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A REVISION OF THE GENUS BEJARIA MUTIS EX L. (ERICACEAE)

City University of New York PH.D. 1984

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A REVISION OF THE GENUS BEJARIA Mutis ex L. (ERICACEAE).

by

STEVEN E. CLEMANTS

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1984

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

A REVISION OF THE GENUS BEJARIA Mutis ex L. (ERICACEAE).

by

Steven Earl Clemants

Adviser: Professor James L. Luteyn

Bejaria, found in South America, Central America, Mexico, W Cuba, and SE USA, is recognized as having fifteen species. Past workers relied heavily on characters of the indumentum, but observations in the field show that indumentum is very variable within populations and to some extent on individuals. Floral characters are found to be more consistent and are used to characterize species or species groups. Five distinct corolla shapes are seen. They are: spreading or bell-shaped, trumpet-shaped, tube-shaped, cup-shaped, and funnel-shaped. Analysis of wood anatomy showed tremendous variation within species in quantitative characters. Furthermore, there are quantitative changes with the age of the wood, therefore studies of wood anatomy in the Rhododendroideae that do not take into account this variation may be suspect. Flavonoid aglycone and flavonoid glycoside spot-patterns showed much the same variation as was found with the wood.

Acknowledgements

I wish to express my deep gratitude to all the people who helped and encouraged me during my doctoral studies. I want to thank Grace Markman who helped in many ways for the past year and a half, Dwight Kincaid who was very generous with his time and equipment, Fred Seaman who enabled me to learn, first-hand, chemotaxonomy, to the New York Botanical Garden who gave me support in the form of an Herbarium Fellowship for the past three years, to Lehman College who gave my Teaching positions for the two years before that. Special thanks go to Dr. James L. Luteyn, my adviser, for the patience he showed through the years, and the willing advice he gave.

I want to thank Bobbi Angel and Grace Markman for the fine drawings of *Bejaria* plants found in this volume.

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INTRODUCTION

Bejaria, a neotropical genus of 15 shrubby or arborescent species, is characterized by its 7-merous flowers, free petals, capsular fruits, non-appendaged anthers, and viscin threads mixed with the pollen grains. It is abundant in the mountains of northern and western South America (from Bolivia northward and Guyana westward). It is also found in southeastern United States, western Cuba, central and southern Mexico, and in scattered localities in Central America. Four of the species are widespread and variable, while the others are more uniform and have local distributions.

Two revisions of *Bejaria* were published in this century (Fedchenko & Basilevskaja, 1926, 1928; Mansfeld & Sleumer, 1935), but because many researchers have been unable to use these works to identify recent collections, the genus was in need of a more comprehensive revision. Four species were described since 1935, and, in 1941, Camp revised the North American species suggesting that much of the variation in *Bejaria* was due to hybridization.

In the present work corolla shape, of which there are a number of markedly different types, is used to divide the genus into a number of groups. Further definition of species is accomplished by using leaf shape and size, petiole length, and a variety of other characters.

Fifteen species are here recognized of which four are variable and account for most of the variation which caused problems in the past. One species is thought to be of hybrid origin (_B_. _subsessilis_) and one hybrid swarm has been found.

HISTORY

Bejaria was first collected and described by José Celestino Mutis in 1867. He made numerous collections and had illustrations of five specimens drawn for his Flora of Colombia; however, he did not publish on _Bejaria_ himself. He sent descriptions of the genus and two species along with prints from two of his plates to Linnaeus who described the genus with one species (_B_. _aestuans_) in 1771 (see ORTHOGRAPHY AND TYPIFICATION). Linné filius (1781) described the second species (_B_. _resinosa_) and cited the two Mutis plates.

Shortly after the first two species were described, Ruiz and Pavon (1794) described the genus _Acunna_ based on specimens they collected in Peru. Evidently they were unfamiliar with the genus _Bejaria_. The congeneric status of _Bejaria_ and _Acunna_ was first noted by Ventenat (1802) and formal transfers were made by Persoon (1806) and G. Don (1834).

Two additional genera have been described based on _Bejaria_ specimens. _Jurgensenia_ was named by von

Turczaninov (1847) for a collector of Mexican plants and aide of Galeotti. He compared his new genus to *Zygophyllum* and *Juliana* but did not place the genus in any family. A second genus, *Heptacarpis*, was described by Conzatti (1940) on nearly the same material, i.e. collected 20 km from the type locality of *Jurgensenia*. He placed his new genus in the Ternstromiaceae.

Most of the early collections of *Bejaria* were made by men working for seed houses and nurseries in Europe. *Bejaria racemosa* was described from a plant grown at Cels, France. The specimen was grown from seed sent by A. Michaux from Charlestown, South Carolina (Ventenat, 1802) and probably represented the first introduction of *Bejaria* into Europe. Later, in the 1840's and 1850's, a number of collectors brought back live plants, seeds, and most importantly, herbarium specimens. These collectors included William Purdie, who collected for the Duke of Northumberland; William Lobb and R. W. Pearce, who collected under contract to Messrs. Veitch; and J. J. Linden, Nicolas Funck, and Louis Joseph Schlim, who collected for Mr. Linden's seed house in Belgium. Specimens brought back by these collectors, plus those of Andreas Hartweg, represent the largest number of *Bejaria* collections from the early to middle 19th century.

The first revision of *Bejaria*, by Fedchenko and Basilevskaja (1926, 1928), brought together all the names in *Bejaria*, and provided descriptions for many species, however, the revision was based on specimens from few herbaria (LE, S, W) and was superseded by the more thorough revision of Mansfeld and Sleumer (1935).

The second revision of *Bejaria*, by Mansfeld and Sleumer (1935), was based on specimens from numerous herbaria (including B, K, NY, S, W). The authors also consulted the numerous collections by Weberbauer from Peru and other European collectors. Although this revision is commonly consulted recent workers, such as Wilbur and Luteyn (1978) and Maguire, Steyermark, and Luteyn (1978), have found it to be unsatisfactory. Wilbur and Luteyn stated "The most recent revision of the genus (Mansfeld & Sleumer, 1935) is unsatisfactory due to the extreme variation encountered in such "key" characters as plant indumentum and corolla size." Maguire, Steyermark, and Luteyn stated "... the present authors are unable to assign many specimens with clarity to the entities so presented by Mansfeld and Sleumer."

Camp (1941) believed that much of the difficulty with *Bejaria* -- namely the great variation in indumentum, leaf shapes and sizes, and flower size -- could be explained by hybridization. He suggested that hybridization amoung four species could account for most of the variation in *Bejaria*.

ORTHOGRAPHY AND TYPIFICATION.

In 1771 Linnaeus published *Befaria* *aestuans* as a new genus and species based upon a description sent to him by Mutis in 1767. The spelling *Befaria* was again used by Linné filius (1781) when he published *Befaria* *resinosa*. In 1802, however, Mutis' student Zea (as a footnote in Ventenat, 1802) pointed out that *Befaria* was named for Don Bejar a professor of botany at Cadiz and, further, that Mutis had wanted the genus spelled *Bejaria*. It can be seen from the description Mutis sent Linnaeus (Fig. 1, a transcription and translation of this description follows this section) that *Bejaria* could be misread as *Befaria*, and that Mutis intended to name the genus *Bejaria* after Don Bejar. Because Linnaeus attributed the name of the genus to Mutis (Linnaeus, 1771) and Mutis intended to spell the genus *Bejaria*, as indicated by the description (Fig. 1) and by Zea, *Befaria* needs to be changed to *Bejaria* as required by Article 73.1 of the International Code of Botanical Nomenclature (Voss, 1983). The reservations on making orthographic changes do not apply in this instance because 1) the change does not affect the first syllable of the name (Article 73.3), and 2) there is no indication that the change was intentional (Article 73.7). Conservation of *Befaria* is not justified as there is no consistent use of the spelling. Humboldt and Bonpland (1809), Bentham and Hooker (1880), Mansfeld and

Fig. 1. Description of Bejaria sent to Linnaeus in 1769 by J. C. Mutis. Reprinted with permission of the Linnaean Society of London.

Promont. [illegible], [illegible]; [illegible] [illegible], [illegible] [illegible] [illegible]. 1(8)

8. [illegible]

Frutex 1-2 orgyiarum altitudine; 3-4 pollicum diametro, ramosus; rami [illegible] patentes, [illegible], subdivisi, [illegible].

Folia alterna, [illegible] opposita, conferta, petiolata, [illegible] [illegible], [illegible] oblonga, [illegible], obtusa, [illegible], supra [illegible], viridia, subtus tomentosa, [illegible], 1-2 pollicaria. Petioli brevissimi, planiusculi.

Flores sparsi ad alas foliorum, [illegible] [illegible] in pedunculis [illegible], pedicellis [illegible], hirsutis, pollicaribus. Corollae color [illegible].

Bractea ad singulum pedicellum, [illegible], lanceolata, [illegible], [illegible], subhirsuta.

Cal. Perianthium monophyllum, [illegible] [illegible] [illegible], 7-fidum, [illegible] [illegible] subaequalibus, [illegible], [illegible] exterioribus paulo brevioribus, [illegible], [illegible], [illegible], persistens.

Cor. Petala septem, [illegible] infra [illegible] [illegible], [illegible] oblonga, [illegible] [illegible], [illegible] [illegible] longiora.

Stam. Filamenta [illegible] [illegible] infra [illegible] [illegible], [illegible], filiformia, [illegible], [illegible] [illegible] [illegible], oblonga, [illegible].

Pist. Germen superum, [illegible], [illegible] [illegible]. Stylus [illegible], [illegible], longitudine corollae, [illegible]. Stigma [illegible], [illegible].

Per. Bacca [illegible], [illegible], [illegible], [illegible], [illegible].

Sem. [illegible], minima, oblonga, [illegible], [illegible].

Bergia dixi in honorem Cl. Dn. Bergii Botanices Professoris [illegible].

Sleumer (1935), and Camp (1941) used the Linnaean spelling Befaria, (though they indicated the derivation of the name from Bejar), on the other hand Ventenat (1802), G. Don (1834), A. P. De Candolle (1839), Fedchenko and Basilevskaja (1926, 1928), Sprague (1928), and Macbride (1959) used the Mutis spelling, Bejaria.

In addition to demonstrating the orthography of Bejaria, the Mutis description also indicates a new application for the name Bejaria aestuans. This name has been applied to populations of B. mathewsii from southern Colombia (formerly B. phillyriaefolia) by Mansfeld and Sleumer (1935). This application is inconsistent with the Mutis description and results from the use of unpublished Mutis plates to indicate types without consulting the Mutis description. The Berlin and Madrid specimens of Mutis 4639 were selected as types by Mansfeld and Sleumer (1935, p. 206). They stated "Mutis 4639, mit der unveröffentlichten Tafel von Mutis übereinstimmend und daher als Typus anzusehen ..." (Mutis 4639 agrees with the unpublished plate of Mutis and therefore [should be] regarded as the type). Unfortunately the copy of the Mutis plate and the Mutis specimen at Berlin have been destroyed. The specimens of Mutis 4639 at MA and US lack flowers but the leaves are acute to acuminate and therefore inconsistent with the Mutis description.

Other Mutis plates exist which have been connected with B. aestuans but they also are inconsistent with the

Mutis description. Linné filius cited one Mutis plate under the name B. aestuans (copies at Linnaean Society library, plate #7 & Madrid herbarium, slide #1838c). A second plate (copy at Madrid herbarium, slide #1838a) has B. aestuans engraved on it. Both these plates portray plants with tube-shaped flowers, slightly spreading at the tip and leaves with acute or acuminate apices, whereas the description (Fig. 1) indicates a plant with petals spreading at a 45° angle and leaves with obtuse leaf apices. Therefore, because neither the plates nor the specimens selected as types are consistent with the Mutis description they should not be considered types. Instead, I have chosen as the neotype a color plate at the Madrid herbarium (Madrid slide #1840) which depicts a plant with spreading pink flowers and obtuse leaf apices and is consistent with the Mutis description for other characters. This plate depicts a specimen formerly named B. glauca to which the name B. aestuans is here applied.

The correct citations are, therefore:

Bejaria Mutis ex Linnaeus, Mantissa plantarum altera 152. 1771, "Befaria". Type. Bejaria aestuans.

Bejaria aestuans Linnaeus, Mantissa plantarum altera 242. 1771, "Befaria". Neotype. Unpublished Mutis Plate at MA n.v. (Madrid slide #1840!).

Transcription of Mutis description (Fig. 1).

Line 1. 8 Bejaria

Line 2. Frutex 1-2 orgyarum altitudine, 3-4 pollicum diametro, ramosus, ra=

Line 3. mulis patentibus, varie subdivisis, teretiusculis . . .

Line 4. Folia alterna, raro opposita, conferta, patentia, nonnulla obovata,

Line 5. plurima oblonga; integerrima, obtusa, avenia, supra viridia, nitida;

Line 6. infra tomentosa, subincana, 1-2 pollicaria. Petioli brevissimi, planiusculi.

Line 7. Flores pauci ex alis folioium, plurimi terminales in pedunculis racemosis,

Line 8. pedicellis teretibus, hirsutis, pollicaribus. Corollae color incarnatus.

Line 9. Bractea ad singulum pedicellum, brevissima, lanceolata, acuta, con=

Line 10. cava, subhirsuta.

Line 11. Cal. Perianthium monophyllum, deorsum parum ventricosum, 7-fidum, laci=

Line 12. niis subaequalibus, ovatis, acutis, exterioribus paulo latioribus; conniven=

Line 13. tibus; parvis; persistens . . .

Line 14. Cor. Petala septem, receptaculo inserta. Unques brevissimi; laminae oblongae, sursum

Line 15. latiores obtusae, erecto-patentes; calyce quinquies longiores . . .

Line 16. Stam. Filamenta quartuordecim, receptaculo inserta; inferne crassiuscula, hirsuta,

Line 17. deinde filiformia, corolla paulo breviora, alterna minora. Antherae parvae,

Line 18. oblongae, incumbentes.

Line 19. Pist. Germen supernum, parvum, obsolete heptagynum. Stylus teres, erectus, longitu=

Line 20. dine corollae, persistens. Stigma crassiusculum. 7-striatum . . .

Line 21. Peri. Bacca heptagona, depressa, ubilicata, septem locularis, exsucca

Line 22. Sem. Numerosissima, minima, oblongo-teretia, imbricatim posita.

Line 23. Bejariam dixi in honorem Cl. Dn. Bejar Botanices Professoris Gadensis.

Translation of Mutis description.

Shrub of 1-2 fathoms in height, of 3-4 inches in diameter, branched, branches spreading, variously subdivided, somewhat terete. Leaves alternate, rarely opposite, crowded, spreading, some obovate, most oblong; entire, obtuse, veinless, green, shiny on upper surface, tomentose, subwhite below, 1-2 inches. Petals very short, fairly flat. Flowers few from the axis of leaves, mostly terminal on racemose pedicels, pedicels terete, hirsute, 1 inch. Corolla flesh-colored. Bract one on each pedicel, very short, lanceolate, acute, curved inward, subhirsute. Calyx monophyllus, not very swollen below, 7-divided, lacinia subequal, ovate, acute, outer a little wider; connivent; small; persistent. Petals seven, inserted on receptacle. Claws very short; blades oblong, upwards wider obtuse, spreading at an angle of ca. 45°; five times longer than calyx. Filaments 14, inserted on recptacle; lower moderately thick, hirsute, then filiform, slightly shorter than corolla, alternate smaller. Anthers small, oblong, incumbent. Ovary superior, small, obsoletely 7-carpellate. Style terete, erect, with length of corolla, persistent. Stigma moderately thick, 7-striate. Pericarp. Berry 7-angled, flat on top, depressed in center, 7-locular, juiceless. Seeds. Very numerous, very small, oblong-terete, imbricately placed. _Bejaria_ named in honor of the celebrated Don Bejar, Botanical Professor of Cadiz.

MORPHOLOGY

Habit

Bejaria species are erect or spreading shrubs 1-6 m tall or, in _B. aestuans_ and _B. sprucei_, trees up to 15 m tall. _Bejaria tachirensis_ and _B. nana_ are small shrubs, 0.3-2 m tall, sometimes considered suffruticose. All species are terrestrial. Stems and twigs are terete or subterete, sometimes bluntly angled. Bark is usually fissured or deeply fissured.

The general habit appears to be influenced by the environment. Low shrubs are common in exposed habitats while trees are usually found in cloud forests, protected areas, or in pine-oak forests.

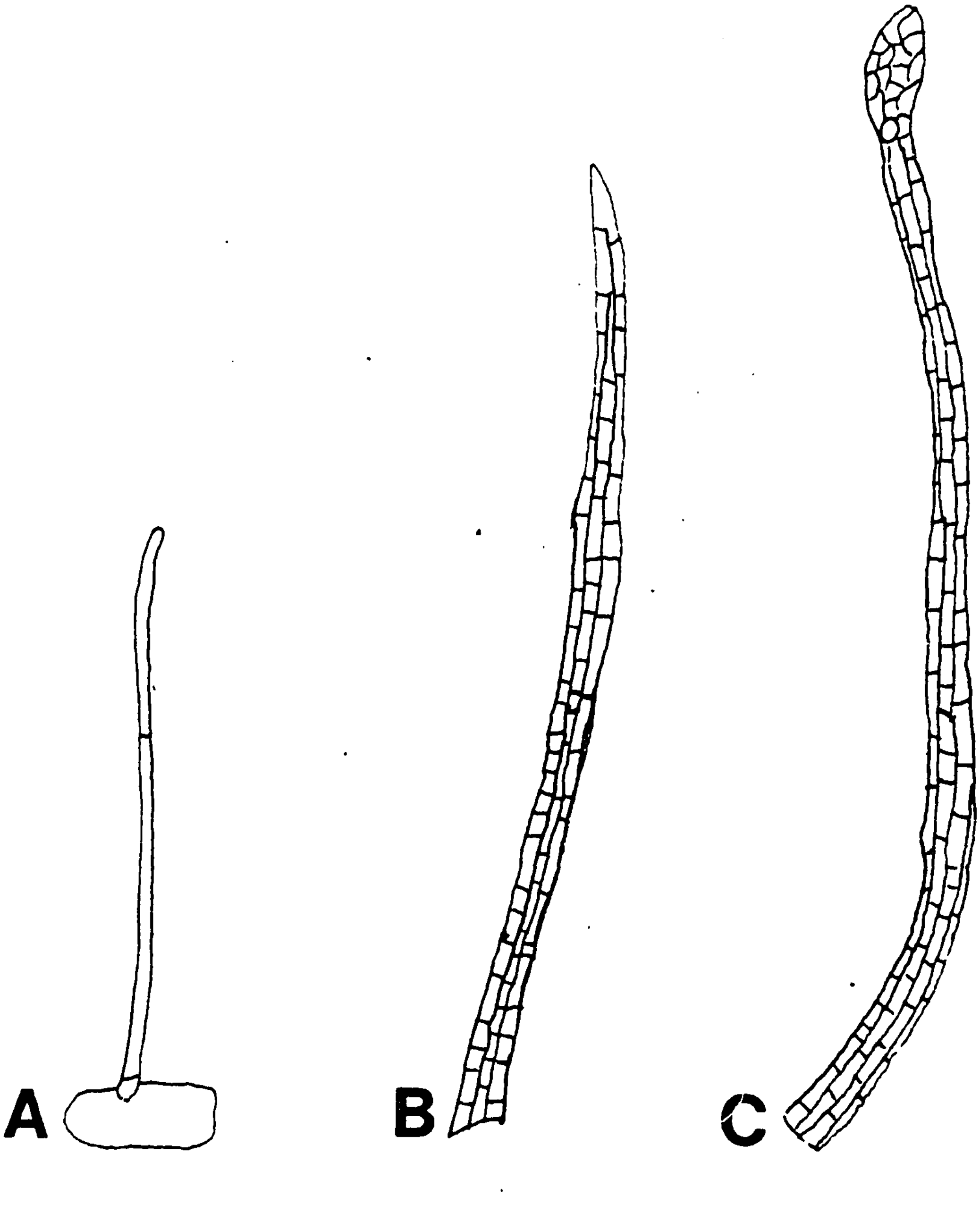
Indumentum

Three types of hairs --unicellular or multicellular-uniseriate hairs (Fig. 2A), multicellular-multiseriate hairs (Fig. 2B), and multicellular-multiseriate capitate (glandular) hairs (Fig. 2C)-- are found in *Bejaria*. Hairs may be found on all plant parts but are usually restricted to certain organs following topographic rules. The unicellular and multicellular-uniseriate hairs rarely exceed 1 mm in length, whereas the other two hair types reach 5 mm in length.

Unicellular and multicellular-uniseriate hairs. The unicellular and multicellular-uniseriate hairs (Fig. 2A), corresponding, in part, to the filiform hairs of Cowan (1950) and Seithe (1980), may be found on all organs of the plant. They are usually twisted and contorted and are nearly always present on immature foliage and flowers.

Multicellular-multiseriate hairs. The multicellular-

Fig. 2. Hair types in <u>Bejaria</u>. A. Multicellular-uniseriate hair. B. Multicellular-multiseriate hair. C. multicellular-multiseriate capitate hair.


A
B
C

multiseriate hairs (Fig. 2B), corresponding to the setose hairs of Cowan (1950) and the setiform hairs of Seithe (1980), may be found on most vegetative organs of the plant but are absent from the flower (except the calyx). Although the variation in topography is not as great as for the unicellular and multicellular-uniseriate hairs, there is still variation within populations. For example, individuals of *B. aestuans* growing side by side on Páramo La Negra, Venezuela may show different hair types on the rachis (*Clemants & Dugarte 2427*-with tomentose rachis, *Clemants & Dugarte 2428*-with hispid rachis, and *Clemants & Dugarte 2429*-with glandular-hispid rachis).

Multicellular-multiseriate capitate hairs. The multicellular-multiseriate capitate hairs (Fig. 2C), corresponding to the setose-glandular hairs of Cowan (1950) and the setiform gland hairs of Seithe (1980), are also found on all organs except the flowers (they are, however, found on the calyx). This hair type and the preceding (the multicellular-multiseriate hairs) appear to be mutually exclusive, either capitate or non-capitate hairs but not both together are found on an individual. Either hair type can be found in combination with the unicellular and multicellular-uniseriate hairs, however.

Some of the topographic rules presented by Seithe (1980) for *Rhododendron* apply to *Bejaria*. The nerve rule -- hairs on the nerves are often longer than those between the nerves -- applies to *Bejaria*. In addition, I have noted that the midrib is often the only pubescent part of the leaf, rarely is the remainder of the leaf pubescent and the midrib not. The surface rule -- hairs on the adaxial leaf surface are often larger than those on the abaxial surface -- also applies of Bejaria. In addition, I have noted that the adaxial hairs are often fewer and more scattered than the abaxial hairs. The margin rule -- hairs on the margin are often longer and thinner than those on the lamina -- does not always apply to Bejaria; more often the marginal hairs are shorter or at least thicker than the hairs on the plane. The margin and midrib are often pubescent and the lamina glabrous, but a pubescent lamina with glabrous midvein and margin or a pubescent margin and glabrous lamina and midvein are rare.

Within some populations, individuals with capitate hairs are more common in exposed areas and individuals with non-capitate hairs or glabrous are more common in protected areas. For example individuals of B. aestuans from Páramo La Negra, Venezuela with glandular-hispid rachises (Clemants & Dugarte 2427) are more common in the paramo edge while individuals with hispid or glabrous rachises (Clemants & Dugarte 2428, Clemants & Dugarte 2429) are found in the subparamo. Although glandular-hispid individuals are more common in exposed areas in some populations, in others (i.e. B. imthurnii on Cerro Roraima) individuals with glandular-hispid rachises (Clemants & Delascio 2454) and individuals with hispid rachises (*Clemants & Delascio 2453*) grow side by side.

The presence, density, and topography of hairs was used by Mansfeld and Sleumer (1935) to characterize species. For instance, they recognized three closely related species, *B. grandiflora*, *B. resinosa*, and *B. congesta*. The differences between these species related to the presence of dense tomentum on the abaxial leaf surface (*B. grandiflora*), absence of indumentum on the abaxial leaf surface (*B. resinosa*), and presence of multicellular-multiseriate hairs on the abaxial leaf surface (*B. congesta*). Mansfeld and Sleumer also recognized five varieties within *B. glauca*, four of these based on hair types. *Bejaria glauca* var. *typica* lacked hairs on the pedicels; var. *tomentella* had tomentose pedicels; var. *setosa* had hispid pedicels, and var. *glandulosa* had glandular-hispid pedicels.

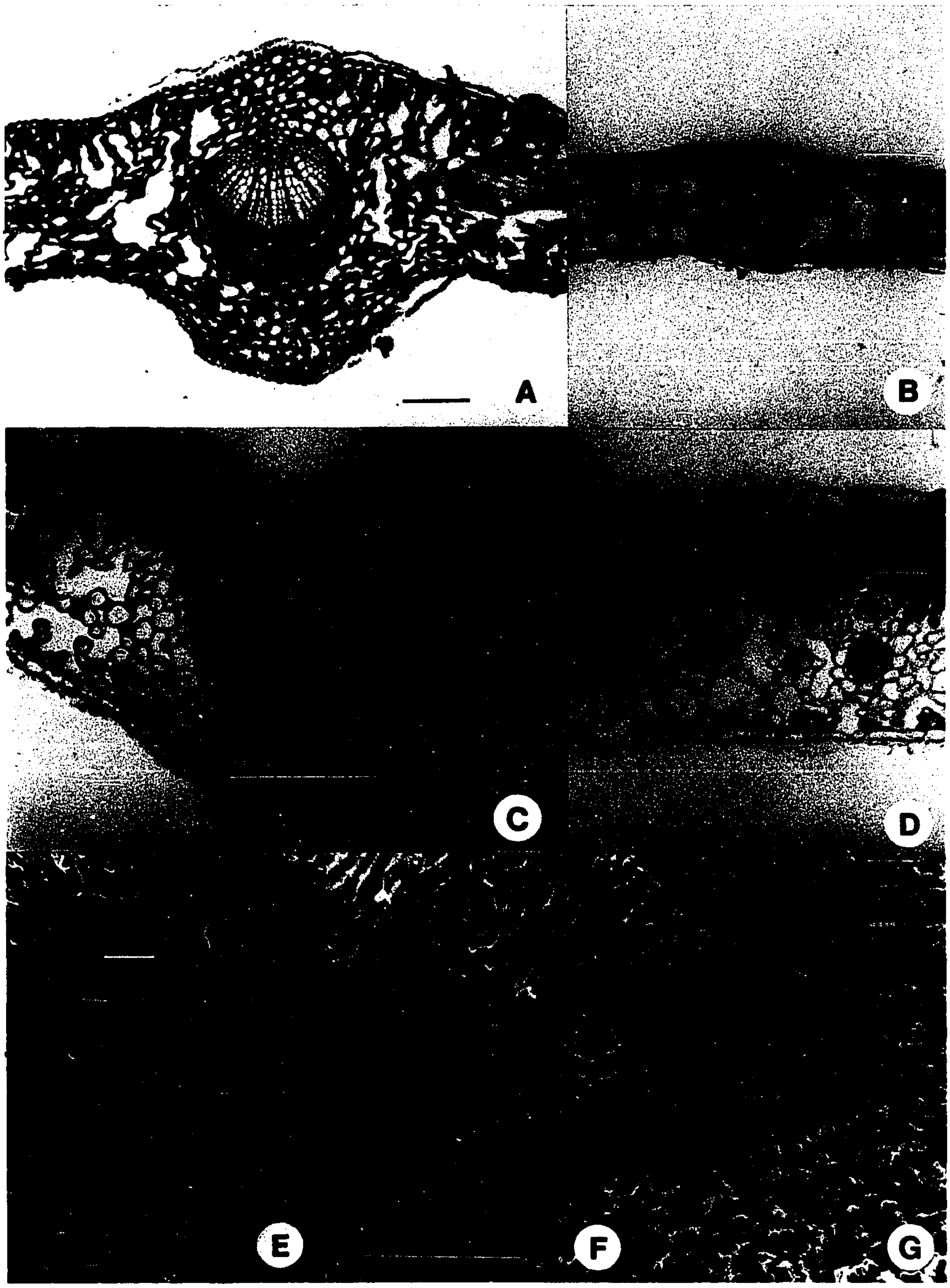
I have found that the presence and, in particular, the topography of hairs varies within species, populations, and in some instances individuals. Because of this variation I do not consider hair type and topography to be taxonomically useful.

Leaves

The leaves of *Bejaria* are simple, alternate, estipulate, evergreen, chartaceous or usually coriaceous, and usually brochidodromous. All leaves are green when mature but may be red when young and flushing. Most of the species are abaxially glaucous. The leaf shape varies from linear to nearly orbicular with the most common shapes being lanceolate, elliptic, and ovate. Leaf size varies from 0.85 x 0.15 cm in *B. nana* to 12.5 x 3.5 cm in *B. aestuans*. The lamina is usually flat and marginally revolute. Three species, *B. cubensis*, *B. ledifolia*, and *B. nana*, however, have strongly longitudinally curled leaves, and three others, *B. aestuans*, *B. sprucei*, and *B. resinosa*, rarely have curled leaves (becoming strongly curled in *B. resinosa*). Petioles are 1.2-12 mm long and usually channeled adaxially or flattened in cross-section. Stomata are weakly tetracytic (Watson et al., 1966; Stevens, 1971), a type of stomate not found elsewhere in the Ericaceae except in *Epigaea*. Stevens (1969) reported that in some species of *Bejaria* the stomata are all aligned perpendicular to the axis.

Leaf anatomy is very important in delimiting two sections of *Bejaria*: section *Racemosae* and section *Bejaria*. The monotypic section *Racemosae* (with *B. racemosa*) is characterized by one layer of palisade parenchyma, the cells of which are nearly square (Fig. 3B), absence of a hypodermis (Fig. 3B), a pieris-type midrib bundle (Fig. 3A) (see Stevens, 1969 for a description of the different types of midrib bundles in Ericaceae), and the presence of stomata on both leaf surfaces (Fig. 3E and 3F). Section *Bejaria* (with the

Fig. 3. Leaf anatomy of *Bejaria*. Figs. A-B. *Bejaria racemosa* (coll. *Clemants* *&* *Miller* *1607*). A. Leaf midvein cross-section. Bar = 0.1 mm. B. Leaf lamina cross-section. See bar in Fig. A for scale. Figs. C-D. *Bejaria* *imthurnii* (coll. *Clemants* *&* *Delascio* *2454*). C. Leaf midvein cross-section. See bar in Fig. A for scale. D. Leaf lamina cross-section. See bar in Fig. A for scale. Figs. E-F. *Bejaria* *racemosa* (coll. *Clemants* *&* *Miller* *1607*). E. SEM photo of adaxial leaf surface. See bar in Fig. F for scale. F. SEM photo of abaxial leaf surface. Bar = 0.1 mm. Fig. G. *Bejaria* *imthurnii* (coll. *Clemants* *&* *Delascio* *2454*). SEM photo of adaxial leaf surface. See bar in Fig. A for scale.


A
B
C
D
E
F
G

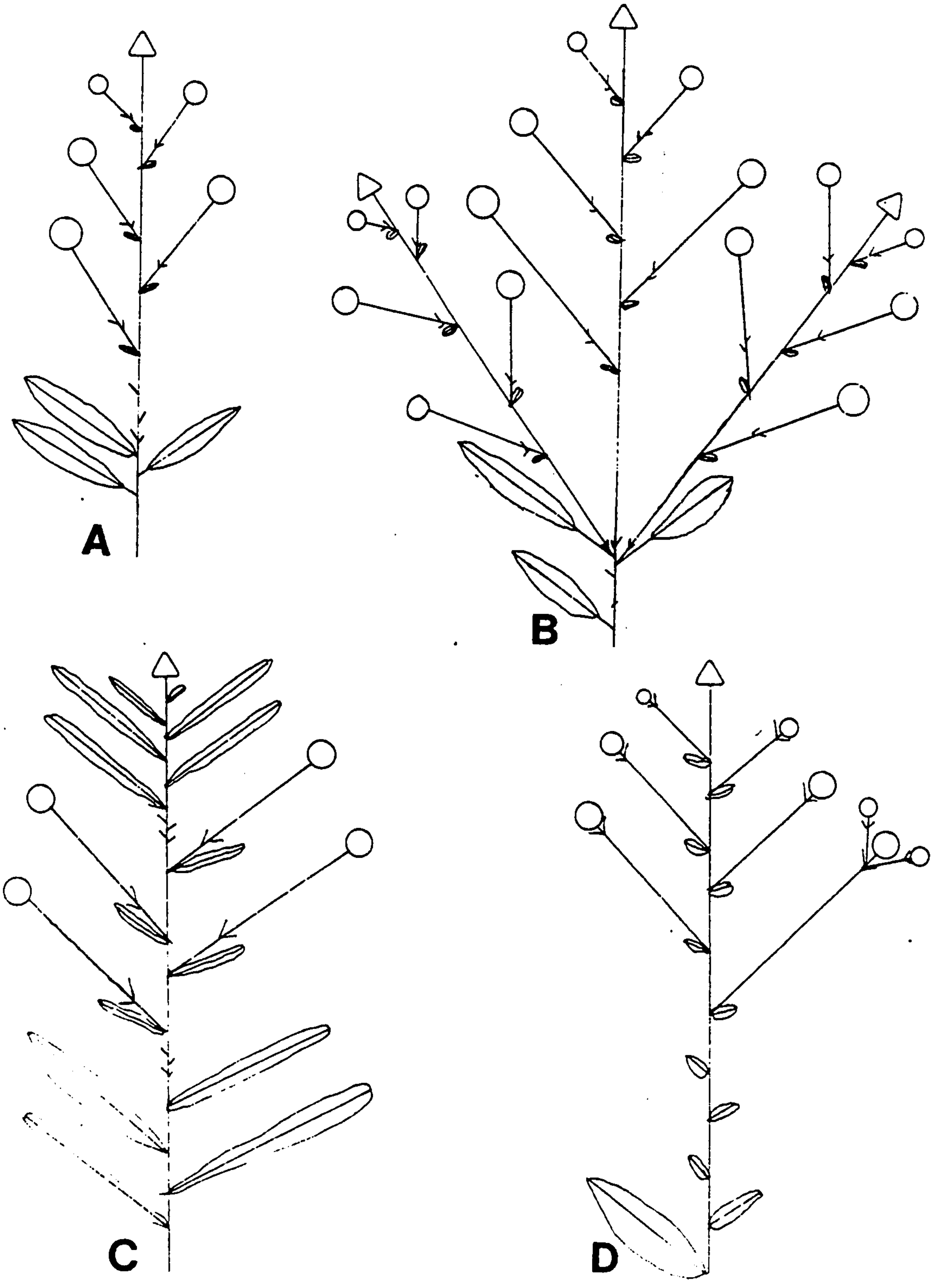
remaining species) is characterized by two or more layers of palisade parenchyma, the cells of which are usually elongate (Fig. 3D), a "mucilaginous hypodermis" (Stevens, 1969 p. 117), composed of an epidermis and a hypodermis (apparently) which bulges into the mesophyll (Fig. 3D), an oxydendron-type of midrib bundle (Fig. 3C), and stomata only on the abaxial leaf surface (Fig. 3G).

I consider the shape, size, and curling of the leaf and the length of the petiole to be taxonomically useful, while the indumentum hair type and topography, although diverse, I do not consider taxonomically useful.

Inflorescence

Bejaria inflorescences are usually large terminal or axillary, indeterminate racemes (Fig. 4A). The inflorescences are, however, functionally determinate. I have seen only one specimen (of *B. cubensis*) in which the terminal bud of the inflorescence continues to grow after the inflorescence has flowered (Fig. 4C). The rachis ranges from 0.6 to over 16 cm long and has from three to over 20 flowers. The pedicels are usually inclined toward the rachis, but the distal portion may decline to a horizontal position. In *Bejaria racemosa* and *B. cubensis* three-flowered branches with a terminal flower (cymules) occasionally occur (Fig. 4D). A similar type of determinate inflorescence branch is found in *Elliottia*

Fig. 4. Inflorescences of *Bejaria*. Figs. A-B. Inflorescences of *B. aestuans*. C. Inflorescence of *B. cubensis*. D. Inflorescence of *B. racemosa*.


A
B
C
D

(Ericaceae: Cladothamneae) (Bohm et al., 1978).

One or more inflorescences are commonly found at the ends of the current growth in *Bejaria* (Fig. 4B), and, occasionally, in *B. aestuans* and *B. sprucei*, the inflorescences are in lower leaf axils. These clusters of racemes often appear paniculate but each raceme has bud scales or scars at the base of the rachis. Spike-like inflorescences are found in *B. nana*, where the pedicels are extremely short making the flowers appear sessile. The inflorescence of *B. racemosa* (Fig. 4D) is unique in the genus, the leaves subtending the inflorescence are reduced in size creating a stalked (pedunculate) effect and the inflorescences are always terminal. This unique inflorescence type is one of the criteria used for placing *B. racemosa* in a separate section.

Although Fedchenko and Basilevskaja (1928) used the type of inflorescence (paniculate, racemose, and corymbose) as a taxonomic criterion, the paniculate inflorescences which they recognized are actually numerous simple racemes clustered at the growing point. Their distinction between racemose and corymbose inflorescences is taxonomically insignificant, because there is no correspondence with other characters in *Bejaria*.

Floral bracts and bracteoles

Floral bracts are green, coriaceous or chartaceous, and range in length from 2.3-50 mm. The lower floral bracts resemble the leaves in size and shape; the upper ones are usually narrower and smaller. Floral bracts were considered important to the taxonomy of *Bejaria* by Mansfeld and Sleumer (1935). They used the size of the floral bracts to characterize species, but floral bracts are extremely variable and do not correspond with other characters. Therefore, I do not use them in this revision.

The bracteoles are usually subopposite and inserted on the middle or basal part of the pedicel. They are green or tan, and range in length from 0.8-6.6 mm. In *B. racemosa* and *B. nana* they are consistently inserted near the calyx at the distal end of the pedicel. Although the position of the bracteoles is useful in distinguishing the two species just mentioned, elsewhere there is much variation in position from the middle to near the base of the pedicel (occasionally on the apical part). The bracteoles are usually caducous but sometimes, on copiously glandular pedicels, they persist.

Flowers

Floral characters, thought to be of little taxonomic use by Mansfeld and Sleumer (1935) because flower shape and size were so variable in their species, are here used as the primary set of characters for separating species.

The diameter of the pedicel, number and length of the sepals, number and length of the petals, shape of the corolla, length of the stamens relative to the corolla, and indumentum of the filaments are all useful and important characters.

Pedicels. In *Bejaria* the pedicels articulate with the rachis but are continuous with the calyx, and they range from 0.4-1.7 mm in diameter. *Bejaria sprucei* and *B. zamorae* have very thin pedicels (less than 0.6 mm diam.) while all other species have thicker pedicels (usually more than 0.6 mm diam.).

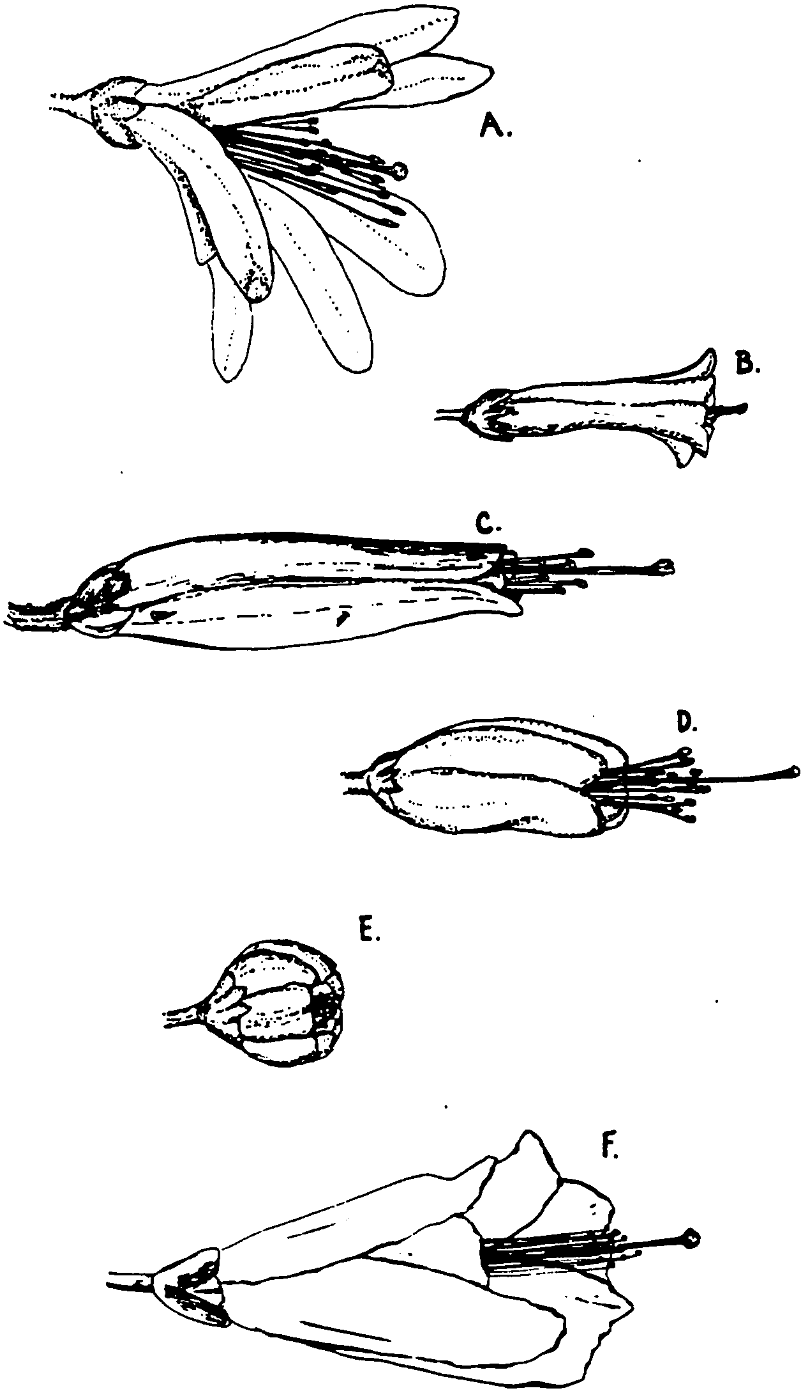
Calyx. The calyx is composed of two parts; the tube which is crateriform or shallowly crateriform, and the lobes. The calyx lobes are usually seven in number, and are arranged with two fully inside, three half inside-half outside, and two fully outside. They are ovate to widely depressed ovate, sometimes elliptic or deltate; the length varies from 0.8 to 7.5 mm. The margin varies from smooth to ciliolate, ciliate, or erose. Both the shape and size of the lobes vary on all individuals in the genus, the inner ones generally being smaller and narrower than the outer ones. The lobes are not articulate with the tube and are basally truncate.

Corolla. Petals are free, white to dark red, usually oblanceolate, with an entire or commonly undulate margin, and commonly tomentose distally.

Corolla shape provides a very good and distinctive taxonomic character. A number of corolla shapes are found in *Bejaria*. Because the petals are free the common terms for shapes of sympetalous corollas such as "tubular" can not be used, therefore I have appended "-shaped" to these terms to indicate that the petals are not fused. The most common is a spreading or bell-shaped corolla (Fig. 5A) as found in *B. racemosa*, *B. aestuans*, *B. imthurnii*, *B. cubensis*, *B. steyermarkii*, and *B. subsessilis*. Rarely *B. aestuans* has a trumpet-shaped corolla (Fig. 5B). A tube-shaped corolla (Fig. 5C-D) is found in *B. mathewsii*, *B. resinosa*, *B. ledifolia*, *B. zamorae*, and *B. sprucei* and cup-shaped ones (Fig. 5E) in *B. tachirensis* and *B. nana*. Funnel-shaped corollas (Fig. 5F) characterize only *B. infundibula*. These different corolla shapes are probably related to different pollinators; for instance, *B. racemosa* and *B. aestuans*, both with spreading or bell-shaped, pink corollas, are visited by honey (and other unknown) bees, whereas *B. resinosa* with large red tube-shaped corollas is visited by a variety of hummingbirds. Stevens (1976) has similarly suggested different pollinators for species of *Rhododendron* with different corolla shapes.

Andoecium. The androecium is usually composed of 14 stamens. The filaments are tomentose in all species but *B. cubensis* which has glabrous filaments. Stamens are consistently long-exserted in *B. sprucei* (Fig. 5D) and often so in *B. mathewsii* and *B. resinosa*, whereas in the

Fig. 5. Corolla shapes in *Bejaria*. Figs. A-B. Corollas of *B. aestuans*. Fig. C. Corolla of *B. resinosa*. Fig. D. Corolla of *B. tachirensis*. Fig. E. Corolla of *B. sprucei*. F. Corolla of *B. infundibula*.

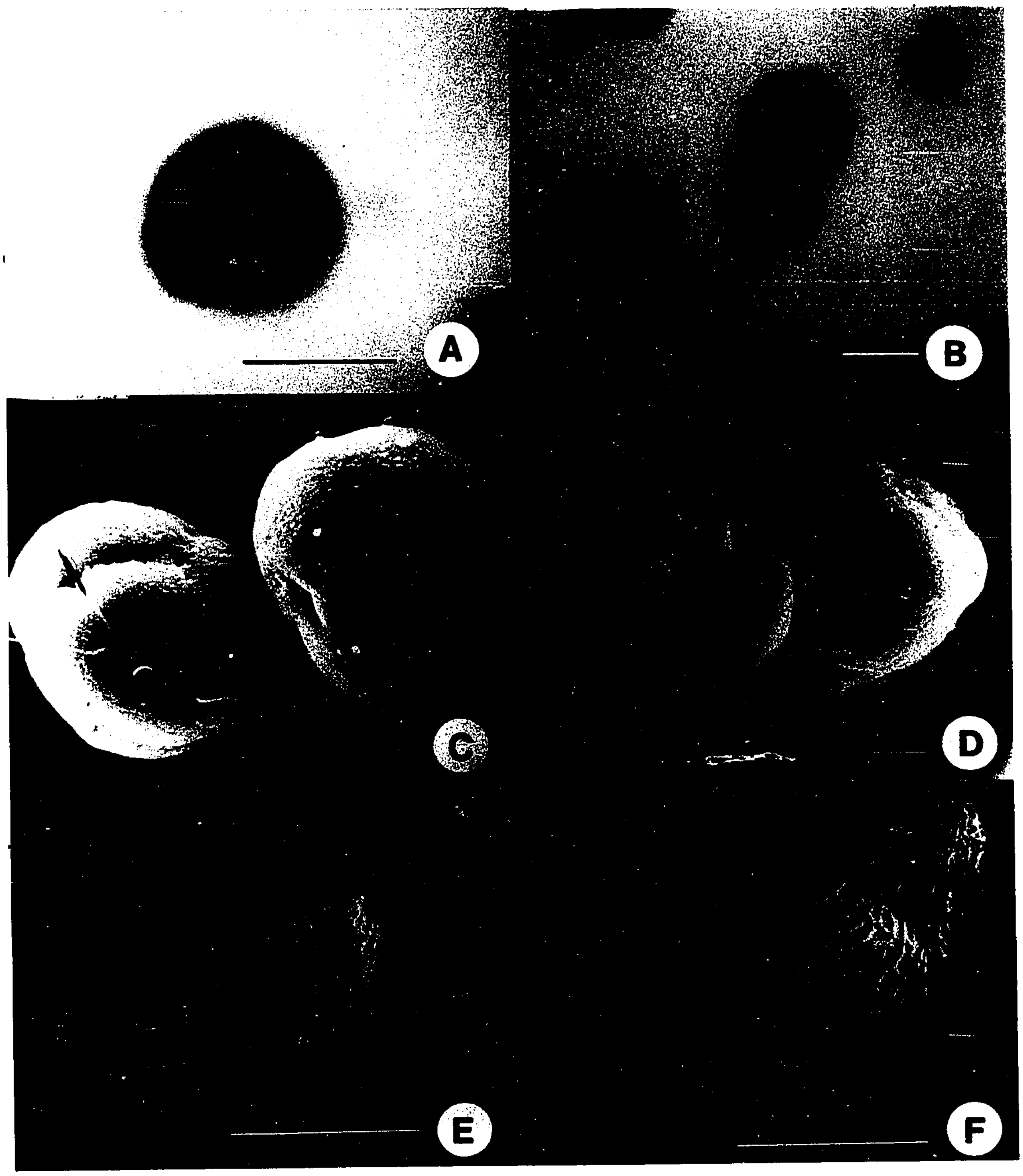

A.
B.
C.
D.
E.
F.

other species the stamens are subequal to the corolla or included. The anther is unappendaged throughout the genus, although sometimes there are fine hairs at the base in *B. aestuans*. Dehiscence is by terminal clefts. In *B. raceomosa* resorption tissue is present but it does not include the epidermis, the actual dehiscence is by separation of intact epidermal cells (Copeland, 1943).

Pollen. *Bejaria* pollen grains are held in tetrahedral tetrads (Figs. 6A-D). They are isopolar; radiosymmetric; zonotreme, tricolporate; fixiform, globose. The AMB is peritreme, the exine pertectate, and viscin threads are present (Figs. 6C-D). Pollen is not useful taxonomically in *Bejaria*, as all species examined are qualitatively identical with only slight quantitative differences.

Gynoecium. The ovary is superior and usually 7-locular except in *B. sprucei* where it is commonly 5- or 6-locular. It normally is glabrous but in one population of *B. aestuans* from near Pie de Cuesta, Colombia (*Luteyn et al. 7614*), the ovaries are beset with long hairs. Placentation is apical-axial (Pyykkö, 1969). In some species the exocarp separates from the endocarp and falls separately (i.e. *B. racemosa*) whereas in other species the exocarp never separates from the endocarp but simply erodes off the endocarp.

Fig. 6. Pollen and seed of *Bejaria*. Figs. A–B. Pollen of *B*. *resinosa* (coll. *Clemants & Luteyn 1675*). Fig. A. Bar = 0.1 mm. Fig. B. Bar = 0.1 mm. Fig. C. SEM photo of pollen of *B*. *resinosa* (coll. *Clemants & Luteyn 1676*). Bar = 0.01 mm. Fig. D. Pollen of *B*. *aestuans* (*Clemants & Luteyn 1677*). Bar = 0.01 mm. Fig. E. Seed of *B*. *aestuans* (coll. *Clemants & Luteyn 1677*). Bar = 1 mm. Fig. F. See bar in Fig. A for scale. Seed of *B*. *resinosa* (coll. *Clemants & Luteyn 1676*). Bar = 1 mm.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Fruits and seeds

The fruits of Bejaria are woody brown capsules ranging in size from 4-9 mm long and 6.2-15 mm in diameter. They are depressed-ovoid, or depressed, transversely ellipsoid. the style usually falling after pollination. Dehiscence is septicidal except in B. racemosa which is slightly loculicidal at the apex.

Seeds are spindle-shaped, 1.2-2 mm long by and 0.3-0.7 mm in diameter, and usually caudate. There is little sculpturing (Fig. 6E-F) but the testa cells are long as is common in the Rhodoreae (Stevens, 1971).

WOOD ANATOMY

The placement of Bejaria in a monogeneric tribe by Copeland (1943) was supported by wood anatomy. Cox (1948 p. 229) stated "Not only has Bejaria evolved along characteristically different lines from the other tribes..., but the genus itself evidences much anatomical variation in its species." Indeed Cox found more variation between the four species of Bejaria he examined than he found among the genera of the Cladothamneae. Record (1932) had earlier observed that "Generic and some specific differences [in the Ericaceae] often are pronounced."

Materials and Methods

Wood specimens were collected in the field or removed from herbarium specimens. A total of 46 samples from ten species were examined in this study; two other species (*B. racemosa* and *B. cubensis*), not examined here, were examined earlier by Cox (1948).

Wood samples of *Bejaria* were dry or in some instances preserved in alcohol. The dried specimens were wetted in either Contrad 80 or Aerosol OT. All specimens were sectioned on a sliding microtome and stained with haematoxylon and Bismarck Brown. Macerations were made using an ultrasonic cleaner following a technique described by Schmid (1982).

Terms used in this paper follow Metcalfe and Chalk (1983).

Results

Vessels elements. Vessel diameter (measured in macerations) is very small to moderately small (Table 1), vessel length (measured from tip to tip) is very small (Table 1), and the vessels are very numerous (Table 1). Vessel elements are variable within species, for example the mean lengths for different samples of *B. aestuans* range from 298-561 um. Furthermore, both the vessel diameter and length increase with distance from the center of the wood (Fig. 7) indicating that they increase with age of the sample.

Perforation plates vary throughout the genus. Within individuals, and even on the same vessel element, simple and scalariform perforation plates occur (Fig. 8A). The number of bars is small, rarely being more than nine per perforation plate. The median number of bars per perforation plate is recorded in Table 1. I consider the median to be a better statistic of central tendency than the mean because the number of bars is often strongly skewed toward zero. A distinction was made between the two ends of a vessel; the end with the largest number of bars was treated separately from the end with the fewest. This was done to illustrate the difference found in a single vessel. Bars are occasionally branched (Fig. 8B) or form reticulate perforation plates.

Vessels of Bejaria are angular in cross-section (Fig. 9B), with very thin walls. While usually solitary, they are occasionally paired. Lateral wall pitting is predominately scalariform on vessel-ray contacts and sparse elsewhere.

Tracheids. Long tracheids (Fig. 8D) with fully bordered pits and ellipsoid pores no longer than the edge of the pit are very numerous in Bejaria woods. Length and wall thickness of tracheids are given in Table 2. Growth rings are often noticeable by a sudden change in the tracheid wall thickness.

Fig. 7. Graph showing the mean change in size of wood elements with distance from center of wood. for each point n=100. (coll. Clemants & Stevenson 2502)

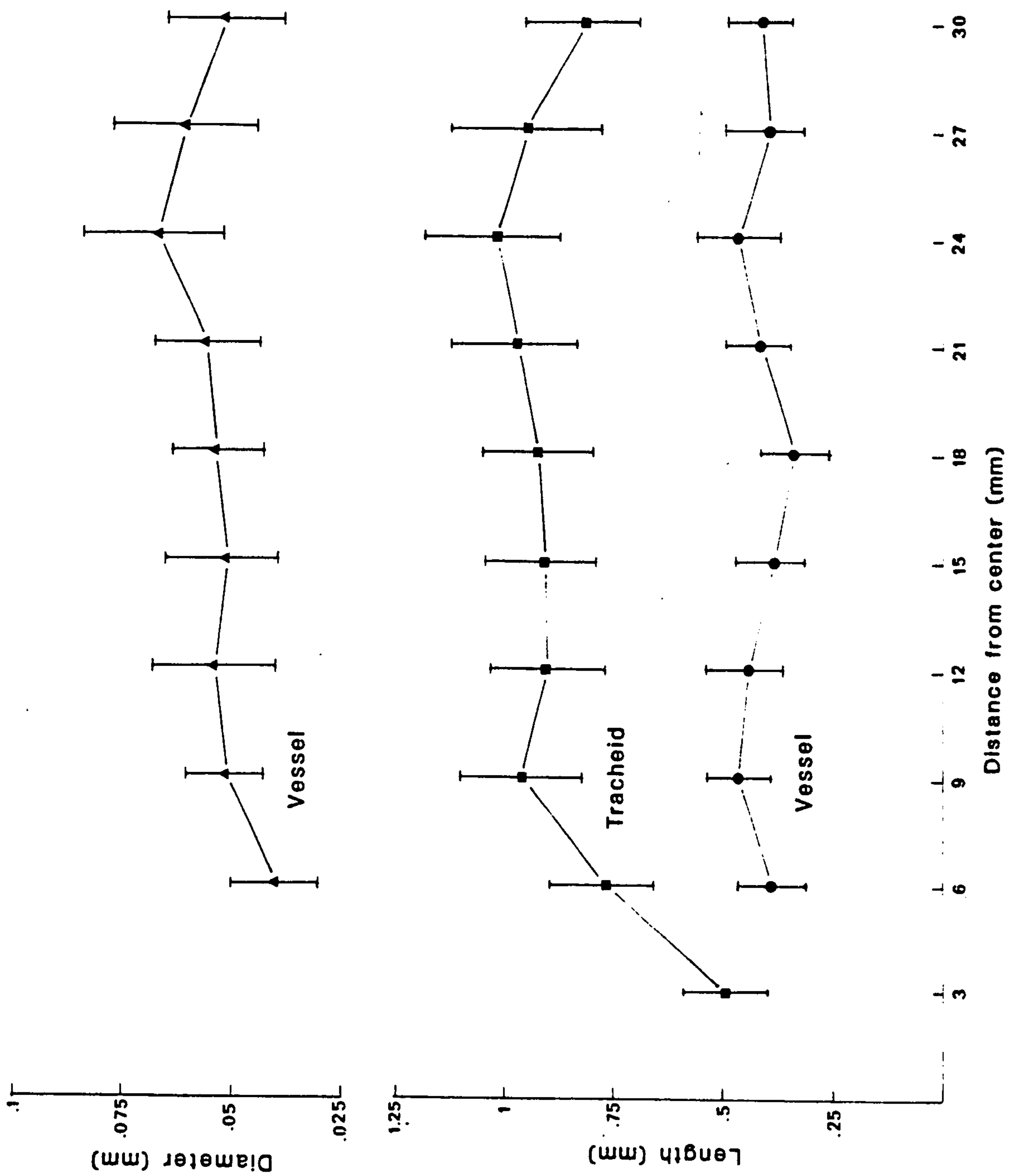
Diameter (mm)
.1
.075
.05
.025
Vessel
Length (mm)
1.25
1
.75
.5
.25
Tracheid
Vessel
3
6
9
12
15
18
21
24
27
30
Distance from center (mm)

Fig. 8. Wood characteristics of Bejaria. Figs. A-C. Vessel elements. Fig. A. Vessel with scalariform perforation plates. Bar = 0.1 mm. Fig. B. Vessel with reticulate perforation plates. Bar = 0.1 mm. Fig. C. Vessel with simple and scalariform perforation plates. Bar = 0.1 mm. Fig. D. Tracheid. Bar = 0.1 mm. Fig. E. Druse in pith. Bar = 0.05 mm. Fig. F. Starch grains in rays. Bar = 0.05 mm.

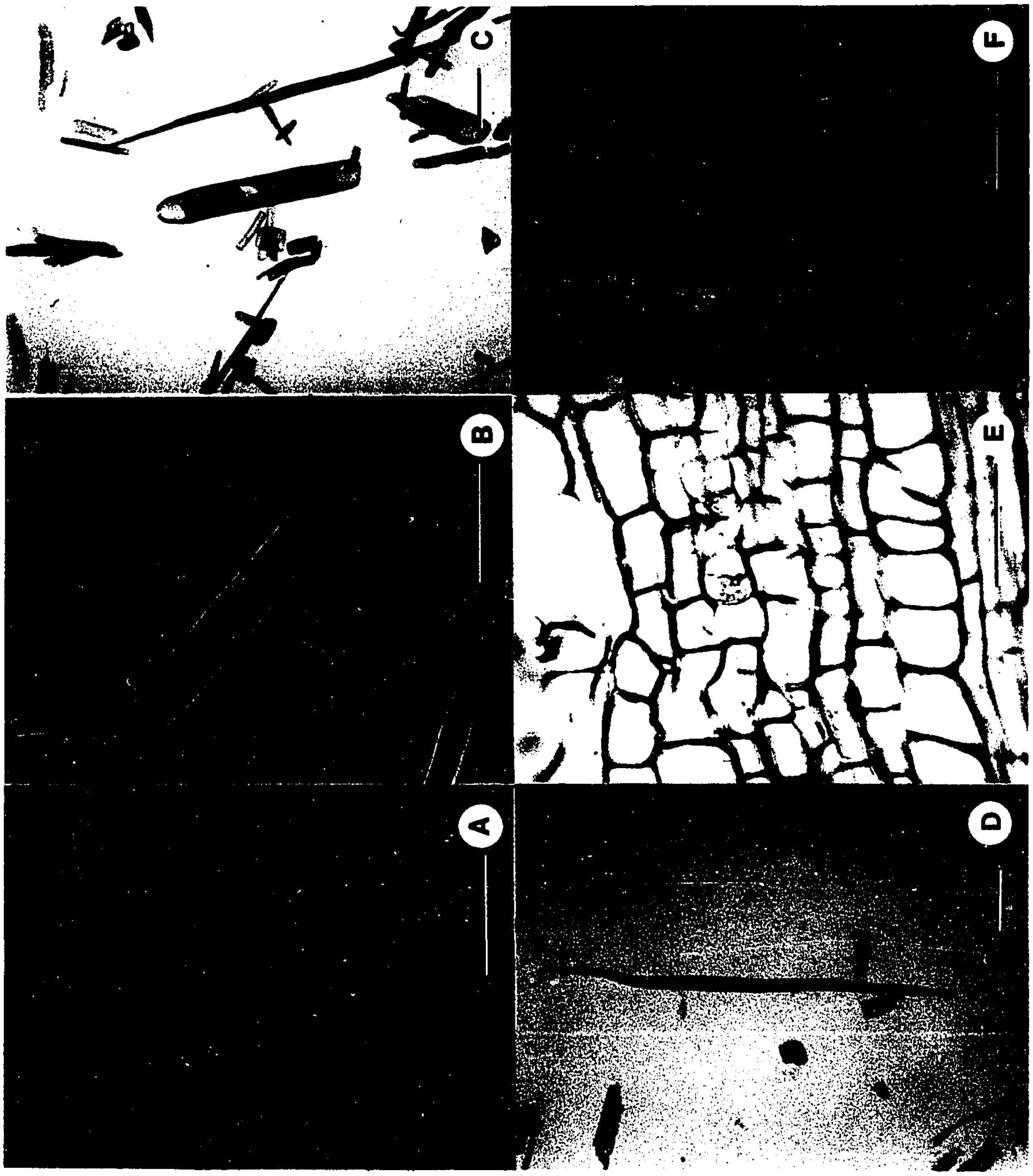
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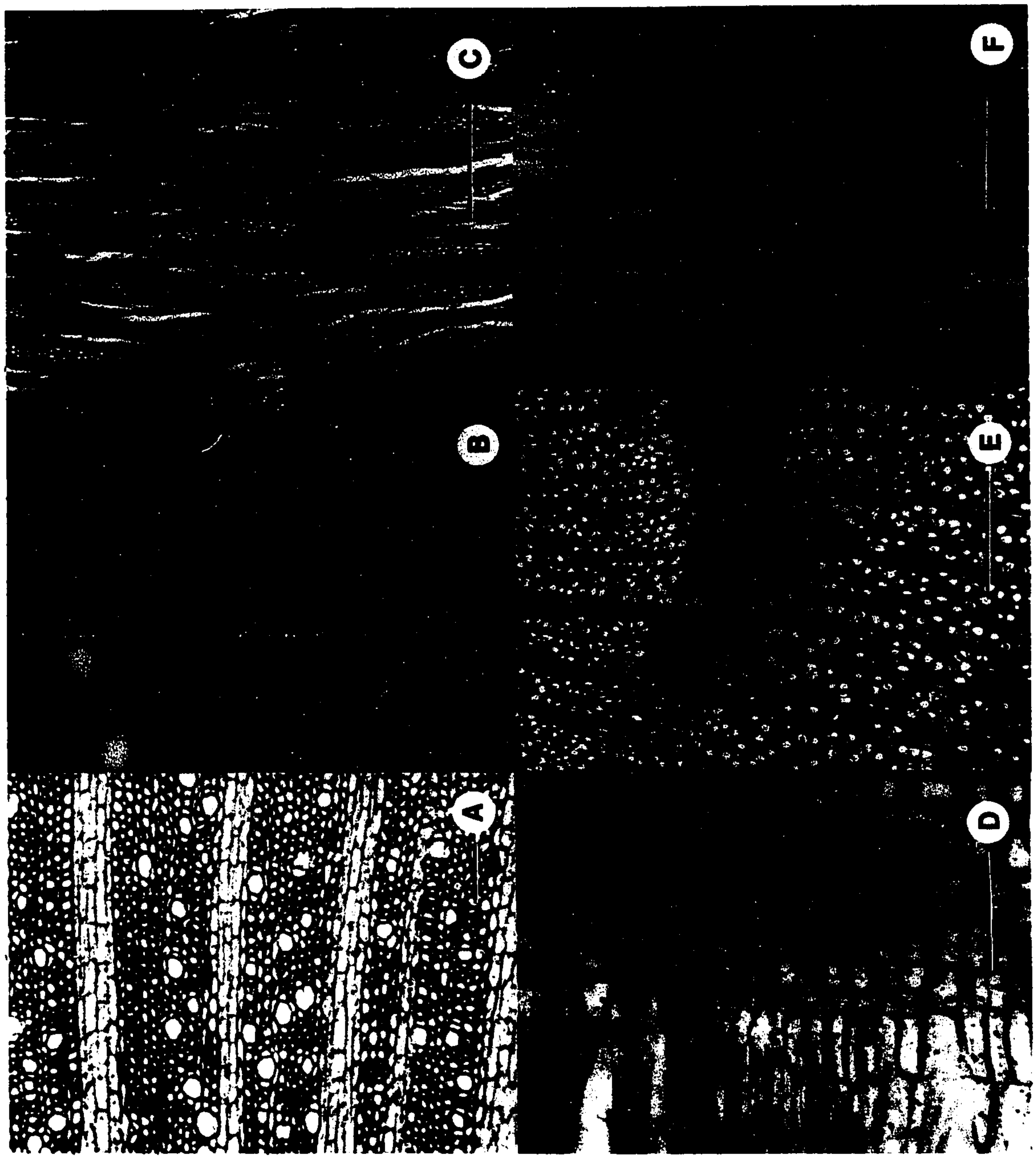
Fig. 9. Wood characteristics of Bejaria. Figs. A-B. Cross-section. Fig. A. Bar = 0.1 mm. Fig. B. Bar = 0.05 mm. Fig. C. tangential section. Bar = 0.5 mm. Fig. D. Radial section through ray. Bar = 0.1 mm. Fig. E-F. Ray islands. Fig. E. Cross-section. Bar = 0.5 mm. Fig. F. Radial section. Bar = 0.5 mm.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Parenchyma. Axial parenchyma is sparse (Fig. 9A) though that that occurs is often near the vessels. Pitting is simple. The length of axial parenchyma cells is given in Table 2. Parenchyma strands are sometimes very difficult to distinguish from unicellular rays.

Rays. Rays in *Bejaria* are Heterogenous Type II (Metcalfe & Chalk, 1983) (Fig. 8C). The margins are made up of erect cells while the bulk of the ray is composed of procumbent and square cells. The rays are frequently filled with large amounts of starch as well as dark staining amorphous material. Taller rays are often found in younger wood. In a few species the rays appear to form aggregates. Intercellular pitting within the rays is simple. Multiseriate rays are usually 3-4 cells wide, length and width are given in Table 3 along with the number of multiseriate rays per square mm.

Ergastic substances. Starch grains are common in the rays and the pith of *Bejaria* species (Fig. 8F). Druses occur occasionally in the pith (Fig. 8E) and are frequent in the bark.

Bark. *Bejaria* bark is often characterized by bands of elongate thick-walled sclereids. In a few species (*B. racemosa*, *B. ledifolia*) these bands are absent.

Ray islands. In many specimens amorphous parenchymatous zones are found usually concentric with growth rings (Fig. 9E). These zones are called ray islands here because they tend to occur along the rays.

These zones run up the stem sometimes for considerable distances (Fig. 9F). They may represent regions in which cracks in the bark occurred, the parenchyma then being callus tissue produced as a wound response.

Discussion

Comparison of Bejaria wood characteristics with the description of the Ericaceae in Metcalfe and Chalk (1950) shows that Bejaria fits very well into the Ericaceae. The only discrepancy is the density of vessel elements which are listed in Metcalfe and Chalk (1950) as rarely exceeding 200 per square mm, whereas in Bejaria the vessel density often exceeds 200 per square mm and sometimes reaches 400 per square mm.

Quantitative wood characteristics of Bejaria species cannot be used for specific delimitation or phylogenetic analysis because of the variation encountered within species and especially within individuals. Multiple state qualitative characters are few in Bejaria wood. Those characters which do occur, such as growth rings, ray islands, and sclereids in the bark, occur sporadically within species and are therefore not very useful taxonomically.

Comparison of Bejaria wood with the wood of other Rhododendroideae can only be made cautiously. Cox did not take into account variation within species (particularly

Table 1. Wood characteristics of *Bejaria*.

Collection	Growth	Wood	Vessel length[a]				Vessel diameter[b]			
	rings	diam.	mean	min	max	SD	mean	min	max	SD
		(mm)		(um)				(um)		
Bejaria aestuans										
Clemants and Luteyn 1668a	+	14	368	157	627	99	47.7	26.4	66.0	9.
Clemants and Luteyn 1670	+	19	416	246	605	82	54.5	39.6	74.8	9.
Clemants and Luteyn 1679c	-	12.5	363	246	538	76	55.9	30.8	83.6	15.
Clemants and Luteyn 1682	+	13	387	179	650	98	48.8	30.8	74.8	10.
Clemants and Fernåndez 2019c	-	17	370	224	560	77	71.6	48.4	132.0	13.
Clemants and Dugarte 2415	+	6	420	202	672	107	46.8	26.4	66.0	7.
Clemants and Dugarte 2423	+	7	409	246	605	76	41.0	30.8	52.8	6.

ria.

sel length^{a}			Vessel diameter^{b}				Bars^{c}		Vessel density^{d}			
min	max	SD	mean	min	max	SD	median		mean	min	max	SD
(um)			(um)				(no.)		(no./mm^{2})			
157	627	99	47.7	26.4	66.0	9.6	0	0	129	90	153	25
246	605	82	54.5	39.6	74.8	9.9	0	0	122	92	189	32
246	538	76	55.9	30.8	83.6	15.2	0	0	142	114	170	22
179	650	98	48.8	30.8	74.8	10.8	12	9	75	52	142	26
224	560	77	71.6	48.4	132.0	13.5	1	0	107	58	161	41
202	672	107	46.8	26.4	66.0	7.4	4	2	212	168	251	32
246	605	76	41.0	30.8	52.8	6.0	0	0	185	117	268	53

Table 1. cont.

Collection	Growth rings	Wood diam. (mm)	Vessel length[a] mean	min (um)	max	SD	Vessel diameter[b] mean	min (um)	max	SD
Clemants and Dugarte 2441a	+	8	422	202	672	102	40.0	26.4	57.2	7.8
Clemants and Dugarte 2441d	+	10.5	374	202	605	90	71.0	35.2	110.0	17.9
Clemants and Dugarte 2443	+	32	567	336	784	111	53.2	30.8	83.6	11.9
Clemants 2482	–	13.5	458	291	694	96	60.2	30.8	110.0	19.0
Clemants and Stevenson 2500a	+	9	367	179	560	76	57.6	35.2	74.8	8.4
Clemants and Stevenson 2501a	+	10	366	134	538	96	46.8	30.8	57.2	7.3
Luteyn et al. 5192	–	11	415	202	582	89	55.3	26.4	83.6	15.5
Luteyn et al. 5270a	+	11	361	202	560	78	39.8	26.4	52.8	6.0
Luteyn et al. 5270b	–	8	363	179	650	103	45.9	26.4	70.4	10.7
Luteyn et al. 5276	–	16	436	269	627	97	49.6	35.2	66.0	8.5

l length[a]			Vessel diameter[b]				Bars[c]		Vessel density[d]			
min	max	SD	mean	min	max	SD	median		mean	min	max	SD
(um)				(um)			(no.)		(no./mm^2)			
202	672	102	40.0	26.4	57.2	7.8	0	0	302	193	536	100
202	605	90	71.0	35.2	110.0	17.9	0	0	179	126	235	37
336	784	111	53.2	30.8	83.6	11.9	1	0	70	65	75	4
291	694	96	60.2	30.8	110.0	19.0	4	0	105	75	142	22
179	560	76	57.6	35.2	74.8	8.4	3	0	153	109	226	41
134	538	96	46.8	30.8	57.2	7.3	0	0	308	176	436	117
202	582	89	55.3	26.4	83.6	15.5	3	1	114	67	176	33
202	560	78	39.8	26.4	52.8	6.0	6	4	141	92	218	42
179	650	103	45.9	26.4	70.4	10.7	6	4	141	109	193	26
269	627	97	49.6	35.2	66.0	8.5	0	0	192	84	310	74

Table 1. cont.

Collection	Growth rings	Wood diam. (mm)	Vessel length[a] mean	min	max	SD	Vessel diameter[b] mean	min	max	SD
			(um)				(um)			
Luteyn et al. 5386	+	10	370	224	538	86	43.9	22.0	66.0	9.2
Luteyn et al. 5411	+	14	481	308	748	91	48.1	30.8	74.8	9.
Luteyn and Lebrón-Luteyn 6366	–	10	420	202	762	96	55.3	35.2	83.6	10.0
Liebman 8592	+	4.5	298	134	426	58	40.5	22.0	79.2	9.7
Mexía 8956	+	6.5	362	157	560	81	45.9	30.8	61.6	7.
Ventana 12779	+	4	348	179	493	76	31.5	17.6	48.4	6.2
<u>Bejaria resinosa</u>										
Clemants and Luteyn 1675d	+	14.5	383	179	515	84	42.6	22.0	66.0	11.2
Clemants and Luteyn 1675h	+	13.5	371	179	538	94	36.9	17.6	52.8	6.6
Clemants 2045	+	13	430	269	560	70	42.6	30.8	57.2	6.

length[a]			Vessel diameter[b]				Bars[c]		Vessel density[d]			
in	max	SD	mean	min	max	SD	median		mean	min	max	SD
m)				(um)			(no.)		(no./mm^2)			
224	538	86	43.9	22.0	66.0	9.2	0	0	219	176	251	24
308	748	91	48.1	30.8	74.8	9.1	0	0	202	116	325	86
202	762	96	55.3	35.2	83.6	10.0	6	4	82	59	92	14
134	426	58	40.5	22.0	79.2	9.7	5	3	238	201	268	31
157	560	81	45.9	30.8	61.6	7.1	4	2	327	268	377	45
179	493	76	31.5	17.6	48.4	6.2	5	3	404	268	544	102
179	515	84	42.6	22.0	66.0	11.2	5	1	166	92	310	86
179	538	94	36.9	17.6	52.8	6.6	3.5	1	168	105	191	27
269	560	70	42.6	30.8	57.2	6.1	4	0	127	101	159	27

Table 1. cont.

Collection	Growth	Wood	Vessel length^{a}				Vessel diameter		
	rings	diam.	mean	min	max	SD	mean	min	max
		(mm)		(um)				(um)	
Clemants et al. 2220	+	10	381	202	560	82	35.6	22.0	48.4
Clemants et al. 2221a	+	10.5	381	264	560	77	35.8	22.0	61.6
Clemants et al. 2221b	+	14	340	202	515	59	37.0	26.4	48.4
Clemants 2396	-	10	341	224	448	55	40.2	22.0	61.6
Clemants 2397a	+	28	401	202	672	101	42.2	22.0	66.0
Luteyn et al. 5314	+	16	344	157	560	83	48.4	30.8	96.8
Luteyn and Lebrón-Luteyn 7726	+	17	339	157	493	75	39.9	26.4	57.2
<u>*Bejaria sprucei*</u>									
Clemants and Fernández 2000	-	6	489	269	739	105	52.8	26.4	79.2

length[a]			Vessel diameter[b]				Bars[c]		Vessel density[d]			
n	max	SD	mean	min	max	SD	median		mean	min	max	SD
)				(um)			(no.)		(no./mm^2)			
2	560	82	35.6	22.0	48.4	4.9	0	0	276	218	327	48
4	560	77	35.8	22.0	61.6	6.4	6	4.5	164	142	201	23
2	515	59	37.0	26.4	48.4	6.3	5.5	3	172	142	196	22
4	448	55	40.2	22.0	61.6	7.7	7	5	142	92	243	42
2	672	101	42.2	22.0	66.0	9.0	0	0	152	101	218	43
7	560	83	48.4	30.8	96.8	14.3	0	0	186	159	226	20
7	493	75	39.9	26.4	57.2	8.2	0	0	241	142	343	76
9	739	105	52.8	26.4	79.2	8.3	5	1	154	127	202	33

Table 1. cont.

Collection	Growth	Wood	Vessel length^a				Vessel diamete		
	rings	diam.	mean	min	max	SD	mean	min	max
		(mm)		(um)				(um)	
Clemamts and Delascio 2479	+	6	439	246	582	85	45.0	22.0	61.
Clemants and Delascio 2480	-	6.5	441	291	650	75	63.3	44.0	83.
<u>Bejaria</u> <u>infundibula</u>									
Clemants and Fernândez 2007c	+	15	412	134	694	98	53.9	30.8	74.8
Clemants and Fernândez 2007d	+	14.5	426	246	672	95	57.3	35.2	92.
<u>Bejaria</u> <u>mathewsii</u>									
Clemants 2046	+	14	345	179	582	83	44.7	26.4	66.0
Luteyn and Lebrôn-Luteyn 6895	-	4.5	354	224	515	74	35.5	22.0	52.8

el length[a]			Vessel diameter[b]				Bars[c]		Vessel density[d]			
min	max	SD	mean	min	max	SD	median		mean	min	max	SD
(um)				(um)			(no.)		(no./mm^2)			
246	582	85	45.0	22.0	61.6	8.7	0	0	316	243	377	38
291	650	75	63.3	44.0	83.6	8.8	2	0	158	135	213	33
134	694	98	53.9	30.8	74.8	10.0	0	0	100	82	144	20
246	672	95	57.3	35.2	92.4	12.4	0	0	156	75	268	64
179	582	83	44.7	26.4	66.0	8.1	0	0	134	84	184	30
224	515	74	35.5	22.0	52.8	6.5	6	3	233	159	293	58

Table 1. cont.

Collection	Growth	Wood	Vessel length[a]				Vessel diamete		
	rings	diam.	mean	min	max	SD	mean	min	max
		(mm)		(um)				(um)	
Cuatrecasas 27550	+	6.5	306	179	493	68	26.7	17.6	35.
Bejaria tachirensis									
Ruiz-Teran et al. 13399	+	4.5	343	179	470	70	30.6	17.6	61.
Bejaria nana									
Cuarecasas 25039	+	7	257	134	493	58	26.6	17.6	44.
Bejaria steyermark									
Tate 201	-	5	310	179	493	66	26.9	17.6	39.
Bejaria imthurnii									
Clemants and Delascio 2453	-	8	529	336	851	100	46.4	30.8	57.

length[a]			Vessel diameter[b]				Bars[c]		Vessel density[d]			
n	max	SD	mean	min	max	SD	median		mean	min	max	SD
)				(um)			(no.)		(no./mm^2)			
9	493	68	26.7	17.6	35.2	3.8	0	0	397	235	519	133
79	470	70	30.6	17.6	61.6	7.0	6	4	387	243	494	108
34	493	58	26.6	17.6	44.0	5.3	2	0	345	201	469	115
79	493	66	26.9	17.6	39.6	5.3	3	0	370	302	452	65
36	851	100	46.4	30.8	57.2	6.3	0	0	206	159	293	40

Collection	Growth rings	Wood diam. (mm)	Vessel length[a]				Vessel diame		
			mean	min	max	SD	mean	min	ma
			(um)				(um)		
Bejaria ledifolia									
Clemants 2483b	+	13	435	269	627	100	32.3	17.6	5

[a] n=50. [b] n=50. [c] First column median number of bars on vessel end
Second column median number of bars on vessel ends with fewest numb
present, -= absent.

l length[a]			Vessel diameter[b]				Bars[c]		Vessel density[d]			
min	max	SD	mean	min	max	SD	median		mean	min	max	SD
um)				(um)			(no.)		(no./mm^2)			
269	627	100	32.3	17.6	52.8	7.2	7	5	206	67	310	98

umber of bars on vessel end with largest number of bars, n=50.

essel ends with fewest number of bars, n=50. [d] n=10. +=

Table 2. Tracheid and axial parenchyma characteristics of *Bejaria*.

Collection	Tracheid length^a				Axial parenchyma^b				Tracheid wall^c			
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD
	(um)				(um)				(um)			
Bejaria aestuans												
Clemants and Luteyn 1668a	609	291	896	131	132	81	243	28	4.0	2.2	4.4	0.7
Clemants and Luteyn 1670	740	493	1098	120	171	90	261	39	4.8	3.3	6.6	0.9
Clemants and Luteyn 1679c	681	358	1008	131	191	117	270	32	4.4	3.3	5.5	0.5
Clemants 1682	774	515	1008	105	180	126	261	28	5.3	4.4	6.6	0.9
Clemants and Fernândez 2019c	897	605	1232	124	185	106	286	34	5.4	4.4	6.6	1.0
Clemants and Dugarte 2415	752	448	1075	125	147	90	234	33	4.7	3.3	6.6	1.0

Table 2. cont.

Collection	Tracheid length[a]				Axial parenchyma[b]				Tracheid wall[c]			
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD
	(um)				(um)				(um)			
Clemants and Dugarte 2423	605	381	784	104	137	72	225	31	3.6	2.2	5.5	1.0
Clemants and Dugarte 2441a	655	269	918	142	165	99	270	40	3.9	2.2	5.5	0.9
Clemants and Dugarte 2441d	552	336	874	110	127	72	207	27	3.7	3.3	4.4	0.6
Clemants and Dugarte 2443	977	515	1366	174	161	81	279	37	5.0	3.3	6.6	1.2
Clemants 2482	970	538	1344	156	168	99	279	38	4.6	3.3	5.5	0.7
Clemants and Stevenson 2500a	689	470	1008	123	146	90	216	29	4.7	3.3	6.6	0.9
Clemants and Stevenson 2501a	568	358	784	87	140	81	225	32	3.1	2.2	4.4	0.9

Table 2. cont.

Collection	Tracheid length^a				Axial parenchyma^b				Tracheid wall^c			
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD
	(um)				(um)				(um)			
Luteyn et al. 5192	787	448	1232	156	149	81	261	34	3.9	2.2	5.5	1.1
Luteyn et al. 5270a	563	336	739	88	152	90	252	34	3.9	2.2	5.5	0.9
Luteyn et al. 5270b	666	448	1075	116	175	90	324	46	3.5	2.2	4.4	0.7
Luteyn et al. 5276	791	470	1210	154	168	81	279	46	3.6	3.3	4.4	0.5
Luteyn et al. 5386	629	470	918	111	150	90	243	31	2.9	2.2	4.4	0.8
Luteyn et al. 5411	519	224	806	111	184	81	360	42	4.7	3.3	6.6	0.9
Luteyn and Lebrón-Luteyn 6366	700	381	1008	107	145	90	252	33	3.2	2.2	4.4	0.6
Liebman 8592	594	336	986	112	138	90	207	29	2.6	2.2	3.3	0.6
Mexía 8956	584	336	896	105	173	108	261	31	4.3	2.2	6.6	1.2
Ventana 12779	625	426	918	90	122	72	189	24	2.4	2.2	4.4	0.7

Table 2. cont.

Collection	Tracheid length^a				Axial parenchyma^b				Tracheid wall^c			
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD
	(um)				(um)				(um)			
Bejaria resinosa												
Clemants and Luteyn 1675d	816	426	1075	151	131	70	216	31	4.5	3.3	6.6	0.8
Clemants and Luteyn 1675h	644	426	851	89	167	108	243	31	3.9	3.3	4.4	0.6
Clemants 2045	652	403	941	100	162	81	252	34	4.1	2.2	5.5	1.0
Clemants et al. 2220	579	358	829	112	151	90	225	28	3.4	2.2	4.4	0.6
Clemants et al. 2221a	616	381	896	129	155	99	261	35	3.5	2.2	4.4	0.7
Clemants et al. 2221b	615	426	874	104	160	108	234	28	4.4	3.3	5.5	0.7
Clemants 2396	552	291	762	87	136	81	243	34	2.6	2.2	3.3	0.6

Table 2. cont.

Collection	Tracheid length^a				Axial parenchyma^b				Tracheid wall^c			
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD
		(um)				(um)				(um)		
Clemants 2397a	678	381	1098	147	165	81	270	37	4.1	3.3	4.4	0.5
Luteyn et al. 5314	574	336	829	109	150	90	235	33	3.3	2.2	5.5	1.2
Luteyn and Lebrón-Luteyn 7726	635	403	963	112	162	90	243	30	4.0	2.2	6.6	1.4
Bejaria sprucei												
Clemants and Fernández 2000	909	627	1322	125	172	90	279	35	3.4	2.2	4.4	1.0
Clemants and Delascio 2479	635	381	851	101	130	81	225	25	4.4	3.3	5.5	0.7
Clemants and Delascio 2480	658	358	1120	108	157	90	252	34	4.4	4.4	4.4	0.0

Table 2. cont.

Collection	Tracheid length^a				Axial parenchyma^b				Tracheid wall^c			
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD
	(um)				(um)				(um)			
Bejaria infundibula												
Clemants and Fernández 2007c	754	493	1075	154	158	108	225	29	4.1	3.3	4.4	0.5
Clemants and Fernández 2007d	724	358	1165	153	157	90	252	32	4.0	2.2	4.4	0.8
Bejaria mathewsii												
Clemants 2046	654	426	1075	132	169	99	243	32	4.0	3.3	4.4	0.6
Luteyn and Lebrón-Luteyn 6895	506	336	717	88	137	72	243	30	3.1	2.2	4.4	0.9
Cuatrecasas 27550	496	336	672	83	105	54	162	23	2.6	2.2	4.4	0.8

Table 2. cont.

Collection	Tracheid length^{a}				Axial parenchyma^{b}				Tracheid wall^{c}			
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD
	(um)				(um)				(um)			
Bejaria tachirensis												
Ruiz-Teran et al. 13399	526	246	762	112	142	81	216	34	3.0	2.2	3.3	0.5
Bejaria nana												
Cuarecasas 25039	348	202	605	59	99	45	198	29	2.9	2.2	4.4	0.8
Bejaria steyermark												
Tate 201	586	336	672	77	128	72	216	28	3.3	2.2	4.4	0.7
Bejaria imthurnii												
Clemants and Delascio 2453	674	403	963	123	164	90	270	35	3.7	3.3	4.4	0.6

Table 2. cont.

Collection	Tracheid length[a]				Axial parenchyma[b]				Tracheid wall[c]			
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD
	(um)				(um)				(um)			
Bejaria ledifolia												
Clemants 2483b	712	426	1075	124	134	90	261	28	4.0	2.2	5.5	0.9

[a] n=100. [b] n=100. [c] n=10.

Table 3. Multiseriate ray characteristics of Bejaria.

Collection	Ray height^a				Ray width^b				Ray density^c				Ray
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD	islands
	(um)				(um)				(no./mm^2)				
Bejaria aestuans													
Clemants and Luteyn 1668a	657	381	1075	196	90	57	128	16	10.6	8.4	5.7	2.8	+
Clemants and Luteyn 1670	439	269	672	103	56	48	70	6	9.2	7.8	1.1	1.3	-
Clemants and Luteyn 1679c	633	314	1232	244	57	44	70	9	5.9	4.7	6.8	0.7	+
Clemants and Luteyn 1682	598	291	1344	239	54	26	79	10	6.5	5.2	8.4	1.0	-
Clemants and Fernández 2019c	692	381	1344	236	86	57	128	15	12.9	11.5	14.7	1.3	-
Clemants and Dugarte 2415	737	224	2150	437	43	26	57	6	8.1	6.8	10.5	1.1	-

Table 3. cont.

Collection	Ray height^a				Ray width^b				Ray density^c				Ray islands
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD	
	(um)				(um)				(no./mm^2)				
Clemants and Dugarte 2423	547	179	1008	227	52	26	70	9	8.1	5.2	9.9	1.8	-
Clemants and Dugarte 2441a	815	336	2150	416	46	31	66	8	3.8	2.6	5.8	1.2	-
Clemants and Dugarte 2441d	478	246	851	145	86	66	114	14	13.2	10.5	14.1	1.4	-
Clemants and Dugarte 2443	956	314	2106	418	41	22	53	7	8.1	6.3	10.5	1.6	-
Clemants 2482	757	314	1523	322	44	35	75	10	6.6	4.2	8.9	1.5	-
Clemants and Stevenson 2500a	987	403	2934	605	49	70	35	8	7.9	4.7	9.9	1.8	-
Clemants and Stevenson 2501a	660	314	1322	250	39	31	48	5	7.2	5.2	11.0	1.9	-

Table 3. cont.

Collection	Ray height^a				Ray width^b				Ray density^c				Ray
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD	islands
	(um)				(um)				(no./mm^2)				
Luteyn et al. 5192	719	426	1456	261	74	35	101	15	7.4	6.3	9.9	1.5	-
Luteyn et al. 5270a	758	246	1590	341	42	22	62	9	8.3	6.3	10.5	1.5	-
Luteyn et al. 5270b	660	269	1389	234	48	26	62	9	7.3	6.8	7.8	0.6	-
Luteyn et al. 5276	762	314	1702	311	55	35	79	10	8.5	7.3	11.0	1.5	-
Luteyn et al. 5386	1044	358	2195	443	62	44	88	12	5.3	3.7	7.3	1.2	-
Luteyn et al. 5411	752	269	2688	519	41	26	79	10	7.8	5.8	9.9	1.8	-
Luteyn and Lebrón-Luteyn 6366	536	291	1344	228	53	31	79	13	10.0	8.4	14.1	1.8	-
Liebman 8592	903	291	2957	708	23	22	40	9	9.9	4.2	16.7	5.2	-
Mexía 8956	567	314	1187	212	37	26	48	6	29.2	19.4	38.7	7.7	-
Ventana 12779	1352	336	3584	983	31	22	40	5	16.8	15.0	17.2	1.0	-

Table 3. cont.

Collection	Ray height^a				Ray width^b				Ray density^c				Ray islands
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD	
	(um)				(um)				(no./mm^2)				
Bejaria resinosa													
Clemants and Luteyn 1675d	755	448	2352	405	65	44	84	10	9.4	5.8	12.0	2.3	-
Clemants and Luteyn 1675h	803	493	1277	188	67	48	92	9	7.4	6.3	8.9	0.8	+
Clemants 2045	952	448	3136	548	68	35	132	20	5.3	2.6	8.9	2.1	+
Clemants et al. 2220	818	179	2262	519	42	35	57	6	6.6	3.7	9.4	1.8	+
Clemants et al. 2221a	926	314	3158	636	68	48	97	13	7.0	4.2	9.4	1.4	+
Clemants et al. 2221b	606	336	1277	248	60	44	84	11	24.9	21.5	28.0	2.5	+
Clemants 2396	749	246	2419	442	52	35	70	9	7.1	5.2	9.9	1.7	+

Table 3. cont.

Collection	Ray height[a]				Ray width[b]				Ray density[c]				Ray islands
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD	
	(um)				(um)				(no./mm^2)				
Clemants 2397a	621	291	1120	235	51	40	66	7	9.5	7.3	11.5	1.8	+
Luteyn et al. 5314	610	291	1120	180	60	44	101	13	7.9	6.8	9.9	1.1	+
Luteyn and Lebrón-Luteyn 7726	663	291	1546	270	48	31	66	9	7.2	5.2	9.9	1.5	+
<u>Bejaria sprucei</u>													
Clemants and Fernández 2000	574	336	986	178	45	26	66	10	9.0	7.8	11.0	1.2	-
Clemants and Delascio 2479	624	202	1747	332	40	22	70	10	7.1	5.8	9.4	1.5	-
Clemants and Delascio 2480	682	246	1299	281	45	26	57	8	6.5	4.7	7.8	1.2	-

Table 3. cont.

Collection	Ray height^{a}				Ray width^{b}				Ray density^{c}				Ray islands
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD	
	(um)				(um)				(no./mm^{2})				
Bejaria infundibula													
Clemants and Fernândez 2007c	712	336	1075	157	80	62	110	3	7.2	4.7	8.4	1.5	+
Clemants and Fernândez 2007d	943	381	1770	338	37	22	66	9	6.6	4.2	8.4	1.4	+
Bejaria mathewsii													
Clemants 2046	822	291	1837	400	88	48	119	18	6.8	4.7	8.9	1.4	+
Luteyn and Lebrôn-Luteyn 6895	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	-
Cuatrecasas 27550	1001	202	2330	636	41	31	57	8	8.5	2.6	11.5	3.5	-

Table 3. cont.

Collection	Ray height[a]				Ray width[b]				Ray density[c]				Ray islands
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD	
	(um)				(um)				(no./mm^2)				
Bejaria tachirensis													
Ruiz-Teran et al. 13399	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	-
Bejaria nana													
Cuarecasas 25039	668	202	1792	329	69	35	106	19	7.7	6.8	9.9	1.4	-
Bejaria steyermark													
Tate 201	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	-
Bejaria imthurnii													
Clemants and 2453	1168	403	2397	450	52	22	70	12	4.2	3.1	5.8	1.0	-

Table 3. cont.

Collection	Ray height[a]				Ray width[b]				Ray density[c]				Ray
	mean	min	max	SD	mean	min	max	SD	mean	min	max	SD	islands
	(um)				(um)				(no./mm^2)				
Bejaria ledifolia													
Clemants 2483b	885	202	2486	437	79	44	106	17	7.0	5.2	9.4	1.8	-

[a] n=25. [b] n=25. [c] mn=10. ND - not done. += present, -= absent.

in Rhododendron) nor did he describe the change in quantitative characters with age. Although Bejaria wood is diverse, as stated by Cox, it is not drastically different from other ericaceous wood and there is no reason to suppose Bejaria did not arise from an ericaceous ancestors.

CHEMISTRY

Flavonoids are phenolic compounds which, because of their conjugated double bond system, are easily identified and therefore interesting to systematists. Much has been written about the taxonomic usefulness of flavonoids (i.e., Harborne, 1967) and will not be repeated here. Flavonoids of many of the temperate members of the Ericaceae have been studied. Harborne and Williams (1973) surveyed many genera in the family for flavonoid aglycones, while other studies have concentrated on flavonoid surveys of specific genera including Rhododendron (King, 1975, 1977; Harborne, 1980; Harborne & Williams, 1971), Elliottia (Bohm et al., 1978), and Cavendishia (Luteyn et al., 1980).

The aglycones of three Bejaria species have been examined by Harborne and Williams (1973). They stated "The Bejariae ... is chemically a very distinct and uniform group...". Similar studies of Elliottia (Bohm et al., 1978) and Rhododendron (King, 1975, 1977), have been useful in clarifying interspecific relationships.

Materials and Methods

Methods generally follow the University of Texas laboratory manual on isolation and identification of flavonoids (Newman et al., 1979).

Two grams of leaf material from specimens collected in the field (heat dried) or obtained from herbarium specimens were rinsed with dichloromethane (Fraction 1). The leaves were ground twice in 80% MeOH and once in 50% MeOH with a tissue homogenizer. The methanol solutions were combined, rotary evaporated to H_2O, and centrifuged to remove particulate matter. This solution was separated with $CHCl_3$ (Fraction 2), and EtOAc (Fraction 3); the remaining aqueous solution was saved (Fraction 4).

Fraction 1 was not analyzed further.

Fraction 2 was chromatographed on silica gel TLC in Benzene: $CHCl_3$ (24:1). One compound near the solvent front in *B. imthurnii* (Clemants & Delascio 2454) was identified as 3',5-dihydroxy-3,4',5',6,7-pentamethoxyflavone. Specimens from five other species are tentatively identified as containing the same compound based on chromatography (Table 4).

Fractions 3 & 4 were chromatographed on Whatman #1 or #3 paper in TBA and 15% HOAc. The results are presented in Figs. 10-22 and Tables 5-42. Complete identification of the compounds was not possible due to the temporary closing of the laboratory .

Aglycones-- The EtOAc fractions were further hydrolyzed with 1.2 N HCl over a steam bath (100°C) and separated between H_2O and EtOAc. The EtOAc fractions were evaporated and chromatographed on cellulose TLC in BAW and Forestal with quercetin as a marker. Identification of the aglycones was based on Rf values (Harborne, 1967) in these two solvents and on the 2D paper chromatographs (Rf values and color reactions in King, 1975, 1977).

Identification of 3',5-dihydroxy, 3,4',5',6,7-pentamethoxyflavone.

UV spot purple with no change under NH_3.

UV spectra. MeOH: 272, 336 nm. MeOH + NaOMe: 287, 321(sh), 400(sh) nm. MeOH + $AlCl_3$: 265(sh), 281, 300(sh), 365, 405(sh) nm. MeOH, $AlCl_3$ + HCl: 265(sh), 282, 302(sh), 356, 405(sh) nm. MeOH + NaOAc: 273, 335 nm. MeOH, NaOAc + H_3BO_3: 272, 335 nm.

NMR spectra in $CDCl_3$: 3.91 δ (ppm)(ca. 3 protons), 3.96 δ (ca. 3 protons), 3.98 δ (ca. 6 protons), 4.00 δ (ca. 3 protons), 6.49 δ (1 proton), 7.36 δ (2 protons).

The spot color under UV and UV with NH_3 vapor is typical of a flavone or flavonol with 5-OH.

The single proton peak at 6.49 in NMR can indicate either a 6 or 8-H while the two proton peak at 7.36 demonstrates a 2', 6'-H. The absence of other proton signals downfield from the methoxyl signals suggests that the compound is completely substituted except for these three positions.

The low UV Band I value in MeOH suggests a 3-substitution, the absence of sugar signals in the NMR spectra suggests that the substitution is a methoxyl. A UV Band I bathochromic shift of 20 nm in $AlCl_3$ + HCl relative to MeOH is characteristic of a 5-OH, 6-OMe pattern. Therefore, since the 6 position is apparently substituted, the free B-ring proton (6.49) is at the 8-position. The 7-OMe substitution is supported by the absence of a UV Band II bathochromic shift of 7-20 nm in NaOAc relative to MeOH. A UV Band I hypsochromic shift of 9 nm in $AlCl_3$ + HCl relative to $AlCl_3$ is typical of a 3'-OH, 4'-OMe pattern. The only position not accounted for is the 5' position. The placement of a methoxyl group at 5' is based on a comparison of the UV spectra of 3',5,5'-trihydroxy-3,6,7,4'-tetramethoxyflavone (Mabry et al., 1971) and the UV spectra of the present compound. Although these spectra are very similar (the distribution of peaks in the NMR spectra are identical) Band II of the NaOMe spectra differ (269 nm in 3',5,5'-trihydroxy-3,6,7,4'-tetramethoxyflavone vs. 287 nm in this compound). This difference suggests that the compounds are different but very similar. The 5'-OMe is also suggested by the number of methoxyl signals.

Results

The results of the aglycone survey (Table 43) illustrate that in many species, in which more than one sample were examined, aglycone patterns vary. Although this variation might be expected in such morphologically variable species as *B. aestuans*, *B. resinosa*, and *B. sprucei*, it is surprising in morphologically stable locally endemic species such as *B. ledifolia*. It also demonstrates a flaw in many studies in which a single specimen is examined and used to characterize species and genera.

The results of the glycoside survey (Tables 5-42, and Figs. 10-22), although incomplete, demonstrate that glycoside spot patterns, as well as aglycone patterns, vary within species. Compare, for instance, *Clemants 2045*, *Clemants 2396*, and *Clemants 2397a* (Tables 32-34, Fig. 19) all samples of *B. resinosa*. The first two samples have four purple compounds (probably quercetin-3-O-rhamnoglucoside, myricetin 3-O-glycoside, quercetin 3-O-glycoside and a flavanone) and the last sample has the same four spots along with two additional purple spots (probably quercetin and myricetin 3-O-glycosides) indicating the presence of a new sugar substituent. While some species, such as *B. resinosa*, are variable, others are not variable or only slightly so. In *Bejaria imthurnii*, for instance, two samples were studied, one with glandular hairs (Clemants & Delascio 2454; Table 39) and the other with non-glandular hairs (Clemants & Delascio 2453a; Table 38). Here flavonoid spot patterns are nearly identical.

Variation within populations is apparently slight. For instance, individuals from a *B. aestuans* population at Páramo La Negra in Venezuela (Table 44), morphologically very similar yet having different hair types, exhibit almost no flavonoid differences.

Discussion

The data on the distribution of aglycones (Table 43) demonstrate that aglycones are not useful in analyzing the phylogeny of *Bejaria* species. Most species have the same aglycone pattern. Variation occurs within species and not between species. Furthermore, because there are few aglycones found (4) and a relatively large number of taxa (13) any phylogenetic analysis would not be fully resolved.

Aglycones of the genera of Rhododendroideae have been compiled (Table 46) but the limited number of compounds makes it impossible to resolve the intergeneric relationships in the Rhododendroideae.

A phylogenetic analysis of the tribes in the Rhododendroideae is, however, possible. The limited number of aglycones does not hinder this analysis, because there are so few tribes in the Rhododendroideae. In order to carry out a cladistic analysis of the chemical data, however, some method had to be devised to deal with the variation. In this study a convention was used. Tribes in which a compound was present in some member and absent in others were scored positive for the presence of the compound. It is considered easier to lose a compound through the loss of an enzyme in the biosynthetic sequence or through degradation during preparation than it is to evolve a biosynthetic sequence more than once in the same tribe (Mabry & Bohlmann, 1978).

Data for this analysis was gathered from Harborne and Williams (1973) who analyzed the aglycones of all genera in the Rhododendroideae, from studies of the Cladothamneae (Bohm et al., 1978), the North America Azaleas (King, 1975, 1977), and from this study. Harborne and Williams' work (1973) needs to be used cautiously for three reasons (1) methods used in preserving herbarium material may extract flavonoids (Coradin & Giannasi, 1980), (2) the leaf extracts were hydrolyzed with HCl (as was done here) which can degrade 5-OMe flavonoids (Bohm, pers. comm.), and (3) often only one specimen per genus was examined.

Hennigian methods of phylogenetic analysis (Hennig, 1969), in which taxa are grouped based on shared derived characters, was used to produce a cladogram (Fig. 23). A data matrix (Table 48) was created by encoding the flavonoid data (Table 47). A method of encoding, in which both position and type of substitution are scored separately, is used. This method follows the procedure presented by Richardson (1983). An outgroup (the other subfamilies of the Ericaceae) was used to polarize the character states.

The cladogram produced using all other Ericaceae subfamilies as an outgroup (Fig. 23A) has only one synapomorphy (6-OMe) with two tribes (Bejarieae and Rhodoreae) having this synapomorphy. If, however, the presence of azaletin and caryotin in only one sample each of the Ericoideae and Vaccinoideae is an error or a parallel derivation then more resolution is possible (Fig. 23B). Either cladogram suggest that *Bejaria* is not the most chemically archaic member of the Rhododendroideae and that *Bejaria* is chemically related to the Rhodoreae. *Bejaria* was once considered archaic in the Ericaceae because of its free petals and floral anatomy (Copeland, 1943). The presence, however, of a number of derived flavonoids suggest that *Bejaria* is not primitive with respect to all characters. In the cladograms, *Bejaria* is the sister group of the Rhodoreae. A relationship of *Bejaria* with the Rhodoreae is possible: they share, for instance, long testa cells on the seeds. The second cladogram (Fig. 23B) suggests a relationship of *Bejaria* and the Phyllodoceae such a relationship is possible since the Phyllodoceae often have inflorescences similar to that of *Bejaria* (Bohm et al., 1978).

The limited information available from the glycoside spot patterns supports the hybrid nature of Clemants 2276. A comparison of the spots (Table 45) demonstrates that Clemants 2276 combines compounds of both parents (compounds 2, 4, 9, and 12) but rarely lacks compounds found in both parents (compound 1) or contains unique compounds (compound 15). This addition of flavonoid profiles in a hybrid occurs elsewhere. In certain instances the hybrid profiles can be used to identify the parents, for example in *Asplenium* (Smith & Levin, 1963; Harborne et al., 1973), *Baptisia* (Alston & Turner, 1962), and *Cavendishia* (Luteyn et al., 1980).

The results of this flavonoid survey based on spot patterns suggest that flavonoids are not going to be taxonomically useful at the species level in *Bejaria*.

Table 4. Taxa in which 3',5-dihydroxy-3,4',5',6,7-pentamethoxyflavone is present.

B. cubensis

Van Hermann s.n.
(year 1914)

B. aestuans

Clemants & Dugarte 2421
Clemants & Dugarte 2427
Clemants & Dugarte 2441
Clemants & Dugarte 2443
Hinton 14106
Luteyn & Lebrón-Luteyn 6425
Luteyn et al. 7616
Mexía 9276
Ventura 12779

B. sprucei

Clemants & Delascio 2481

B. resinosa

Clemants 2274
Luteyn et al. 5314

B. ledifolia

Clemants 2483a
Clemants 2483b

B. imthurnii

Clemants 2454

Fig. 10. Spot patterns of paper chromatographs. Figs. A-B. *B*. *racemosa* (coll. *Clemants* *&* *Miller* *1591*). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 5. Fig. C-D. *B*. *cubensis* (coll. *Van* *Hermann* *s*.*n*., year 1914). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 6. Fig. E-F. *B*. *infundibula* (coll. *Clemants* *&* *Fernández* *2007c*). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 7.

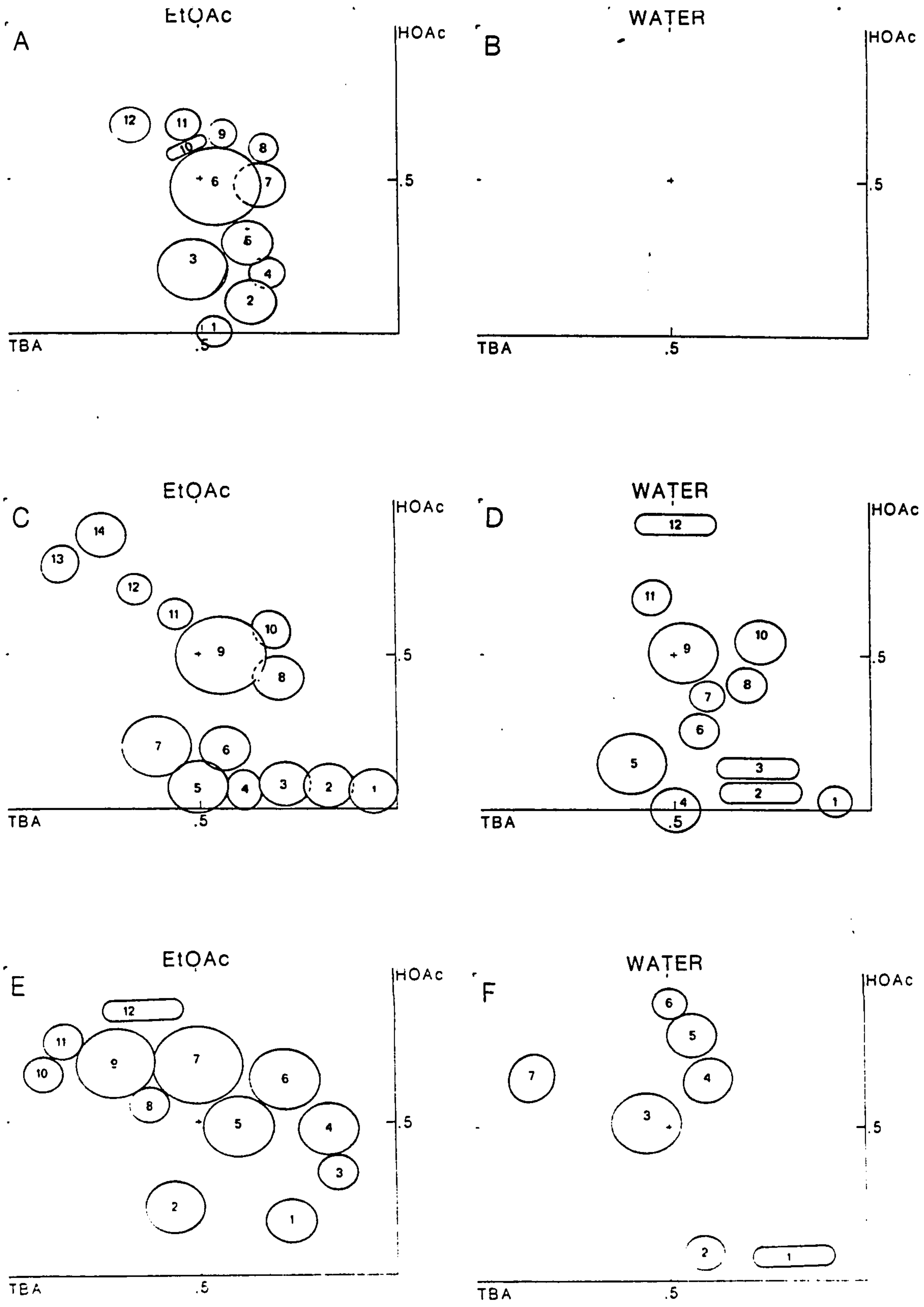

A
EtOAc
HOAc
.5
TBA
.5
12
11
10
9
8
6
7
5
3
4
2
1
B
WATER
HOAc
.5
TBA
.5
C
EtOAc
HOAc
.5
TBA
.5
14
13
12
11
10
9
8
7
6
5
4
3
2
1
D
WATER
HOAc
.5
TBA
.5
12
11
10
9
8
7
6
5
3
2
4
1
E
EtOAc
HOAc
.5
TBA
.5
12
11
10
9
7
6
8
5
4
3
2
1
F
WATER
HOAc
.5
TBA
.5
6
5
7
4
3
2
1

Table 5. Rf values and color reactions of individual spots from paper chromatographs of *B. racemosa*. Coll. *Clemants & Miller 1591*.

EtOAc extract (Fig. 10A)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH$_3$)
1	47/0	Y/Y
2	33/3	fB/fB
3	52/16	fB/fB
4	25/14	fG/fG
5	29/24	fG/fG
6	43/40	P/G
7	29/38	-
8	27/49	-
9	34/54	-
10	41/50	fW/fW
11	46/53	P/P
12	58/58	-

Water extract

Not chromatographed

[1] B=blue, G=green, O=orange, P=purple, Pk=pink, Y=yellow, W=white, f=fluorescent, -=no distinct color.

Spot # refers to accompanying figure.

Table 5 cont.

TBA= tertiary butyl alcohol, glacial acetic acid, water.

HOAc= glacial acetic acid, water.

UV= refers to color of spot under ultraviolet light (360 nm).

UV+NH_3= refers to color of spot under ultraviolet light in the presence of ammonia vapors.

Table 6. Rf values and color reactions of individual spots from paper chromatographs of _B_. _cubensis_. Coll. _Van Hermann_ _s_._n_. (year 1914)

EtOAc extract (Fig. 10C)			Water extract (Fig. 10D)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	2/0	Y/Y	1	39/3	Pk/Pk
2	21/3	Pk/Y	2	26/4	BG/BG
3	34/6	fB/Y	3	28/10	fB/Y
4	44/1	Y/Y	4	51/0	Y/Y
5	56/1	Y/Y	5	58/12	fB/Y
6	45/12	fB/Y	6	34/24	fB/Y
7	63/20	fB/Y	7	32/36	Y/Y
8	25/42	P/O	8	24/38	fB/Y
9	43/50	P/G	9	42/46	P/O
10	28/54	P/Y	10	21/52	fW/Y
11	59/64	-	11	46/65	Pk/Pk
12	67/74	-/fB	12	45/94	fB/fB
13	82/77	-/fB			
14	73/90	-/fB			

[1] See footnote following table 5.

Table 7. Rf values and color reactions of individual spots from paper chromatographs of *B. infundibula*. Coll. *Clemants* *&* *Fernândez* *2007c*

EtOAc extract (Fig. 10E)			Water extract (Fig. 10F)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH$_3$)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH$_3$)
1	28/17	Y/Y	1	19/9	fW/YG
2	55/28	Y/Y	2	40/7	fW/YG
3	15/38	Y/Y	3	54/53	P/O
4	17/49	B/B	4	38/65	Pk/Pk
5	40/49	fW/Y	5	40/82	fB/fB
6	30/61	P/O	6	43/89	fB/G
7	50/71	P/O	7	81/68	fB/fB
8	65/63	fB/BY			
9	69/73	P/G			
10	85/68	fW/B			
11	78/76	P/G			
12	60/87	fB/fB			

[1] See footnote following table 5.

Fig. 11. Spot patterns of paper chromatographs. Fig. A-B. *B. aestuans* (coll. Clemants & Fernández 2019a). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 8. Fig. C-D. *B. aestuans* (coll. Clemants 2275). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 9. Fig. E-F. *B. aestuans* (coll. Clemants 2345). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 10.

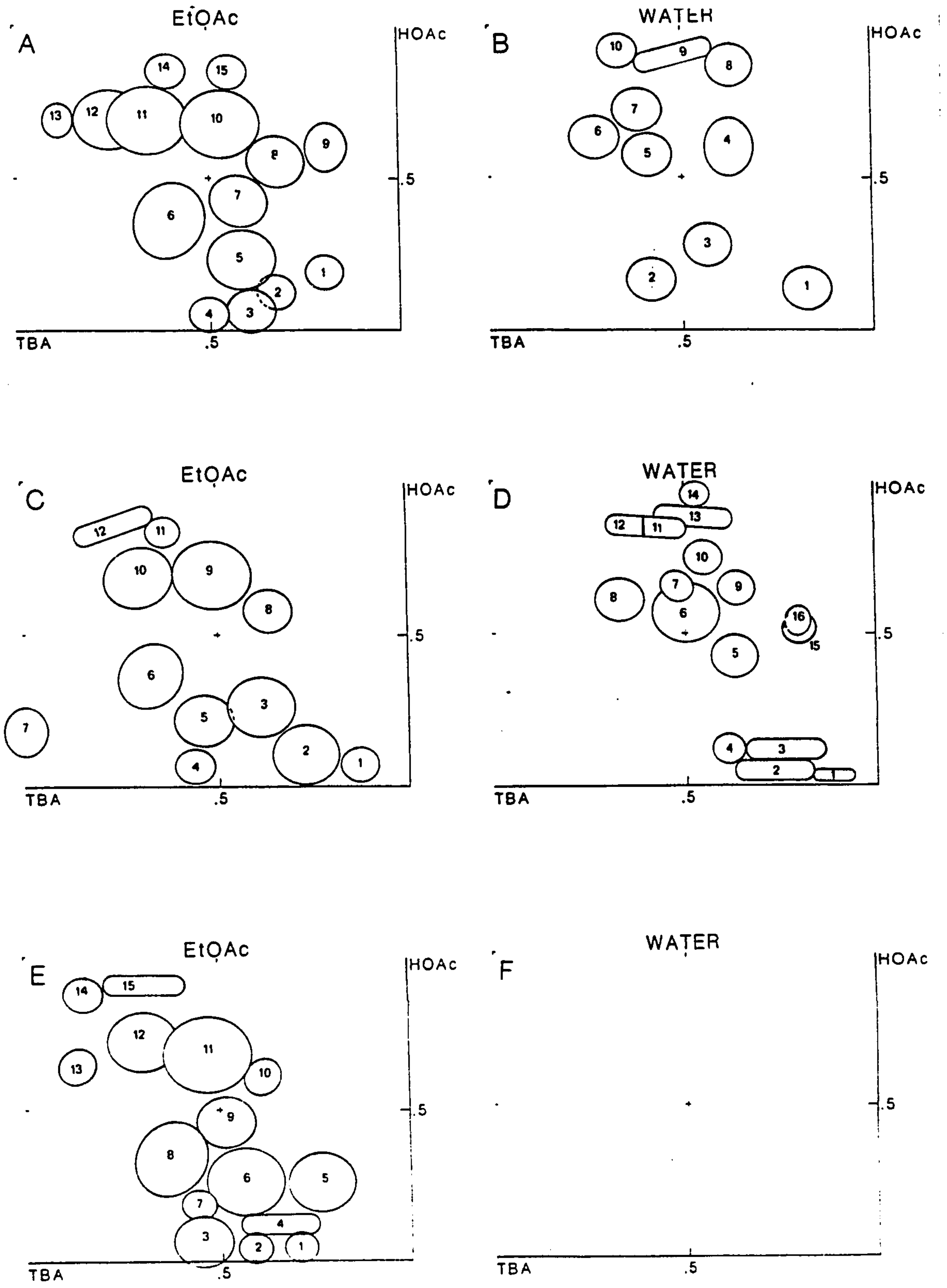

A
EtOAc
HOAc
TBA
.5
.5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
B
WATER
HOAc
TBA
.5
.5
1 2 3 4 5 6 7 8 9 10
C
EtOAc
HOAc
TBA
.5
.5
1 2 3 4 5 6 7 8 9 10 11 12
D
WATER
HOAc
TBA
.5
.5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
E
EtOAc
HOAc
TBA
.5
.5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
F
WATER
HOAc
TBA
.5
.5

Table 8. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*.

Coll. *Clemants & Fernández 2019a*

EtOAc extract (Fig. 11A)			Water extract (Fig. 11B)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	15/15	-/OY	1	20/9	fB/Y
2	28/8	-	2	59/13	fB/Y
3	36/3	Y/Y	3	43/24	fB/Y
4	50/4	Y/Y	4	36/56	-/Y
5	37/19	fB/Y	5	54/51	P/O
6	60/34	fB/Y	6	66/56	P/O
7	41/42	-	7	56/63	-/Y
8	31/54	P/O	8	40/86	B/B
9	19/58	P/P	9	55/84	-/BG
10	47/65	P/G	10	65/86	B/B
11	64/72	P/G			
12	77/70	P/P			
13	85/68	-			
14	56/83	P/P			
15	40/80	-			

[1] See footnote following table 5.

Table 9. Rf values and color reactions of individual spots from paper chromatographs of B. aestuans. Coll. Clemants 2275

EtOAc extract (Fig. 11C)			Water extract (Fig. 11D)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	15/5	Y/Y	1	11/1	Pk/Pk
2	31/6	fB/Y	2	26/2	fW/Y
3	42/25	fB/Y	3	23/10	fW/Y
4	57/9	Y/Y	4	39/8	fW/Y
5	56/21	fB/Y	5	37/43	P/Y
6	66/35	fB/Y	6	50/55	P/O
7	98/17	fB/fB	7	53/67	fW/Y
8	35/56	P/Y	8	67/62	P/O
9	50/68	P/O	9	38/62	Pk/Y
10	72/68	P/GO	10	48/74	Pk/Pk
11	57/81	fB/fB	11	56/86	BG/BG
12	68/85	fB/G	12	69/87	BG/B
			13	42/87	B/B
			14	46/94	fW/fW
			15	22/43	P/O
			16	20/51	fW/fW

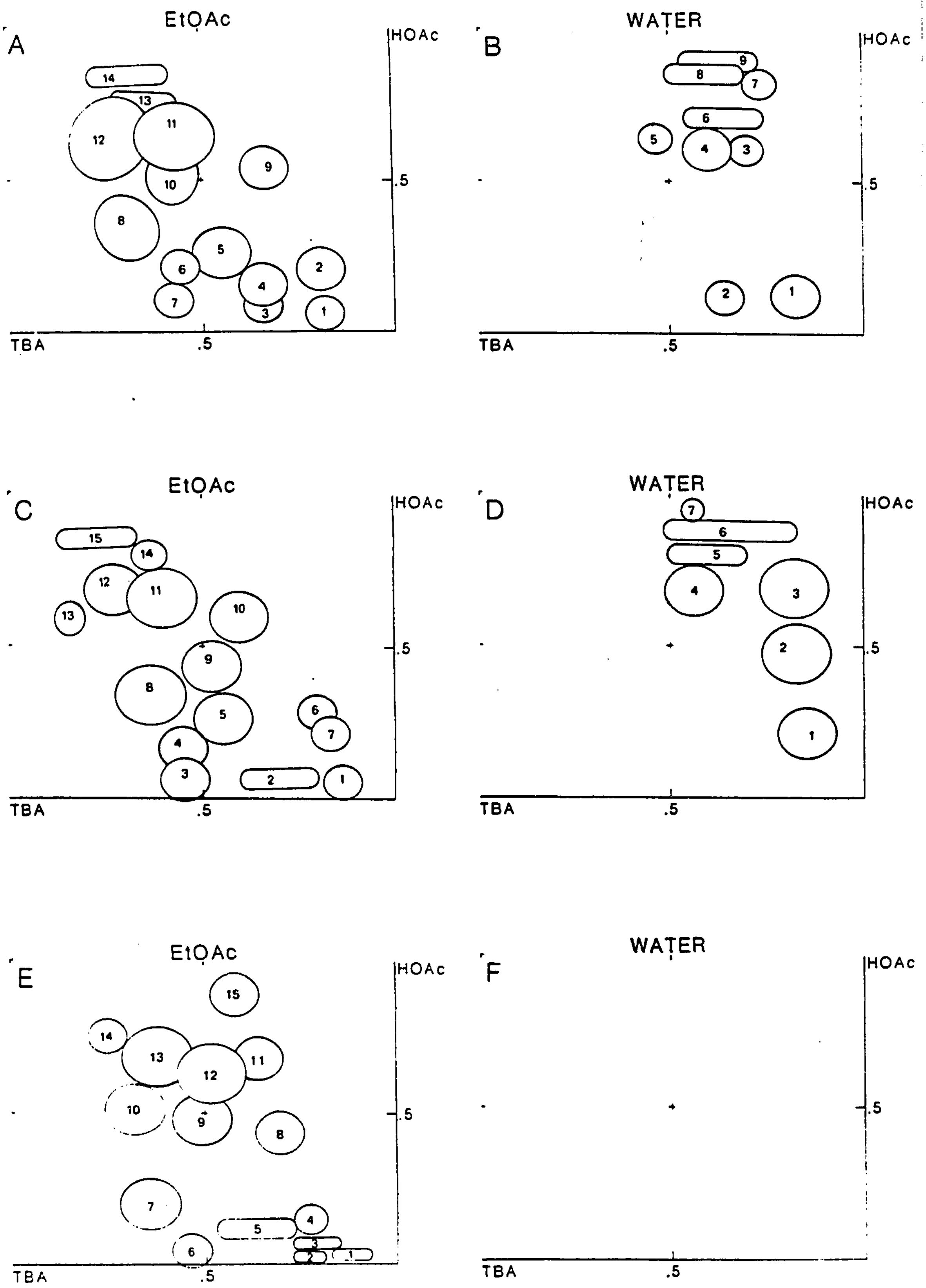
[1] See footnote following table 5.

Table 10. Rf values and color reactions of individual spots from paper chromatographs of B. aestuans. Coll. Clemants 2345

EtOAc extract (Fig. 11E)			Water extract
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	not chromatographed
1	18/4	Y/Y	
2	36/3	Y/Y	
3	57/3	Y/Y	
4	30/10	fB/Y	
5	16/22	-/Y	
6	43/22	fB/Y	
7	60/14	fB/Y	
8	65/30	fB/Y	
9	46/42	fB/Y	
10	33/52	P/Y	
11	52/63	P/Y	
12	72/67	P/OG	
13	85/55	fB/fB	
14	79/79	fB/fB	
15	62/87	fB/G	

[1] See footnote following table 5.

Fig. 12. Spot patterns of paper chromatographs. Fig. A-B. B. aestuans (coll. Clemants & Dugarte 2415). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 11. Fig. C-D. B. aestuans (coll. Clemants & Dugarte 2421). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 12. Fig. E-F. B. aestuans (coll. Clemants & Dugarte 2441). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 13.


A
EtOAc
HOAc
.5
TBA
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6
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B
WATER
HOAc
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TBA
.5
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5
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9
C
EtOAc
HOAc
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WATER
HOAc
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TBA
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EtOAc
HOAc
.5
TBA
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11
12
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15
F
WATER
HOAc
.5
TBA
.5

Table 11. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*. Coll. *Clemants & Dugarte 2415*

EtOAc extract (Fig. 12A)			Water extract (Fig. 12B)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	18/4	Y/Y	1	15/13	W/W
2	18/15	Y/Y	2	36/11	B/B
3	33/4	Y/Y	3	30/60	W/Y
4	32/10	B/Y	4	42/58	P/O
5	42/20	fB/Y	5	56/63	P/G
6	55/15	B/Y	6	36/68	Pk/Y
7	58/7	Y/Y	7	26/82	B/BG
8	65/32	fB/Y	8	42/86	B/BG
9	35/52	P/Y	9	35/89	-/B
10	57/48	P/Y			
11	53/63	-/O			
12	71/68	P/OG			
13	59/77	P/P			
14	60/84	fB/-			

[1] See footnote following table 5.

Table 12. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*. Coll. *Clemants & Dugarte 2421*

EtOAc extract (Fig. 12C)			Water extract (Fig. 12D)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	17/4	Y/Y	1	16/13	W/Y
2	34/8	fB/Y	2	47/19	-/Y
3	57/3	Y/Y	3	59/18	-/Y
4	57/13	fB/Y	4	64/43	-/Y
5	44/23	fBG/Y	5	72/37	Pk/Pk
6	23/27	fB/Y	6	82/30	fB/G
7	17/20	Y/Y	7	99/38	fB/fB
8	66/30	fB/Y			
9	48/40	fB/Y			
10	36/54	P/Y			
11	55/65	P/Y			
12	73/69	P/OG			
13	85/59	fB/-			
14	58/75	fW/-			
15	72/83	fBG/-			

[1] See footnote following table 5.

Table 13. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*. Coll. *Clemants & Dugarte 2441*

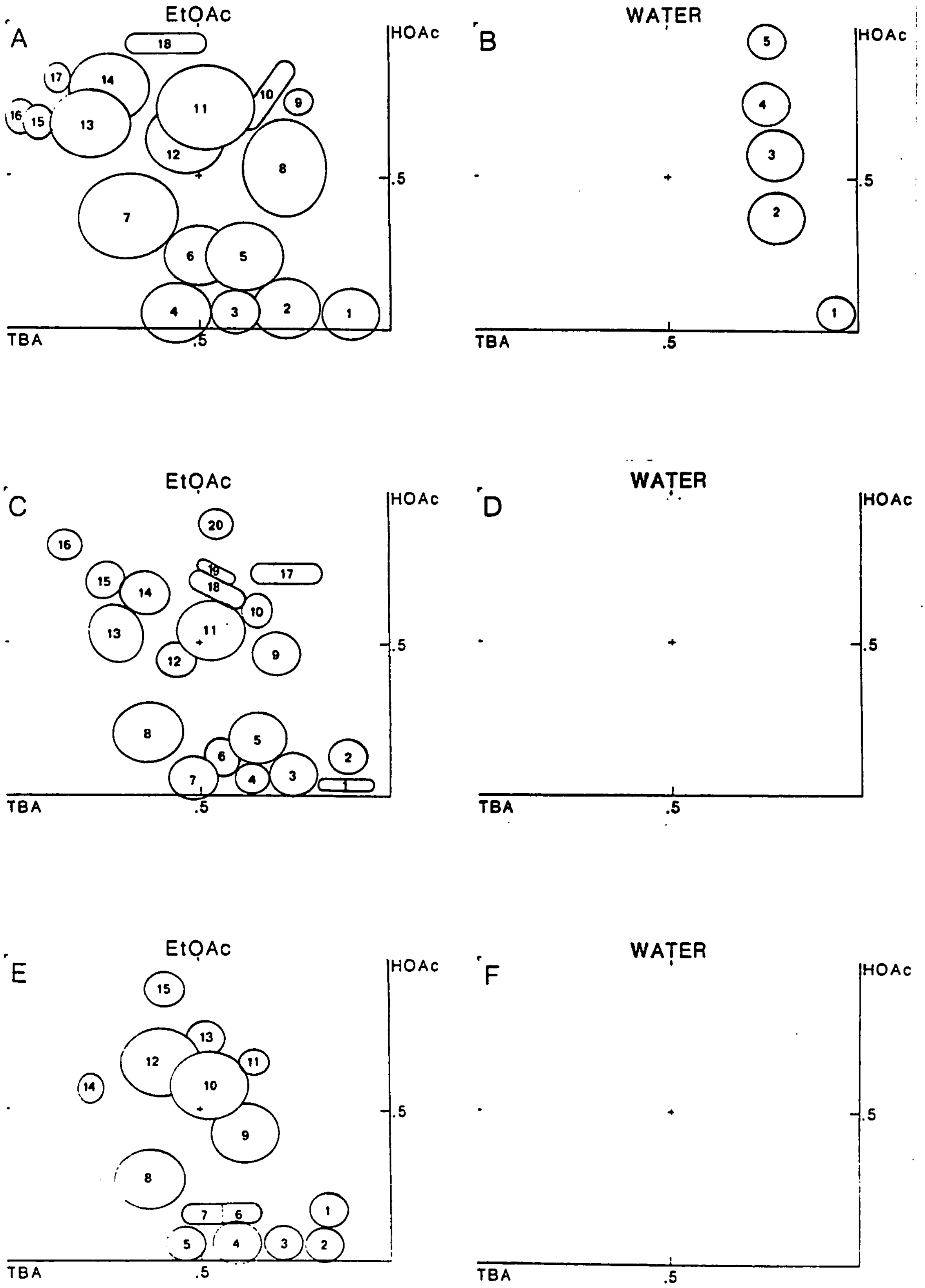
EtOAc extract (Fig. 12E)

Water extract not chromatographed

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	15/1	Y/Y
2	33/1	Y/Y
3	28/4	B/B
4	22/12	B/B
5	41/11	B/W
6	54/2	Y/Y
7	61/20	B/YG
8	31/44	P/P
9	51/41	P/O
10	67/56	P/G
11	35/61	W/W
12	48/62	P/O
13	62/72	P/G
14	72/76	B/B
15	38/88	B/B

[1] See footnote following table 5.

Fig. 13. Spot patterns of paper chromatographs. Fig. A-B. *B. aestuans* (coll. *Clemants* & *Dugarte* 2427). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 14. Fig. C-D. *B. aestuans* (coll. *Clemants* & *Dugarte* 2428). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 15. Fig. E-F. *B. aestuans* (coll. *Clemants* & *Dugarte* 2429). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 16.


A
EtOAc
HOAc
TBA
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WATER
HOAc
TBA
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EtOAc
HOAc
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2
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4
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D
WATER
HOAc
TBA
.5
E
EtOAc
HOAc
TBA
.5
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WATER
HOAc
TBA
.5

Table 14. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*. Coll. *Clemants & Dugarte 2427*

EtOAc extract (Fig. 13A)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	14/5	Y/Y
2	30/7	W/Y
3	43/5	Y/Y
4	59/15	Y/Y
5	41/19	W/Y
6	53/16	B/Y
7	63/35	B/Y
8	33/51	P/O
9	20/63	-
10	34/70	-/Y
11	49/68	P/G
12	56/55	P/O
13	73/63	P/G
14	66/77	P/G
15	85/60	P/P
16	89/62	BW/BW
17	79/74	B/B
18	60/89	B/BO

Water extract (Fig. 13B)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	4/2	Pk/Pk
2	25/39	-/Y
3	27/39	P/Y
4	28/68	Pk/Pk
5	28/89	B/B

Table 14 cont.

[1] See footnote following table 5.

Table 15. Rf values and color reactions of individual spots from paper chromatographs of B. aestuans. Coll. Clemants & Dugarte 2428

EtOAc extract (Fig. 13C)			Water extract
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	not chromatographed.
1	14/2	Y/Y	
2	13/13	Y/Y	
3	29/4	B/W	
4	38/3	Y/Y	
5	38/12	B/W	
6	49/9	B/W	
7	54/4	Y/Y	
8	59/20	B/W	
9	28/40	P/O	
10	31/52	W/Y	
11	43/52	P/G	
12	52/44	-/O	
13	66/49	P/G	
14	59/63	P/G	
15	70/67	B/B	
16	79/75	B/B	
17	25/65	-/Y	

Table 15 cont.

18	44/60	-/0
19	43/66	W/Y
20	47/82	B/B

[1] See footnote following table 5.

Table 16. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*. Coll. Clemants & Dugarte 2429

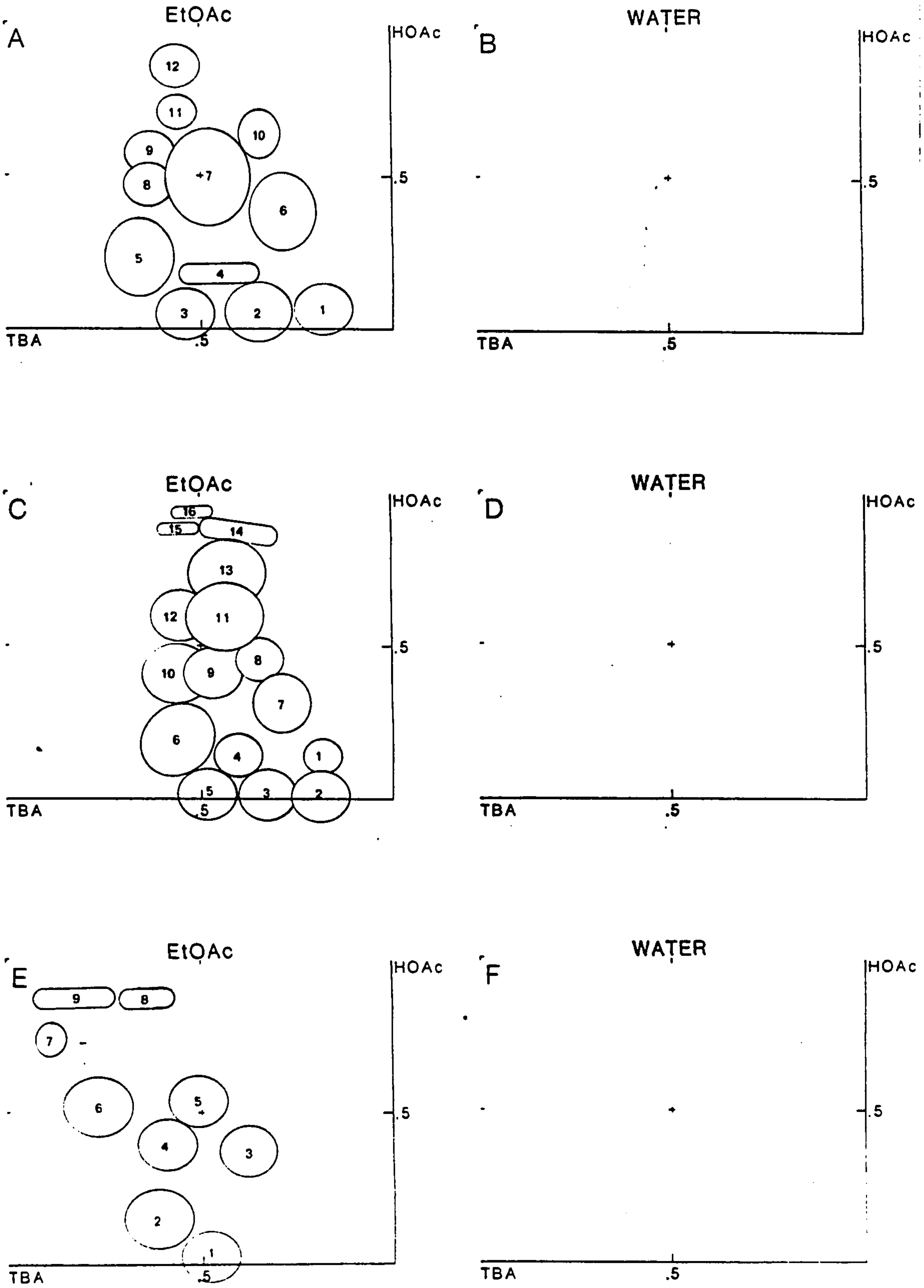
EtOAc extract (Fig. 13E)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	14/14	Y/Y
2	16/3	Y/Y
3	27/7	W/Y
4	39/5	Y/Y
5	55/7	Y/Y
6	37/16	B/B
7	47/16	B/Y
8	61/29	B/Y
9	35/43	P/O
10	47/57	P/G
11	34/63	B/B
12	67/65	P/GP
13	50/71	W/Y
14	85/49	B/B
15	58/86	B/BG

Water extract
not chromatographed

[1] See footnote following table 5.

Fig. 14. Spot patterns of paper chromatographs. Fig. A-B. *B. aestuans* (coll. *Clemants 2482*). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 17. Fig. C-D. *B. aestuans* (coll. *Hinton 14106*). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 18. Fig. E-F. *B. aestuans* (coll. *Luteyn & Lebrón-Luteyn 6366*). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 19.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EtOAc
HOAc
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TBA
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B
WATER
HOAc
.5
TBA
.5
C
EtOAc
HOAc
.5
TBA
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16
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D
WATER
HOAc
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TBA
.5
E
EtOAc
HOAc
.5
TBA
.5
9
8
7
6
5
4
3
2
1
F
WATER
HOAc
.5
TBA
.5

Table 17. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*. Coll. *Clemants 2482*

EtOAc extract (Fig. 14A)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	16/2	Y/Y
2	38/3	B/Y
3	54/3	Y/Y
4	42/14	B/Y
5	58/19	B/Y
6	32/32	P/YO
7	47/46	P/G
8	65/48	P/G
9	62/61	P/GP
10	37/57	B/B
11	50/63	W/W
12	56/79	B/BG

Water extract
not chromatographed

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[1] See footnote following table 5.

Table 18. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*. Coll. Hinton 14106

EtOAc extract (Fig. 14C)			Water extract
Spot	Rf X 100	Color[1]	not chromatographed
#	(TBA/HOAc)	(UV/UV+NH_3)	
1	16/10	W/W	
2	14/1	Pk/Pk	
3	31/1	Y/Y	
4	37/14	fB/Y	
5	47/4	Y/Y	
6	49/17	B/W	
7	26/32	P/O	
8	35/41	P/G	
9	44/42	P/O	
10	57/39	P/G	
11	44/58	P/O	
12	57/54	P/P	
13	45/71	P/P	
14	44/79	B/B	
15	62/84	-/fB	
16	58/90	-/fB	

[1] See footnote following table 5.

Table 19. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*. Coll. *Luteyn & Lebrón-Luteyn 6366*

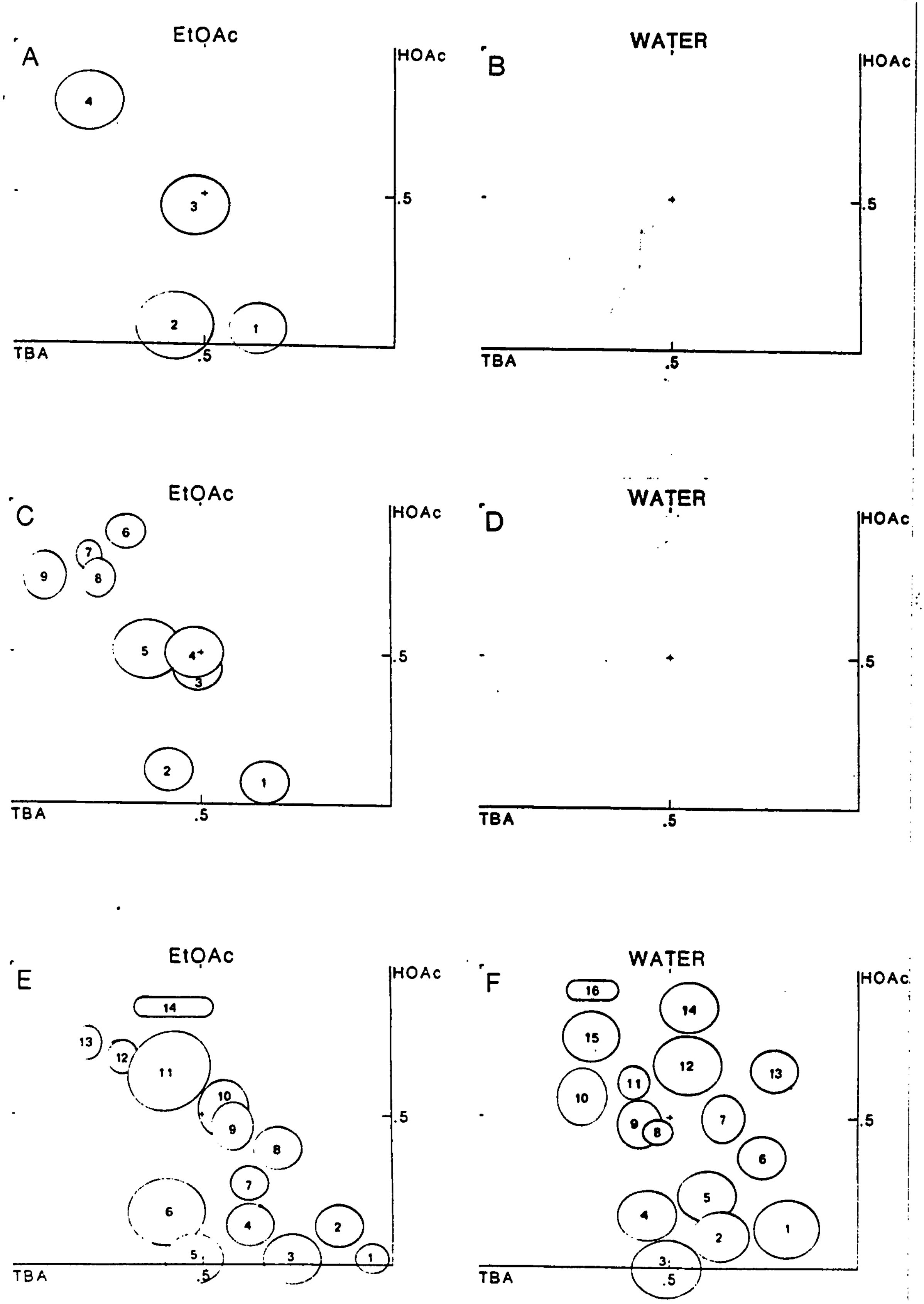
EtOAc extract (Fig. 14E)

Water extract not chromatographed

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	47/2	Y/Y
2	59/14	fB/G
3	34/32	P/Y
4	55/34	P/Y
5	47/42	P/G
6	67/41	P/G
7	82/63	B/B
8	52/85	fB/fB
9	72/83	-/B

[1] See footnote following table 5.

Fig. 15. Spot patterns of paper chromatographs. Fig. A-B. *B*. *aestuans* (coll. *Luteyn* *&* *Lebrón-Luteyn* *6425*). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 20. Fig. C-D. *B*. *aestuans* (coll. *Luteyn* *et* *al.* *7616*). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 21. Fig. E-F. *B*. *aestuans* (coll. *Matuda* *2589*). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 22.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HOAc
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TBA
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WATER
HOAc
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HOAc
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WATER
HOAc
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EtOAc
HOAc
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HOAc
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Table 20. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*. Coll. *Luteyn & Lebrón-Luteyn 6425*

EtOAc extract (Fig. 15A)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	40/3	fB/Y
2	59/10	fB/Y
3	53/41	-/Y
4	71/82	-/B

Water extract

not chromatographed

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[1] See footnote following table 5.

Table 21. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*. Coll. *Luteyn et al. 7616*

EtOAc extract (Fig. 15C)			Water extract
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	not chromatographed
1	36/6	fB/G	
2	58/12	fB/G	
3	48/41	P/Y	
4	52/49	P/O	
5	65/51	P/G	
6	71/83	-/fB	
7	79/71	-/B	
8	78/66	fB/fB	
9	88/70	W/W	

[1] See footnote following table 5.

Table 22. Rf values and color reactions of individual spots from paper chromatographs of *B. aestuans*.
Coll. *Matuda 2589*

EtOAc extract (Fig. 15E)			Water extract (Fig. 16F)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	7/0	Pk/Pk	1	19/9	W/YG
2	16/9	B/B	2	37/7	W/YG
3	29/0	Y/Y	3	52/0	Y/Y
4	39/9	B/Y	4	58/12	B/YG
5	54/1	Y/Y	5	42/18	B/YG
6	60/16	B/Y	6	28/35	B/B
7	41/18	B/B	7	39/50	-/Y
8	31/32	-/Y	8	52/46	-/Y
9	45/42	P/Y	9	53/49	P/O
10	49/52	P/O	10	67/54	P/O
11	61/56	P/Brown	11	56/59	Y/Y
12	71/55	B/B	12	44/67	Pk/Pk
13	79/57	B/B	13	25/66	Y/Y
14	59/72	P/P	14	45/88	B/B
			15	65/76	-/P
			16	67/84	B/B

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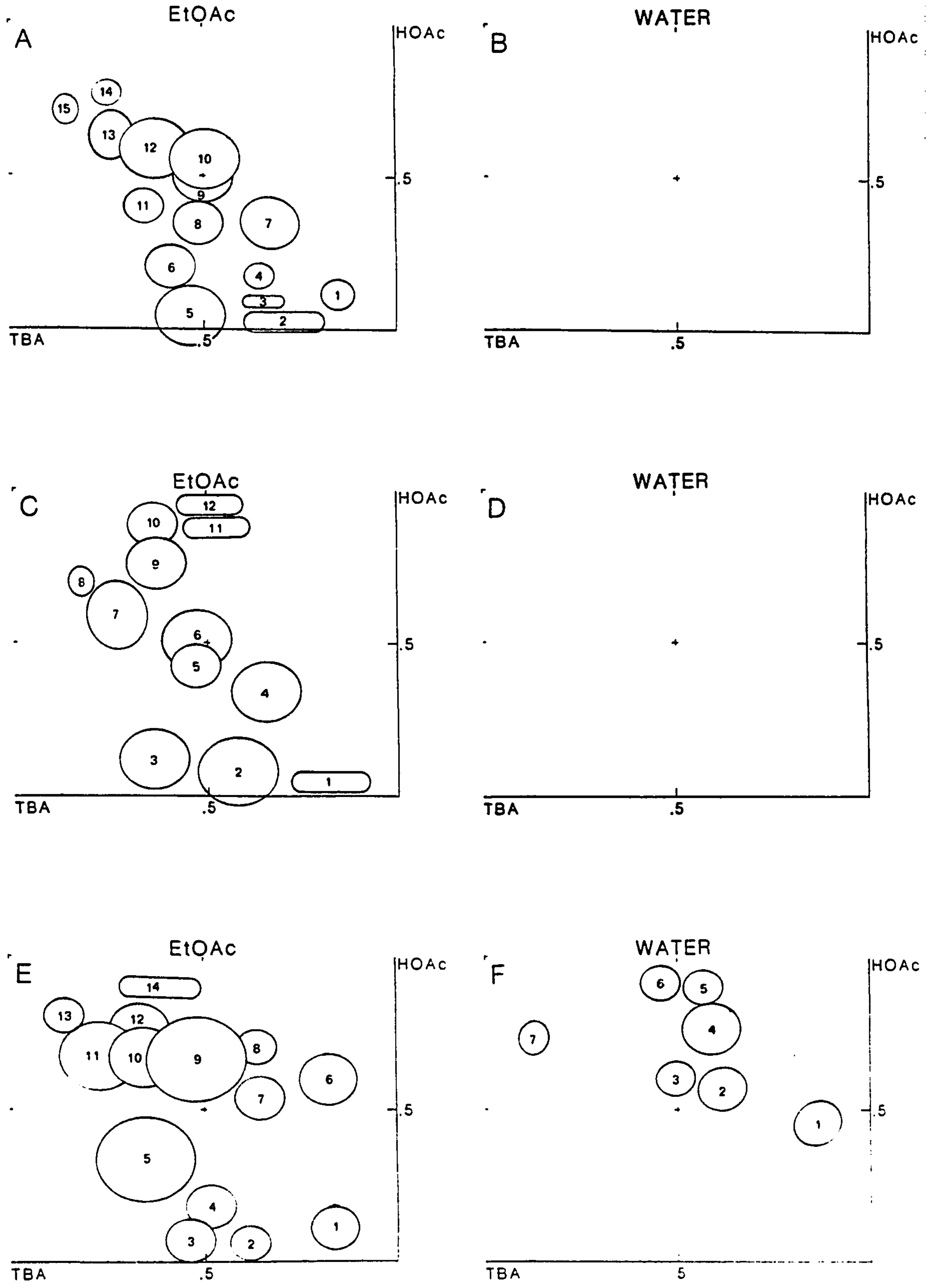
[1] See footnote following table 5.

Fig. 16. Spot patterns of paper chromatographs. Fig. A-B. *B. aestuans* (*Mexía 9276*). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 23. Fig. C-D. *B. aestuans* (coll. *Ventana 12779*). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 24. Fig. E-F. *B. sprucei* (coll. *Clemants & Fernândez 2000*). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 25.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WATER
HOAc
TBA
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EtOAc
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HOAc
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WATER
HOAc
TBA
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Table 23. Rf values and color reactions of individual spots from paper chromatographs of B. aestuans. Coll. Mexía 9276

EtOAc extract (Fig. 16A)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	15/8	Y/Y
2	32/2	Y/Y
3	37/10	fB/fB
4	40/15	Y/Y
5	55/3	Y/Y
6	59/15	fB/fB
7	31/36	P/P
8	51/37	P/P
9	50/48	P/Y
10	49/59	P/O
11	66/42	P/Y
12	62/59	P/G
13	73/63	P/P
14	64/72	B/B
15	82/71	B/B

Water extract not chromatographed

[1] See footnote following table 5.

Table 24. Rf values and color reactions of individual spots from paper chromatographs of *B*. *aestuans*. Coll. *Ventana* *12779*

EtOAc extract (Fig. 16C)

Water extract not chromatographed

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	22/2	Y/Y
2	45/7	W/Y
3	64/8	fB/Y
4	33/33	P/Y
5	54/33	P/Y
6	56/52	P/O
7	68/53	P/G
8	76/62	-
9	63/70	P/P
10	65/79	-/W
11	51/82	-/fB
12	54/89	-/B

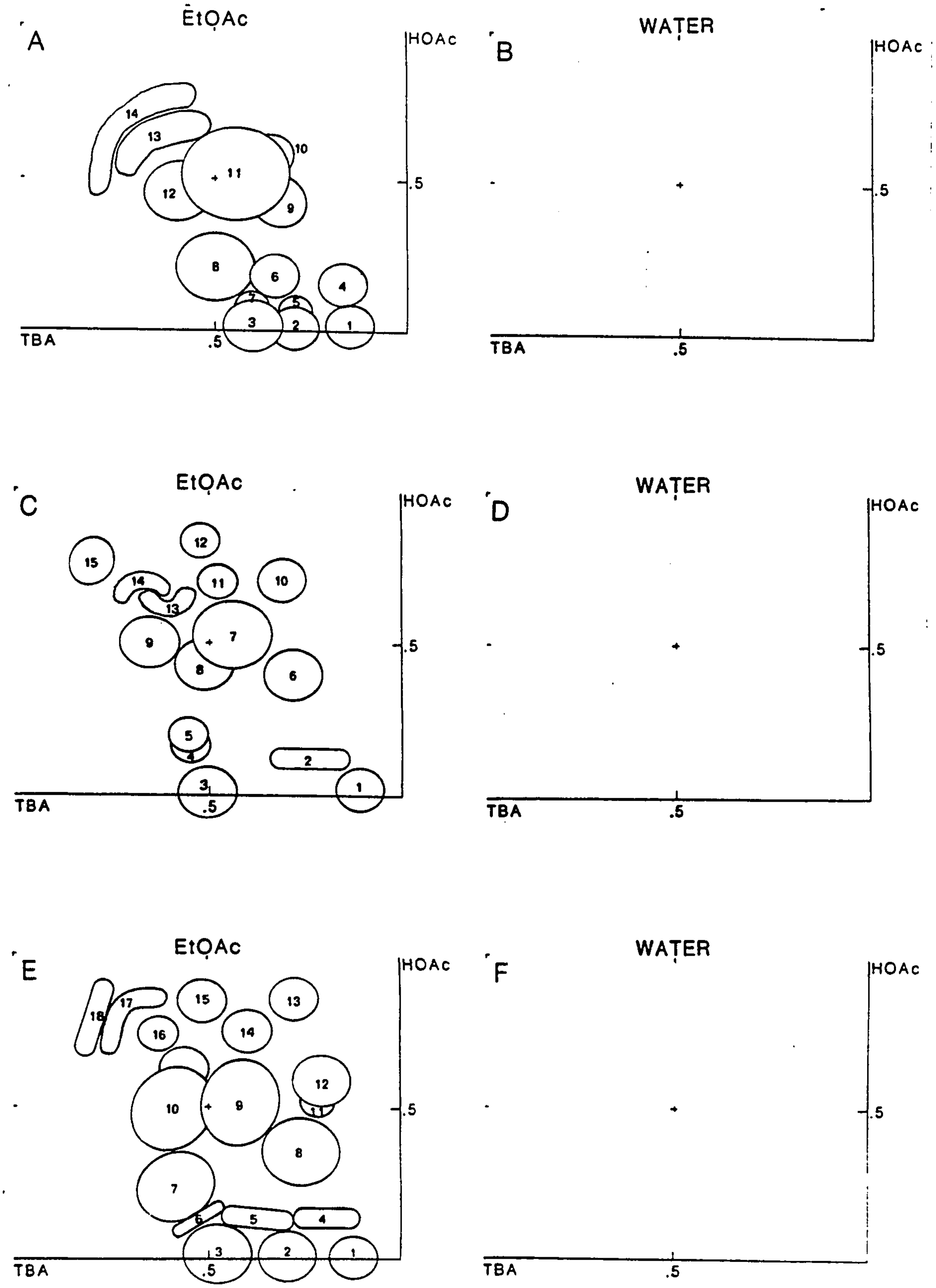
[1] See footnote following table 5.

Table 25. Rf values and color reactions of individual spots from paper chromatographs of *B. sprucei*. Coll. *Clemants & Fernândez 2000*

EtOAc extract (Fig. 16E)			Water extract (Fig. 16F)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	18/13	-/Y	1	18/45	-/Y
2	39/5	Y/OY	2	38/56	P/Y
3	55/6	Y/OY	3	45/60	W/YG
4	50/16	B/Y	4	40/71	Pk/Pk
5	63/34	B/Y	5	43/89	BG/BG
6	17/62	P/P	6	53/96	B/B
7	35/55	P/O	7	86/70	B/B
8	36/68	P/G			
9	51/66	P/O			
10	64/66	P/G			
11	73/63	P/G			
12	67/74	P/PG			
13	79/77	B/BG			
14	60/84	P/P			

[1] See footnote following table 5.

Fig. 17. Spot patterns of paper chromatographs. Fig. A-B. B. sprucei (coll. Clemants & Delascio 2479). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 26. Fig. C-D. B. sprucei (coll. Clemants & Delascio 2480). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 27. Fig. E-F. B. sprucei (coll. Clemants & Delascio 2481). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 28.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WATER
HOAc
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TBA
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EtOAc
HOAc
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TBA
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D
WATER
HOAc
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TBA
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EtOAc
HOAc
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4
3
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TBA
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WATER
HOAc
.5
TBA
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Table 26. Rf values and color reactions of individual spots from paper chromatographs of *B. sprucei*. Coll. *Clemants & Delascio 2479*

EtOAc extract (Fig. 17A)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	10/1	Y/Y
2	25/1	Y/Y
3	44/2	Y/Y
4	17/10	Y/Y
5	28/5	B/Y
6	33/12	W/Y
7	43/9	B/B
8	50/20	B/Y
9	30/38	P/O
10	29/58	W/W
11	40/58	P/G
12	60/46	P/GP
13	62/66	B/B
14	71/73	B/B

Water extract
not chromatographed

[1] See footnote following table 5.

Table 27. Rf values and color reactions of individual spots from paper chromatographs of _B_. _sprucei_. Coll. _Clemants_ _&_ _Delascio_ _2480_

EtOAc extract (Fig. 17C) | Water extract not chromatographed

Spot #	Rf X 100 (TBA/HOAc)	Color[1] $(UV/UV+NH_3)$
1	11/1	Red/Red
2	25/10	Y/Y
3	51/3	Y/Y
4	56/11	Y/Y
5	58/15	fB/fB
6	32/33	P/Y
7	46/46	P/P
8	54/33	-/Y
9	66/44	P/P
10	30/69	-
11	50/62	-
12	55/73	P/P
13	63/52	P/P
14	66/65	fB/fB
15	80/68	fB/fB

[1] See footnote following table 5.

Table 28. Rf values and color reactions of individual spots from paper chromatographs of _B_. _sprucei_. Coll. _Clemants_ _&_ _Delascio_ _2481_

EtOAc extract (Fig. 17E)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	11/1	Pk/Pk
2	50/0	Y/Y
3	47/3	Y/Y
4	21/12	Y/Y
5	36/9	B/YG
6	52/12	Y/Y
7	56/17	YB/YG
8	29/38	-/O
9	43/53	P/G
10	59/47	P/G
11	25/50	Y/Y
12	21/58	Y/Y

Water extract
not chromatographed

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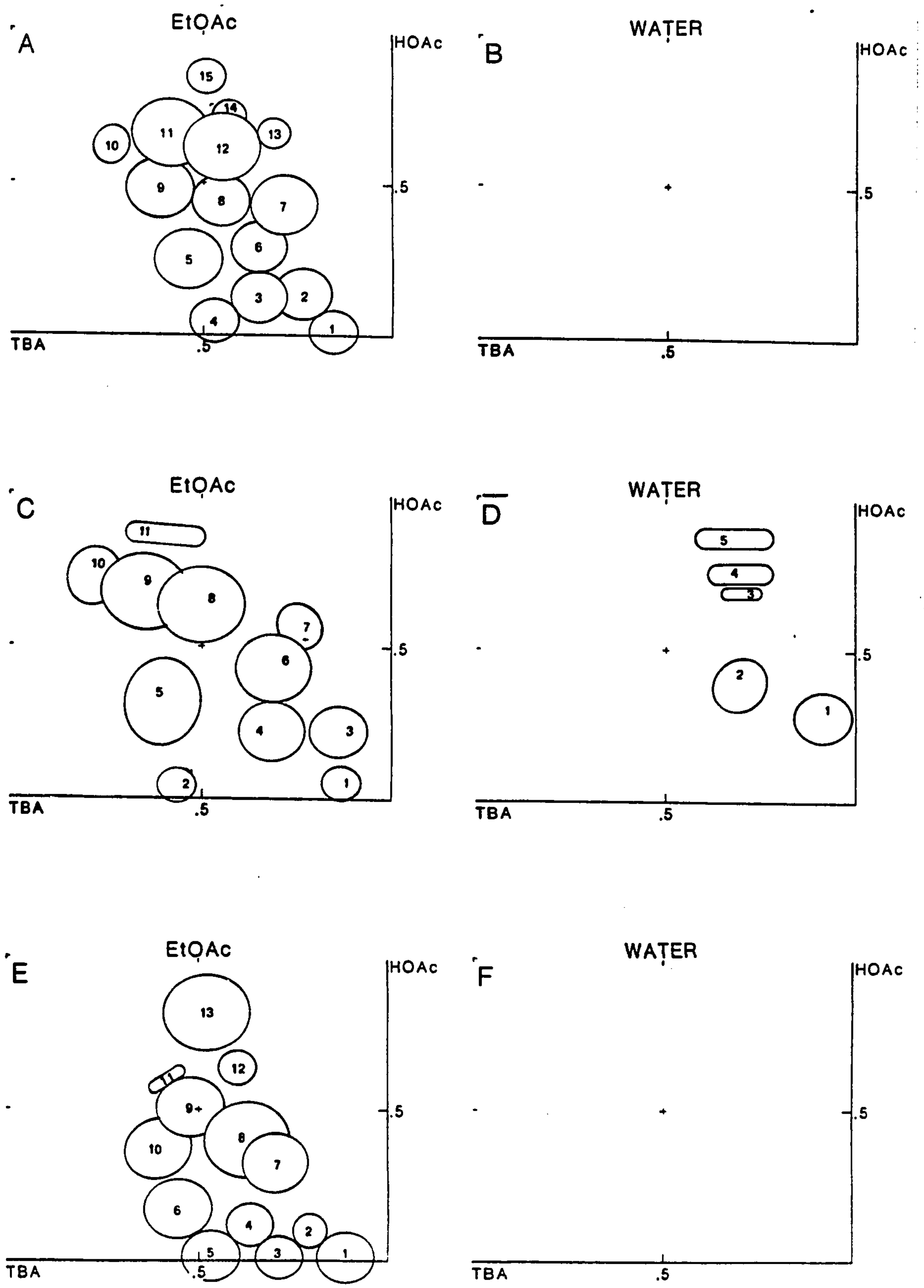
[1] See footnote following table 5.

Fig. 18. Spot patterns of paper chromatographs. Fig. A-B. B. mathewsii (coll. Clemants 2046). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 29. Fig. C-D. B. resinosa (coll. Clemants 2274). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 30. Fig. E-F. B. resinosa (coll. Luteyn et al. 5314). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 31.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F
WATER
HOAc
.5
TBA
.5

Table 29. Rf values and color reactions of individual spots from paper chromatographs of *B. mathewsii*. Coll. Clemants 2046

EtOAc extract (Fig. 18A)

Water extract not chromatographed

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	14/4	Y/Y
2	21/16	P/Y
3	40/16	B/Y
4	49/6	Y/Y
5	56/28	B/Y
6	40/32	W/Y
7	29/44	P/O
8	48/44	P/O
9	62/52	P/G
10	75/60	B/B
11	59/66	P/G
12	46/60	P/GO
13	32/61	W/W
14	45/69	W/W
15	49/81	B/BG

[1] See footnote following table 5.

Table 30. Rf values and color reactions of individual spots from paper chromatographs of B. resinosa. Coll. Clemants 2274

EtOAc extract (Fig. 18C)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	15/4	Y/Y
2	56/4	Y/Y
3	16/21	B/Y
4	37/19	BW/Y
5	64/34	B/Y
6	38/42	BW/Y
7	31/54	P/O
8	50/67	P/O
9	66/70	P/BG
10	76/76	P/BG
11	58/87	B/BG

Water extract (Fig. 18D)

Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	12/25	W/Y
2	31/40	fB/Y
3	32/64	-/Y
4	28/72	W/Y
5	31/83	fB/G

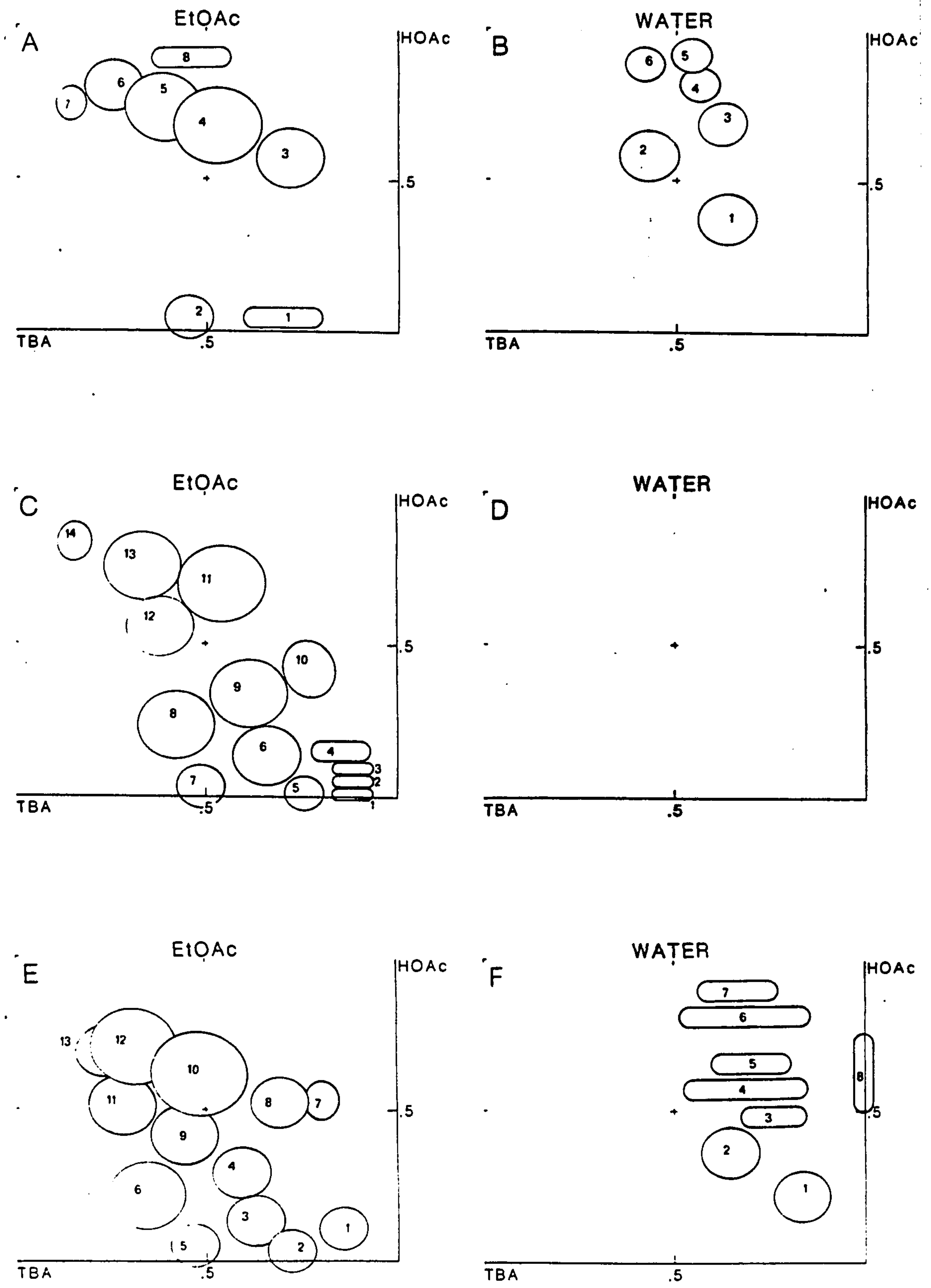
[1] See footnote following table 5.

Table 31. Rf values and color reactions of individual spots from paper chromatographs of *B. resinosa*. Coll. *Luteyn et al. 5314*

EtOAc extract (Fig. 18E)			Water extract
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	not chromatographed
1	10/1	Red/Red	
2	20/10	Tan/Tan	
3	29/0	Y/Y	
4	34/9	fB/Y	
5	48/0	Y/Y	
6	54/14	fB/Y	
7	24/36	P/Y	
8	38/44	P/G	
9	54/55	P/G	
10	59/39	P/G	
11	60/60	fB/fB	
12	40/63	Pk/Pk	
13	48/78	-/B	

[1] See footnote following table 5.

Fig. 19. Spot patterns of paper chromatographs. Fig. A-B. _B_. _resinosa_ (coll. _Clemants_ _2045_). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 32. Fig. C-D. _B_. _resinosa_ (coll. _Clemants_ _2396_). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 33. Fig. E-F. _B_. _resinosa_ (coll. _Clemants_ _2397a_). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 34.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EtOAc
HOAc
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7
8

Table 32. Rf values and color reactions of individual spots from paper chromatographs of B. resinosa.

Coll. Clemants 2045

EtOAc extract (Fig. 19A)			Water extract (Fig. 19B)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	29/4	Y/Y	1	37/40	-/Y
2	53/6	Y/Y	2	59/58	P/O
3	28/56	P/O	3	38/73	Pk/Pk
4	48/71	P/O	4	40/89	B/B
5	67/76	P/G	5	42/97	B/B
6	80/75	P/P	6	57/93	B/B
7	88/70	B/B			
8	56/90	fB/B			

[1] See footnote following table 5.

Table 33. Rf values and color reactions of individual spots from paper chromatographs of B. resinosa. Coll. Clemants 2396

EtOAc extract (Fig. 19C)			Water extract
Spot \#	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	not chromatographed
1	14/0	Y/Y	
2	14/3	B/B	
3	14/7	Y/Y	
4	19/10	B/B	
5	28/2	B/B	
6	38/92	B/YG	
7	53/0	Y/Y	
8	60/9	B/YG	
9	40/27	B/B	
10	29/35	P/O	
11	45/61	P/O	
12	60/51	W/-	
13	63/65	P/G	
14	79/75	P/P	

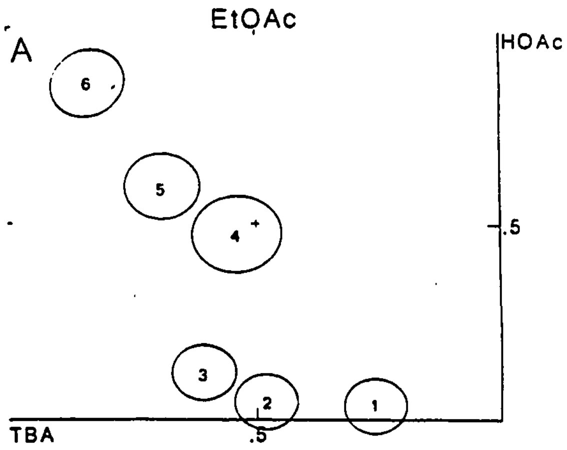
[1] See footnote following table 5.

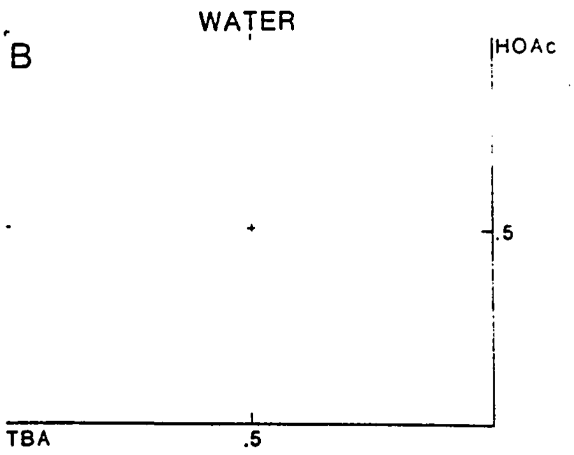
Table 34. Rf values and color reactions of individual spots from paper chromatographs of _B_. _resinosa_. Coll. _Clemants_ _2397a_

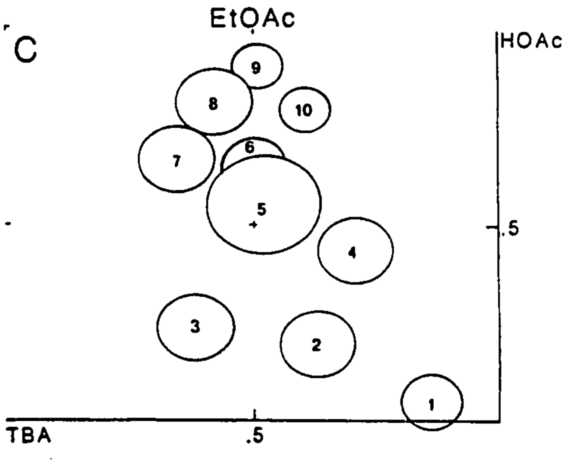
EtOAc extract (Fig. 19E)			Water extract (Fig. 19F)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	17/16	-	1	18/20	W/Y
2	33/9	fB/Y	2	35/37	fB/Y
3	41/18	fB/Y	3	49/25	-/Y
4	43/34	fB/Y	4	59/36	P/Y
5	55/5	Y/Y	5	72/33	Pk/Pk
6	65/28	fB/Y	6	82/30	B/fG
7	24/50	P/-	7	88/38	G/G
8	33/49	P/G	8	64/0	W/W
9	58/48	P/O			
10	52/62	P/OG			
11	73/58	P/G			
12	70/71	P/G			
13	84/66	P/P			

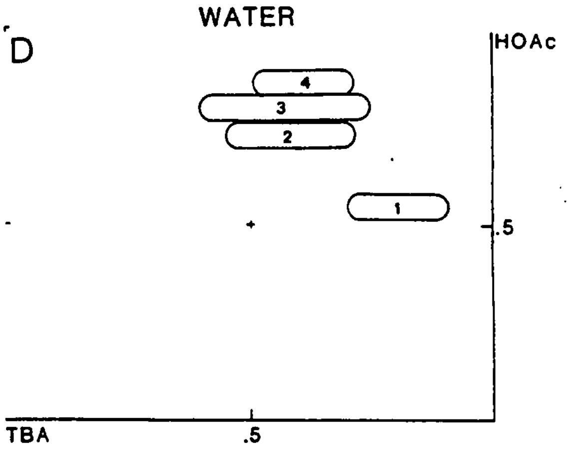
[1] See footnote following table 5.

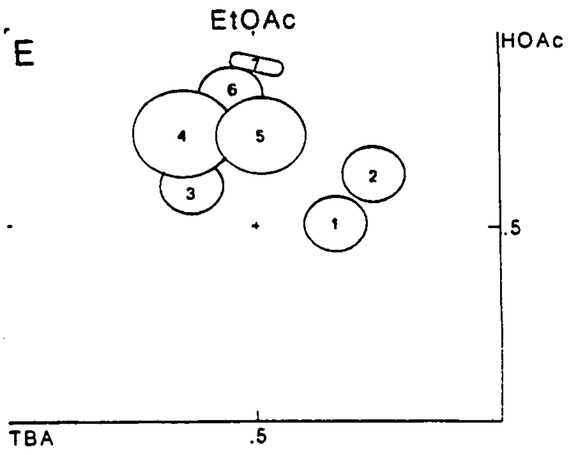
Fig. 20. Spot patterns of paper chromatographs. Fig. A-B. *B. resinosa* (coll. *Luteyn et al. 7580*). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 35. Fig. C-D. *B. ledifolia* (coll. *Clemants 2483a*). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 36. Fig. E-F. *B. ledifolia* (coll. *Clemants 2483b*). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 37.


A
EtOAc
HOAc
.5
TBA
.5
1
2
3
4
5
6


B
WATER
HOAc
.5
TBA
.5


C
EtOAc
HOAc
.5
TBA
.5
1
2
3
4
5
6
7
8
9
10


D
WATER
HOAc
.5
TBA
.5
1
2
3
4


E
EtOAc
HOAc
.5
TBA
.5
1
2
3
4
5
6
7

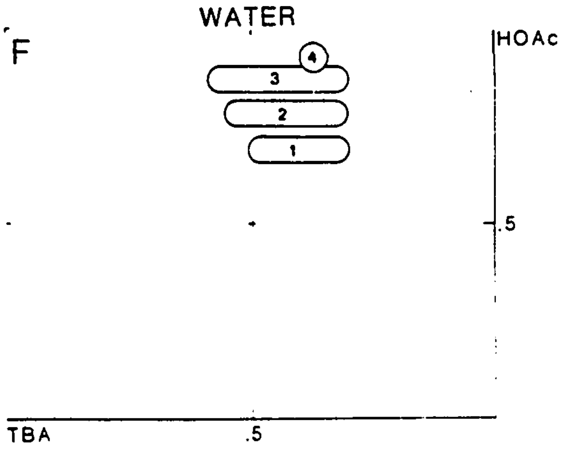

F
WATER
HOAc
.5
TBA
.5
1
2
3
4

Table 35. Rf values and color reactions of individual spots from paper chromatographs of _B_. _resinosa_. Coll. _Luteyn et al. 7580_

EtOAc extract (Fig. 20A)			Water extract
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	not chromatographed
1	25/2	-	
2	47/3	-	
3	60/9	fB/YG	
4	53/46	-/Y	
5	67/53	P/B	
6	78/80	-/B	

[1] See footnote following table 5.

Table 36. Rf values and color reactions of individual spots from paper chromatographs of _B_. _ledifolia_. Coll. _Clemants_ _2483a_

EtOAc extract (Fig. 20C)			Water extract (Fig. 20D)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	15/3	Y/Y	1	28/53	-/Y
2	35/17	W/Y	2	46/76	Pk/Y
3	62/25	B/Y	3	47/82	B/G
4	29/48	P/O	4	37/90	G/G
5	47/59	P/G			
6	50/67	-			
7	65/67	P/G			
8	55/78	P/P			
9	49/86	BW/B			
10	39/78	P/Y			

[1] See footnote following table 5.

Table 37. Rf values and color reactions of individual spots from paper chromatographs of *B. ledifolia*. Coll. *Clemants 2483b*

EtOAc extract (Fig. 20E)			Water extract (Fig. 20F)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	36/50	BW/Y	1	39/59	-/Y
2	30/61	P/O	2	41/73	Pk/Y
3	64/62	B/Y	3	43/82	fB/G
4	68/73	P/G	4	32/90	G/G
5	49/71	P/OG			
6	55/81	P/P			
7	48/84	BW/-			

[1] See footnote following table 5.

Fig. 21. Spot patterns of paper chromatographs. Fig. A-B. *B. imthurnii* (coll. *Clemants & Delascio 2453a*). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 38. Fig. C-D. *B. imthurnii* (coll. *Clemants & Delascio 2454*). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 39. Fig. E-F. *B. tachirensis* (coll. *Luteyn et al. 5903*). Fig. E. Chromatograph of EtOAc extract. Fig. F. Chromatograph of water extract. For Rf values and color reactions see Table 40.

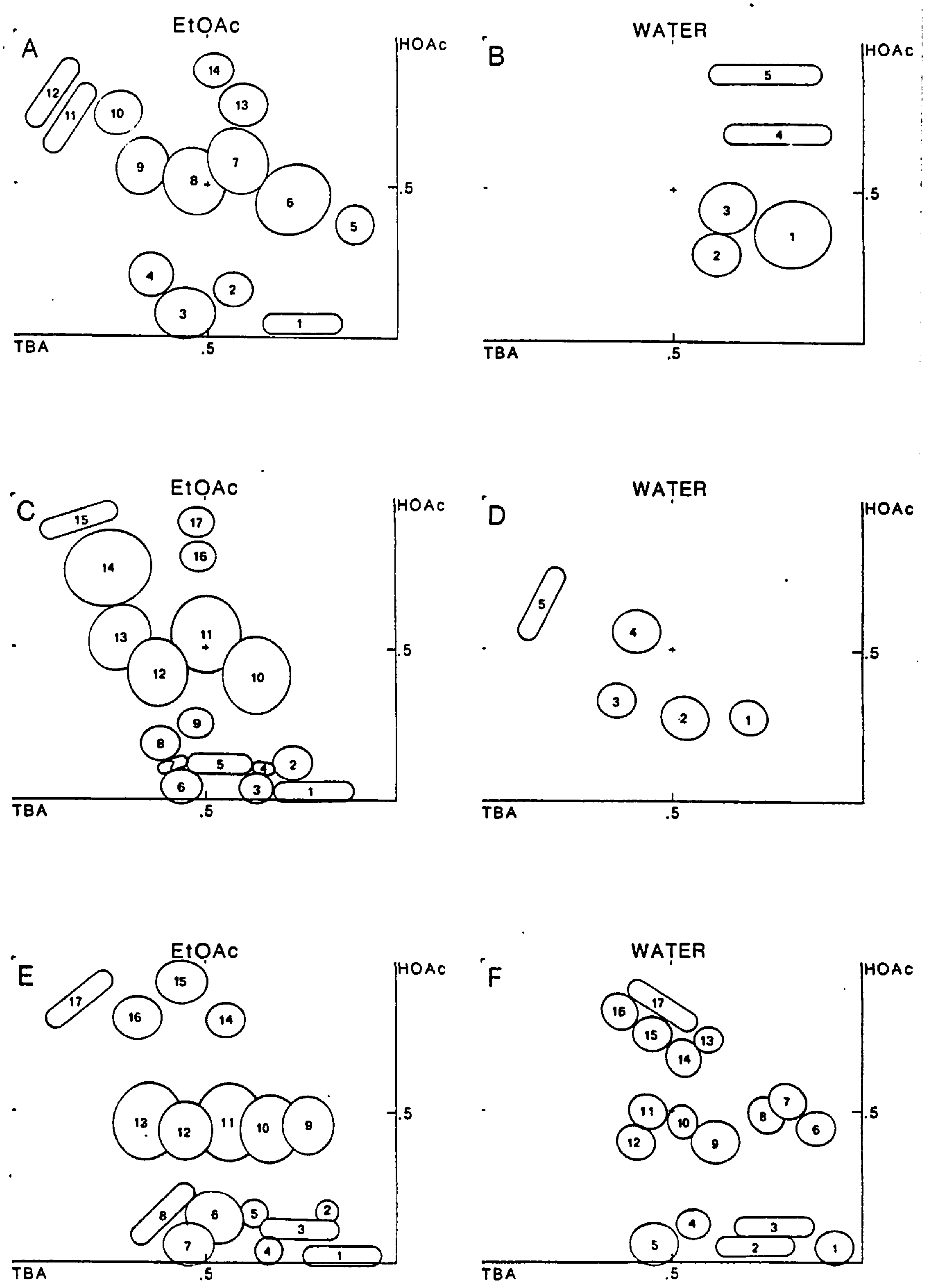

A
EtOAc
HOAc
.5
TBA
.5
1 2 3 4 5 6 7 8 9 10 11 12 13 14
B
WATER
HOAc
.5
TBA
.5
1 2 3 4 5
C
EtOAc
HOAc
.5
TBA
.5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
D
WATER
HOAc
.5
TBA
.5
1 2 3 4 5
E
EtOAc
HOAc
.5
TBA
.5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
F
WATER
HOAc
.5
TBA
.5
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17

Table 38. Rf values and color reactions of individual spots from paper chromatographs of <u>B</u>. <u>imthurnii</u>. Coll. <u>Clemants</u> <u>&</u> <u>Delascio</u> <u>2453a</u>

EtOAc extract (Fig. 21A)			Water extract (Fig. 21B)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	28/1	Y/P	1	19/40	P/O
2	44/11	fB/YG	2	46/35	-/O
3	52/2	Y/Y	3	39/47	-/G
4	60/15	fB/YG	4	25/68	Pk/Pk
5	11/32	-/Y	5	26/87	BG/BG
6	30/38	P/O			
7	45/52	P/G			
8	52/40	P/O			
9	65/45	P/G			
10	66/64	B/B			
11	80/64	B/B			
12	84/80	-/B			
13	41/68	Pk/Pk			
14	49/89	B/B			

[1] See footnote following table 5.

Table 39. Rf values and color reactions of individual spots from paper chromatographs of *B. imthurnii*. Coll. *Clemants & Delascio 2454*

EtOAc extract (Fig. 21C)			Water extract (Fig. 21D)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	25/1	Y/Y	1	31/35	P/Y
2	31/9	B/B	2	45/35	P/Y
3	44/1	Y/B	3	61/40	-/G
4	42/5	BW/Y	4	57/63	Pk/Pk
5	51/8	BW/Y	5	82/65	B/B
6	59/3	Y/Y			
7	64/7	-/O			
8	64/12	B/Y			
9	51/16	-/B			
10	44/32	P/Y			
11	57/47	P/G			
12	60/33	P/Y			
13	73/37	P/G			
14	66/58	B/B			
15	73/72	B/B			
16	46/70	-			
17	47/80	-			

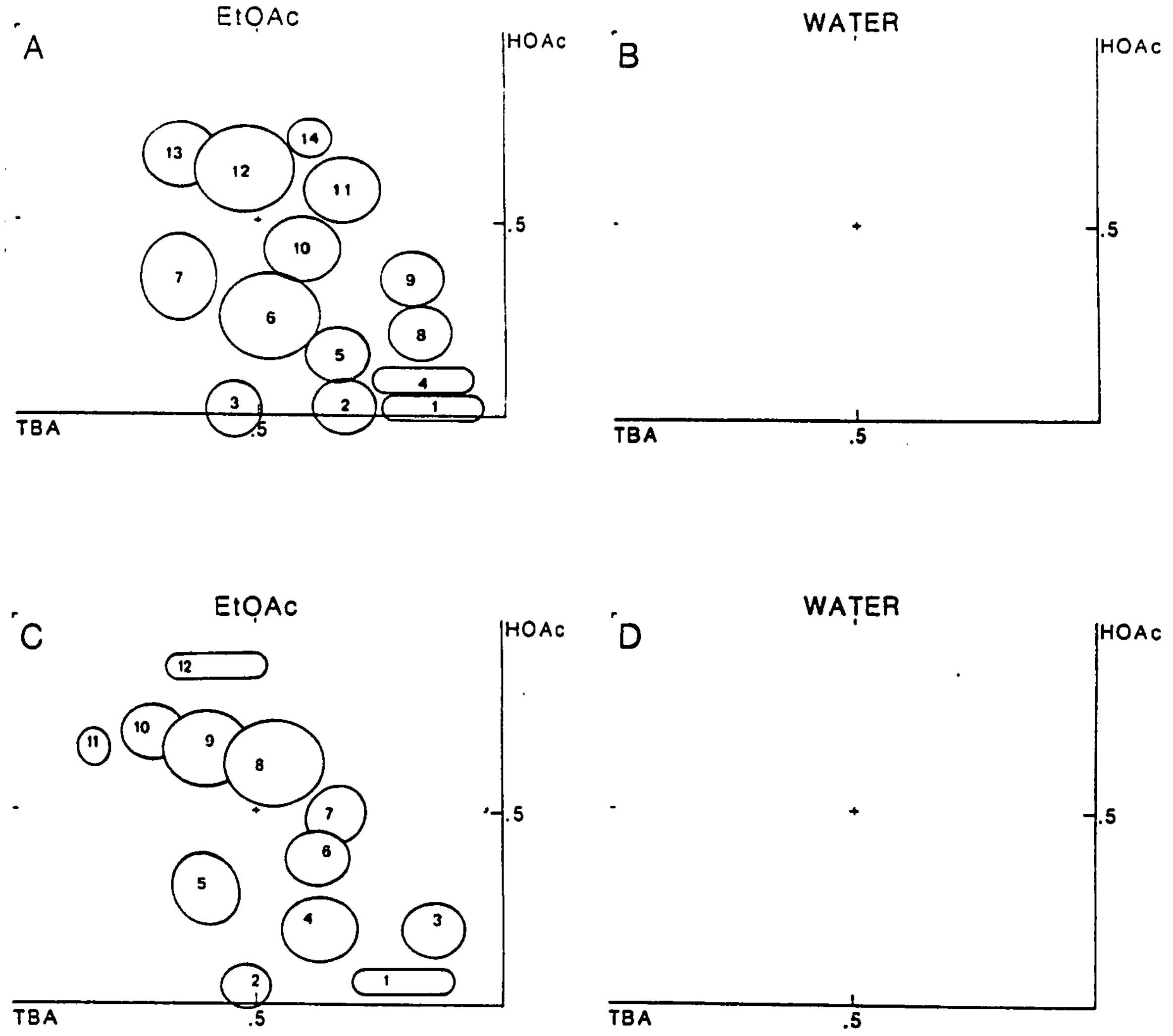
[1] See footnote following table 5.

Table 40. Rf values and color reactions of individual spots from paper chromatographs of B. tachirensis. Coll. Luteyn et al. 5903

EtOAc extract (Fig. 21E)			Water extract (Fig. 21F)		
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)
1	14/2	Y/Y	1	6/2	Pk/Pk
2	25/15	Tan/Tan	2	27/4	fW/Y
3	32/11	fW/Y	3	24/13	-/Y
4	41/3	Y/Y	4	42/10	fB/Y
5	43/16	fW/YG	5	54/6	fB/Y
6	51/13	fB/YG	6	10/40	-/O
7	55/4	Y/Y	7	21/47	P/O
8	63/15	fB/YG	8	27/41	W/W
9	24/46	P/O	9	41/36	P/O
10	33/46	P/O	10	46/47	W/W
11	42/55	P/G	11	55/48	P/G
12	53/45	P/O	12	59/38	-/O
13	66/47	P/G	13	41/69	-/O
14	44/74	Pk/Pk	14	46/64	Pk/Pk
15	57/87	P/P	15	55/75	P/O
16	65/68	B/B	16	64/85	-/G
17	79/73	B/B	17	52/83	BG

[1] See footnote following table 5.

Fig. 22. Spot patterns of paper chromatographs. Fig. A-B. _B_. _subsessilis_ (coll. _Clemants_ _2278a_). Fig. A. Chromatograph of EtOAc extract. Fig. B. Chromatograph of water extract. For Rf values and color reactions see Table 41. Fig. C-D. _Bejaria_ hybrid (betw. _B_. _aestuans_ _&_ _B_. _resinosa_: coll. _Clemants_ _2276_). Fig. C. Chromatograph of EtOAc extract. Fig. D. Chromatograph of water extract. For Rf values and color reactions see Table 42.


A
EtOAc
HOAc
.5
TBA
.5
13
12
14
11
10
7
9
6
8
5
4
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2
1
B
WATER
HOAc
.5
TBA
.5
C
EtOAc
HOAc
12
11
10
9
8
.5
7
6
5
4
3
2
1
TBA
.5
D
WATER
HOAc
.5
TBA
.5

Table 41. Rf values and color reactions of individual spots from paper chromatographs of _B_. _subsesselis_. Coll. _Clemants_ _2278a_

EtOAc extract (Fig. 22A)			Water extract
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	not chromatographed
1	12/2	Y/Y	
2	31/0	Y/Y	
3	58/0	Y/Y	
4	16/6	fBG/Y	
5	31/7	fB/Y	
6	46/16	fBG/Y	
7	66/28	fB/Y	
8	14/14	Y/Y	
9	17/24	fW/Y	
10	45/32	fW/Y	
11	34/45	P/Y	
12	56/60	P/Y	
13	75/63	P/G	
14	37/61	Y/Y	

[1] See footnote following table 5.

Table 42. Rf values and color reactions of individual spots from paper chromatographs of Bejaria hybrid. Coll. Clemants 2276

EtOAc extract (Fig. 22C)			Water extract
Spot #	Rf X 100 (TBA/HOAc)	Color[1] (UV/UV+NH_3)	not chromatographed
1	23/6	W/W	
2	53/3	Y/Y	
3	15/19	W/Y	
4	39/17	B/Y	
5	63/34	B/Y	
6	38/37	W/Y	
7	32/51	-	
8	47/67	P/O	
9	68/72	P/G	
10	79/73	P/G	
11	86/65	B/B	
12	55/89	B/BG	

[1] See footnote following table 5.

Table 43.

Distribution of flavonoid aglycones in *Bejaria* species.

Collection	Source	Aglycones[1]			
		Q	M	A	C
B. racemosa					
Clemants & Miller 1591	Field	+	+	+	+
B. cubensis					
Van Hermann s.n.	Herb.	+	-	+	+
B. infundibula					
Clemants & Fernández 2007c	Field	+	+	+	+
B. aestuans					
Clemants & Luteyn 1672	Field	+	-	+	+
Clemants & Fernández 2019a	Field	+	-	+	+
Clemants 2275	Field	+	+	+	+
Clemants 2345	Field	+	+	+	+
Clemants & Dugarte 2415	Field	+	+	+	+

Table 43 cont.

Collection	Source	Aglycones[1]			
		Q	M	A	C
Clemants & Dugarte 2421	Field	+	+	+	+
Clemants & Dugarte 2427	Field	+	+	+	+
Clemants & Dugarte 2428	Field	+	+	+	+
Clemants & Dugarte 2429	Field	+	+	+	+
Clemants & Dugarte 2441	Field	+	+	+	+
Clemants & Dugarte 2443	Field	+	+	+	-
Clemants 2482	Field	+	-	+	+
Hinton 1416	Herb.	+	+	+	+
Luteyn & Lebrón-Luteyn 6366	Herb.	+	-	-	+
Luteyn & Lebrón-Luteyn 6425	Herb.	+	-	+	+
Luteyn et al. 7616	Herb.	+	-	+	+
Matuda 2589	Herb.	+	+	+	+
Mexía 9276	Herb.	+	+	+	+

Table 43 cont.

Collection	Source	Aglycones[1]			
		Q	M	A	C
B. sprucei					
Clemants & Fernândez 2000	Field	+	-	+	+
Clemants & Delascio 2479	Field	+	-	+	+
Clemants & Delascio 2480	Field	+	+	-	+
Clemants & Delascio 2481	Field	+	+	+	+
B. mathewsii					
Clemants 2046	Field	+	+	+	+
B. resinosa					
Clemants 2045	Field	+	+	-	-
Clemants et al. 2220c	Field	+	+	+	-
Clemants et al. 2221a	Field	+	+	-	-
Clemants 2274	Field	+	+	+	+
Clemants 2396	Field	+	+	+	+
Clemants 2397a	Field	+	+	+	+
Luteyn et al. 5314	Herb.	+	+	+	+

Table 43 cont.

Collection	Source	Aglycones[1]			
		Q	M	A	C
Luteyn et al.					
7580	Herb.	+	-	-	+
B. ledifolia					
Clemants 2483a	Field	+	+	+	+
Clemants 2483b	Field	+	+	+	+
B. imthurnii					
Clemants & Delascio					
2453a	Field	+	+	+	+
Clemants & Delascio					
2454	Field	+	+	+	+
B. tachirensis					
Luteyn et al.					
5903	Herb.	+	+	+	+
B. subsessilis					
Clemants 2278a	Field	+	+	+	+
Bejaria hybrid					
Clemants 2276	Field	+	+	+	+

Table 43 cont.

[1] Q= Quercetin, M= Myrecetin, A= Azaletin (3,7,3',4'-OH, 5-OMe flavonol), C= Caryotin (7,3',4'-OH, 3,5-OMe flavonol), += present, -= absent.

Table 44. Comparison of the Rf values and color reactions of paper chromatographs from three individuals of *B. aestuans* from a single population.

	Clemants 2427[1]		Clemants 2428[1]		Clemants 2429[1]	
Comp. #	Rf X 100 (TBA/HOAc)	Color[2]	Rf X 100 (TBA/HOAc)	Color	Rf X 100 (TBA/HOAc)	Color
1	14/5	Y	14/2	Y	16/3	Y
2	-		13/13	Y	14/14	Y
3	30/7	W/Y	29/4	B/W	27/7	W/Y
4	43/5	Y/Y	38/3	Y	39/5	Y
5	59/5	Y/Y	54/4	Y	55/7	Y
6	41/19	W/Y	38/12	B/W	37/16	B
7	53/16	B/Y	49/9	B/W	47/16	B/Y
8	63/35	B/Y	59/20	B/W	61/29	B/Y
9	33/51	P/O	28/40	P/O	35/43	P/O
10	49/68	P/G	43/52	P/G	47/57	P/G
11	56/55	P/O	52/44	-/O	-	
12	73/63	P/G	66/49	P/G	67/65	P/GP
13	66/77	P/G	59/63	P/G	-	
14	34/70	-/Y	31/52	W/Y	34/63	B/-
15	60/89	B/BO	47/82	B/B	58/86	B/BG
16	79/74	B	79/75	B/B	-	

Table 44 cont.

[1] Collected with Dugarte.

[2] See footnote on Table 5 for abbreviations. Compound number does not refer to spot number. Twelve compounds were found in all three individuals; 4 in only two individuals; 3 unique compounds in _Clemants & Dugarte 2427_; 4 unique compounds in _Clemants & Dugarte 2428_; and 2 unique compounds in _Clemants & Dugarte 2429_. Illustrations of the 2D-paper chromatographs for these three samples can be found on Fig. 13.

Table 45. Comparison of a Bejaria hybrid (Clemants 2276; Table 42) and its putative parents: B. resinosa (Clemants 2274; Table 30) and B. aestuans (Clemants 2275; Table 9).

	B. resinosa		B. aestuans		Bejaria hybrid	
Comp. #	Rf X 100 (TBA/HOAc)	Color[1]	Rf X 100 (TBA/HOAc)	Color	Rf X 100 (TBA/HOAc)	Color
1	15/4	Y	15/5	Y	-	
2	-		32/6	B/Y	23/6	W
3	56/4	Y	57/9	Y	53/3	Y
4	16/21	B/Y	-		15/19	W/Y
5	37/19	BW/Y	42/25	B/Y	39/17	B/Y
6	-		56/21	B/Y	-	
7	64/34	B/Y	66/35	B/Y	63/34	B/Y
8	-		98/17	fB	-	
9	38/42	B/Y	-		38/37	B/Y
10	31/54	P/O	35/56	P/Y	32/51	-
11	50/67	P/O	50/68	P/O	47/67	P/O
12	66/70	P/G	-		68/72	P/G
13	76/76	P/BG	72/68	P/GO	79/73	P/G
14	58/87	B/BG	68/85	B/G	55/89	B/BG
15	-		-		86/65	B
16	-		57/81	fB	-	

[1] See footnote following Table 5 for abbreviations.

Table 46. Distribution of aglycones in the genera of the Rhododendroideae.

Genus	Aglycones[1]					
	Q	G	K	M	A	C
Bejaria	+	−	−	±	±	±
Rhododendron	+	±	+	+	+	+
Tsusiophyllum	+	−	−	−	−	−
Menziesia	+	+	±	±	−	−
Ledum	+	+	±	±	−	−
Cladothamnus	+	−	+	+	−	−
Elliottia	+	−	+	+	−	−
Epigaea	+	−	+	+	+	−
Kalmia	+	+	−	−	−	−
Phyllodoce	+	±	+	±	±	+
Kalmiopsis	+	−	+	+	+	−
Rhodothamnus	+	+	+	−	+	−
Bryanthus	+	+	+	+	−	−
Ledothamnus	+	+	+	−	−	−
Leiophyllum	+	+	+	−	−	−
Loiseluria	+	+	−	−	−	−
Daboecia	+	−	±	+	±	−
Diplarche	+	−	+	+	−	−

Table 46 cont.

[1] Q= Quercetin, G= Gossypetin, K= Kaempferol, M= Myricetin, A= Azaletin, C= Caryotin, += present, -= absent, ±= present and absent in different species or collections.

Table 47. Data Matrix from aglycone oxygenation and methylation patterns.

	Hydroxylation[1]								Methoxylation		
	3	5	6	7	8	3'	4'	5'	3	5	6
1. Bejarieae	+	+	-	+	-	+	+	+	+	+	+
2. Rhodoreae	+	+	-	+	+	+	+	+	+	+	+
3. Cladothamneae	+	+	-	+	-	+	+	+	-	-	-
4. Epigaeae	+	+	-	+	-	+	+	+	-	+	-
5. Phyllodoceae	+	+	-	+	+	+	+	+	+	+	-
6. Daboecieae	+	+	-	+	-	+	+	+	-	+	-
7. Diplarcheae	+	+	-	+	-	+	+	+	-	-	-
8. Ericoideae	+	+	-	+	-	+	+	+	-	(+)	-
9. Vaccinoideae	+	+	-	+	-	+	+	+	(+)	(+)	-
10. Pyroloideae	+	+	-	+	-	+	+	-	-	-	-
11. Monotropoideae	+	+	-	+	-	+	+	-	-	-	-

[1] += present, -= absent, (+)= present in only one sample of many.

Table 48. Data Matrix from aglycone oxygenation and methoxylation patterns.

	Hydroxylation[1]								Methoxylation		
	3	5	6	7	8	3'	4'	5'	3	5	6
1. Bejarieae	+	+	-	+	-	+	+	+	+	+	+
2. Rhodoreae	+	+	-	+	+	+	+	+	+	+	+
3. Cladothamneae	+	+	-	+	-	+	+	+	-	-	-
4. Epigaeae	+	+	-	+	-	+	+	+	-	+	-
5. Phyllodoceae	+	+	-	+	+	+	+	+	+	+	-
6. Daboecieae	+	+	-	+	-	+	+	+	-	+	-
7. Diplarcheae	+	+	-	+	-	+	+	+	-	-	-
8. Ericoideae	+	+	-	+	+	+	+	+	-	(+)	-
9. Vaccinoideae	+	+	-	+	+	+	+	+	(+)	(+)	-
10. Pyroloideae	+	+	-	+	-	+	+	-	-	-	-
11. Monotropoideae	+	+	-	+	-	+	+	-	-	-	-

[1] += present, -= absent, (+)= present in only one sample of many. 6-OMe is present in Rhododendron sp. (King 1976) and Bejaria (this paper).

Fig. 23. Cladogram of tribes in the Rhododendroideae. Fig. A. Cladogram using all other subfamilies as an outgroup. Fig. B. Cladogram assuming an error in reporting the presence of Caryotin and Azaletin in Vaccinoideae and Ericoideae. OUT= outgroup, CLA= Cladothamneae, DIP= Diplarcheae, DAB= Daboecieae, EPI= Epigaeae, PHY= Phyllodoceae, BEJ= Bejarieae, RHO= Rhodoreae.

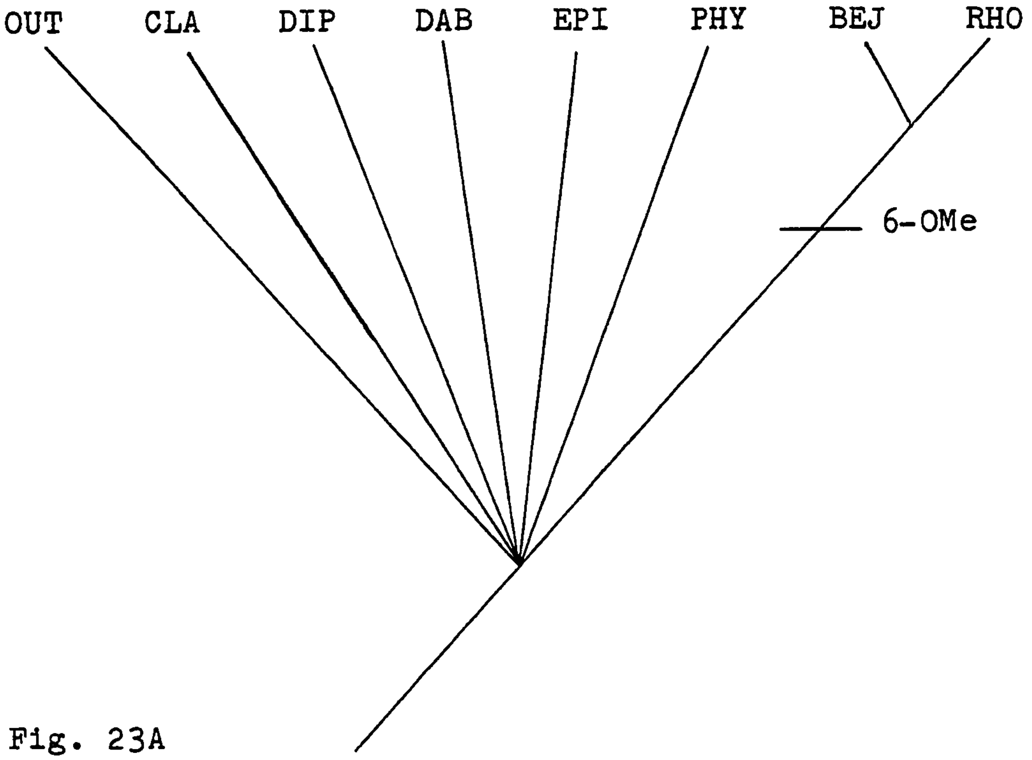


Fig. 23A

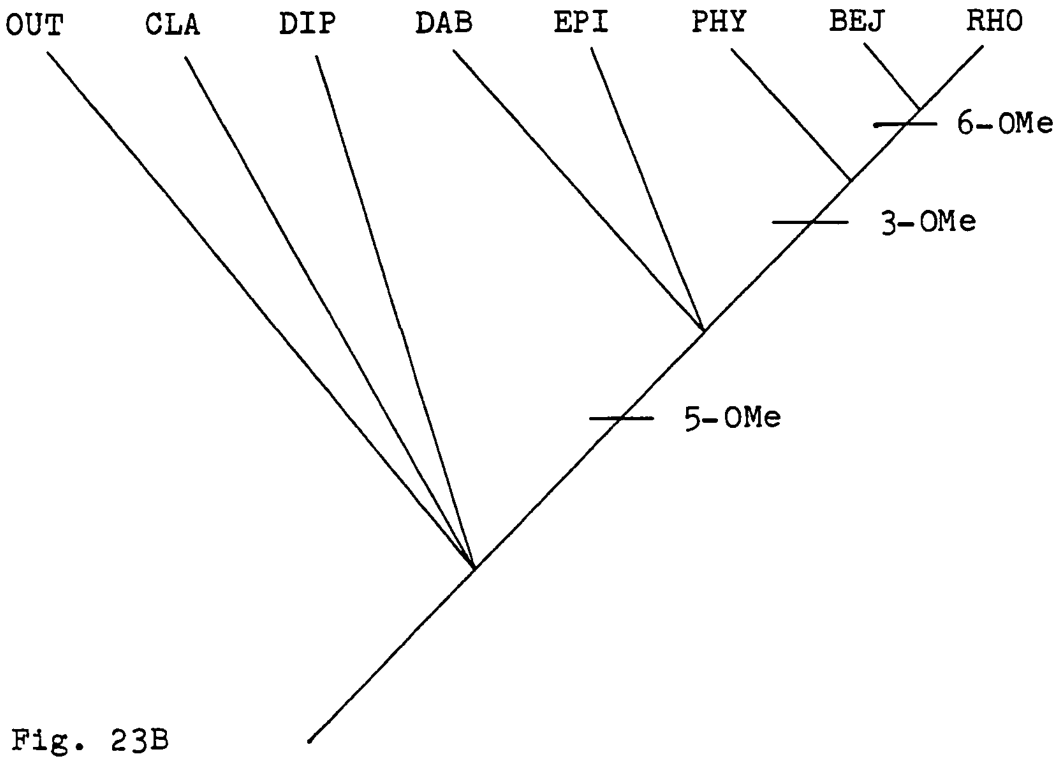


Fig. 23B

POLLINATION

Although no separate study of *Bejaria* pollination was made, field observations suggest that the markedly different floral types found in *Bejaria* (see Morphology: Floral) apparently relate to different pollination mechanisms as they apparently do in Rhododendron (Stevens, 1976).

Spreading and bell-shaped corollas are visited by bees. *Bejaria racemosa* is visited by honey bees, *B. aestuans* is visted by honey bees (*Apis melifera*) and other unknown bees.

Large tube-shaped corollas are visited by hummingbirds. Dr. F. Ortiz C. (Ecuador) found four species visited *B. resinosa* in Ecuador (pers. comm.). I have also seen hummingbirds visit this species.

The tube-shaped flowers with long exserted stamens of *B. sprucei* are visited by oil collecting bees (*Centris flavifrons* Friese) and wasps (*Scolia* sp.?).

HYBRIDIZATION

Hybridization was once considered very important in *Bejaria*. Camp (1941) stated "...one could start with but four of our modern species, *B. ledifola*, *B. glauca* [*B. aestuans*], *B. mathewsii*, and *B. mexicana* [*B. aestuans*] and, in only a comparatively few generations of plants, produce segregate forms indistinguishable from the majority of the species and varieties now recognized in South America." Although Camp believed most of the recognized species could be accounted for by hybridization, he did not suggest that these species were necessarily of recent origin.

Most of the species which Camp wanted to account for through hybridization, are not recognized here but are considered simply infraspecific variants. For example, *B. glauca* (now *B. aestuans*) once had five varieties which Camp specifically believed were of hybrid origin.

Only one species, *B. subsesselis*, is here thought to be of hybrid origin (see discussion following that species). Another population, found on Cerro Villanaco, Ecuador, with presumably the same parents as *B. subsesselis* (*B. aestuans* and *B. resinosa*) is apparently of more recent origin. The first indication that these plants were hybrids was flower shape (slightly spreading) and petal color (pink with red edges). Further analysis of pollen stainability, showed that two grains per tetrad were nonstaining (in cotton blue) and reduced in size. Other evidence for its hybrid nature comes from flavonoid chemistry (see Chemistry section).

ECOLOGY

Bejaria is a common plant of the subparamo and upper montane forests of the Andes. Although *B. aestuans* is found in a variety of habitats including subparamos, cloud forests, and pine-oak woods, most species have more restricted habitats. *Bejaria tachirensis* and *B. nana* are restricted to paramos, *B. steyermarkii* and *B. imthurnii* are restricted to limestone outcrops, and *B. racemosa* and *B. cubensis* are most common in pine woods. *Bejaria sprucei* is exceptional, it is commonly found in savannas of the Guayana Highland and in white sand areas along the Río Vaupes, Colombia.

Bejaria species range in altitude from near sea level to over 4000 m elevation. *Bejaria racemosa* is found at or very near sea level in Florida and Georgia (United States) and *B. cubensis* is found at about 100 m elevation. All other species are usually found between 1500 m and 3000 m elevation. Like other Ericaceae, *Bejaria* is often found in disturbed habitats, particularly roadsides.

A number of *Bejaria* species are sympatric over some of their ranges. For instance *B. aestuans* and *B. resinosa* occur together in Ecuador and parts of Colombia. At Páramo de Tamá *B. aestuans*, *B. resinosa* and *B. tachirensis* occur together.

USES

Bejaria, the rose of the Andes, was once prized for its large brilliantly colored flowers but in recent years it has not been widely cultivated. Four species were known in cultivation by 1857 (Lindley & Paxton, 1854), but in 1953 Preston knew of no cultivated species in Great Britain. I know of only one species (*B. racemosa*) currently cultivated and available from nurseries in the southeastern United States. This horticultural loss is probably due to the difficulty in cultivating the species (Lindley & Paxton, 1854). *Bejaria* requires a cool moist greenhouse (Lindley & Paxton, 1854) but otherwise the procedures for azaleas (Lindley & Paxton, 1854) or *Agarista* (G. Don, 1834) are recommended. Considering the beautiful and diverse flowers, *Bejaria* needs to be reconsidered as an ornamental and proper cultivation techniques identified.

Bejaria is used locally for wood working, as a medicinal, and as fly paper. *Bejaria* wood, one of the few attractive ericaceous woods, is reportedly used to a small extent in turnery and cabinet making (Record & Hess, 1943). A few species are used medicinally, mostly for heart and lung ailments (see the discussion of uses following *B. aestuans* and *B. resinosa* description). One of the more interesting uses of *Bejaria* is as fly paper. Apparently flies are attracted to the flowers of *B.*

racemosa and glandular forms of B. aestuans where they become stuck to the viscous parts (petals, sepals, pedicel, rachis, etc.).

INTERGENERIC RELATIONSHIPS

Bejaria is an isolated genus in the Ericaceae subfamily Rhododendroideae. A review of the past classifications of the Ericaceae has been published elsewhere (Stevens, 1969, 1971) so it will not be reviewed here.

Anatomical characters were used by Copeland to construct a tribe, the Bejariae, whose sole member was Bejaria. He found anther dehiscence in Bejaria was by resorption tissue (as is found in all Rhododendroideae except the members of the Rhodoreae) but unlike other Rhododendroideae the dissolution tissue did not involve the epidermis. The single species of Bejaria examined (B. racemosa) has a prominent endothecium. Further evidence for placing Bejaria in a monogeneric tribe includes the type of leaf stomata, tetracytic, a type of stomatum found elsewhere in the subfamily only in Epigea.

Watson et al. (1966) analyzed the relationships of various genera in the Ericaceae using a phenetic method. They found Bejaria to be the most different of all genera included in their analysis, which included members of the Epacridaceae. Stevens (1971), in the most recent classification of the family, retained the tribal status of Bejaria but did not suggest any close relationships.

Bejaria, although isolated, is sometimes thought to be an archaic member of the Ericaceae (Abbott, 1930; Camp, 1941; Copeland, 1943). The usually 7-merous gamopetalous corolla, the presence of an well developed endothecium, floral vasculature, and the unspecialized inflorescence suggest an archaic position for Bejaria. However, Bejaria has a number of derived flavonoid compounds, a derived type of stomatum, peculiar leaf anatomy in many members, and long testa cells. Therefore I do not think Bejaria is as archaic with respect to all characters.

No phylogenetic analysis of the family or subfamily is presented here because 1) I have not thoroughly studied other genera of the Ericaceae, and 2) problems occur with the tremendous variation found in Rhododendron.

INTERSPECIFIC RELATIONS

Interspecific relationships of Bejaria species were studied using Hennigian (Hennig, 1966) methods of phylogenetic analysis. Using this method taxa were grouped based on shared derived characters (synapomorphies) in the most parsimonious manner. Character state polarity was derived from comparison with an outgroup or from comparison with a functional outgroup. The characters and character states are presented in Table

49, a data matrix in Table 50, and a data matrix with variation removed in Table 51. The resulting cladograms are presented in Figs. 24-25.

The subfamily Rhododendroideae was used as an outgroup for Bejaria. Because this subfamily is so variable both states of many of the characters used in Bejaria can be found in the outgroup. Only characters 1-4 were found not to vary in the outgroup. This variation in the outgroup necessitated using a functional outgroup (using part of Bejaria to polarize the characters in the other part) (see Funk 1981, for a discussion of how to use a functional outgroup). Using characters 1-4, a cladogram (Fig. 24) can be drawn which shows B. racemosa as one side of the first dichotomy with the remaining members of the genus on the other side of the dichotomy. Therefore, B. racemosa can be used as the functional outgroup for the remainder of the genus. It has a uniquely derived character (stomata on both leaf surfaces) and the remaining members of the genus have another uniquely derived character (mucilaginous hypodermis).

Many species have both character states present. In order to make this analysis feasible it was necessary to use a convention for scoring species which are variable for one or more characters. I chose to score species with both states of a two-state character as having the primitive state of the character unless there is a clear

TABLE 49

Character state polarity in *Bejaria*.

Character	primitive state	advanced state	outgroup
1. "mucilaginous hypodermis"	absent	present	subfamily
2. stomata on both surfaces	absent	present	subfamily
3. flower type	bell-shaped or spreading	a. tube-shaped b. cup-shaped c. funnel-shaped	subfamily
4. bracteole position	basal or medial	apical	subfamily
5. leaf shape	elliptic to ovate	linear	*B. racemosa*
6. leaf base	cuneate to narrowly cuneate	obtuse to truncate	*B. racemosa*
7. petiole length	<3.5 mm	>3.5	*B. racemosa*
8. leaf curling	flat	curled	*B. racemosa*

Table 49 cont.

Character	primitive state	advanced state	outgroup
9. rachis length	> 3.5 cm	< 3.5 cm	*B. racemosa*
10. flower color	pink to white	red to purple	*B. racemosa*
11. calyx lobe length	< 3.8 mm	> 3.8 mm	*B. racemosa*
12. petal length	> 12 mm	< 12 mm	*B. racemosa*
13. stamens	not long exserted	long exserted	*B. racemosa*
14. filaments	pubescent	glabrous	*B. racemosa*
15. floral bract length	< 15 mm	> 15 mm	*B. racemosa*
16. # of locules	7	5-6	*B. racemosa*

TABLE 50

Data Matrix for Bejaria species.

Character	Taxon													
	Aes	Cub	Imt	Inf	Led	Mat	Nan	Rac	Res	Spr	Ste	Sub	Tac	Zam
1.	1	1	1	1	1	1	1	0	1	1	1	1	1	1
2.	0	0	0	0	0	0	0	1	0	0	0	0	0	0
3.	0(A)	0	0	C	A	A	B	0	A	A	0	0	B	A
4.	0	0	0	0	0	0	1	1	0	0	0	0	0	0
5	0(1)	1	0	0	0	0	1	0	0	0	0	0	0	0
6.	0(1)	0	0	var.	1(0)	0(1)	0	0(1)	1(0)	0(1)	0	1	0	0(1)
7.	1(0)	0(1)	0	1	0	1(0)	0	0	0(1)	0(1)	0	0	0	1
8.	0	1	0	0	1	0	1	0	0(1)	0(1)	0	0	0	0
9.	var.	0(1)	1(0)	0(1)	var.	var.	1(0)	0(1)	1(0)	0(1)	1	0	1	var.
10.	0	1	0(1)	var.	var.	var.	1	0	1(0)	var.	0	0	0	0

Table 50 cont.

	Aes	Cub	Imt	Inf	Led	Mat	Nan	Rac	Res	Spr	Ste	Sub	Tac	Zam
11.	0(1)	0(1)	0(1)	0	1(0)	1(0)	0	0	1	0(1)	0	var.	0	0
12.	0(1)	0	0	0	0	0	1	0	0	var.	0	0	1	0
13.	0(1)	0	0	0	var.	var.	0	0	var.	1(0)	0	0	0	var.
14.	0	1	0	0	0	0	0	0	0	0	0	0	0	0
15.	0(1)	1	var.	0(1)	0	var.	0	0(1)	0	0	0	1	0	0
16.	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Aes= *B*. *aestuans*, Cub= *B*. *cubensis*, Imt= *B*. *imthurnii*, Inf= *B*. *infundibula*, Led= *B*. *ledifolia*, Mat= *B*. *mathewsii*, Nan= *B*. *nana*, Rac= *B*. *racemosa*, Res= *B*. *resinosa*, Spr= *B*. *sprucei*, Ste= *B*. *steyermarkii*, Sub= *B*. *subsessilis*, Tac= *B*. *tachirensis*, Zam= *B*. *zamorae*.

TABLE 51

Data matrix for <u>Bejaria</u> species after convention for variation was used.

Character	Taxon													
	Aes	Cub	Imt	Inf	Led	Mat	Nan	Rac	Res	Spr	Ste	Sub	Tac	Zam
1.	1	1	1	1	1	1	1	0	1	1	1	1	1	1
2.	0	0	0	0	0	0	0	1	0	0	0	0	0	0
3.a	0	0	0	0	1	1	0	0	1	1	0	0	0	1
b	0	0	0	0	0	0	1	0	0	0	0	0	1	0
c	0	0	0	1	0	0	0	0	0	0	0	0	0	0
4.	0	0	0	0	0	0	1	1	0	0	0	0	0	0
5.	0	1	0	0	0	0	1	0	0	0	0	0	0	0
6.	0	0	0	0	1	0	0	0	1	0	0	1	0	0
7.	0	1	1	0	1	0	1	1	1	0	1	1	1	0
8.	0	1	0	0	1	0	1	0	0	0	0	0	0	0
9.	0	0	1	0	0	0	1	0	1	0	1	0	1	0
10.	0	1	0	0	0	0	1	0	1	0	0	0	0	0

Table 51 cont.

	Aes	Cub	Imt	Inf	Led	Mat	Nan	Rac	Res	Spr	Ste	Sub	Tac	Zam
11.	0	0	0	0	1	1	0	0	1	0	0	0	0	0
12.	0	0	0	0	0	0	1	0	0	0	0	0	1	0
13.	0	0	0	0	0	0	0	0	0	1	0	0	0	0
14.	0	1	0	0	0	0	0	0	0	0	0	0	0	0
15.	0	1	0	0	0	0	0	0	0	0	0	1	0	0
16.	0	0	0	0	0	0	0	0	0	1	0	0	0	0

Aes= *B. aestuans*, Cub= *B. cubensis*, Imt= *B. imthurnii*, Inf= *B. infundibula*, Led= *B. ledifolia*, Mat= *B. mathewsii*, Nan= *B. nana*, Rac= *B. racemosa*, Res= *B. resinosa*, Spr= *B. sprucei*, Ste= *B. steyermarkii*, Sub= *B. subsessilis*, Tac= *B. tachirensis*, Zam= *B. zamorae*.

Fig. 24. Cladogram of Bejaria species using only characters which do not vary in the outgroup (Table 50). For abbreviations see Table 50.

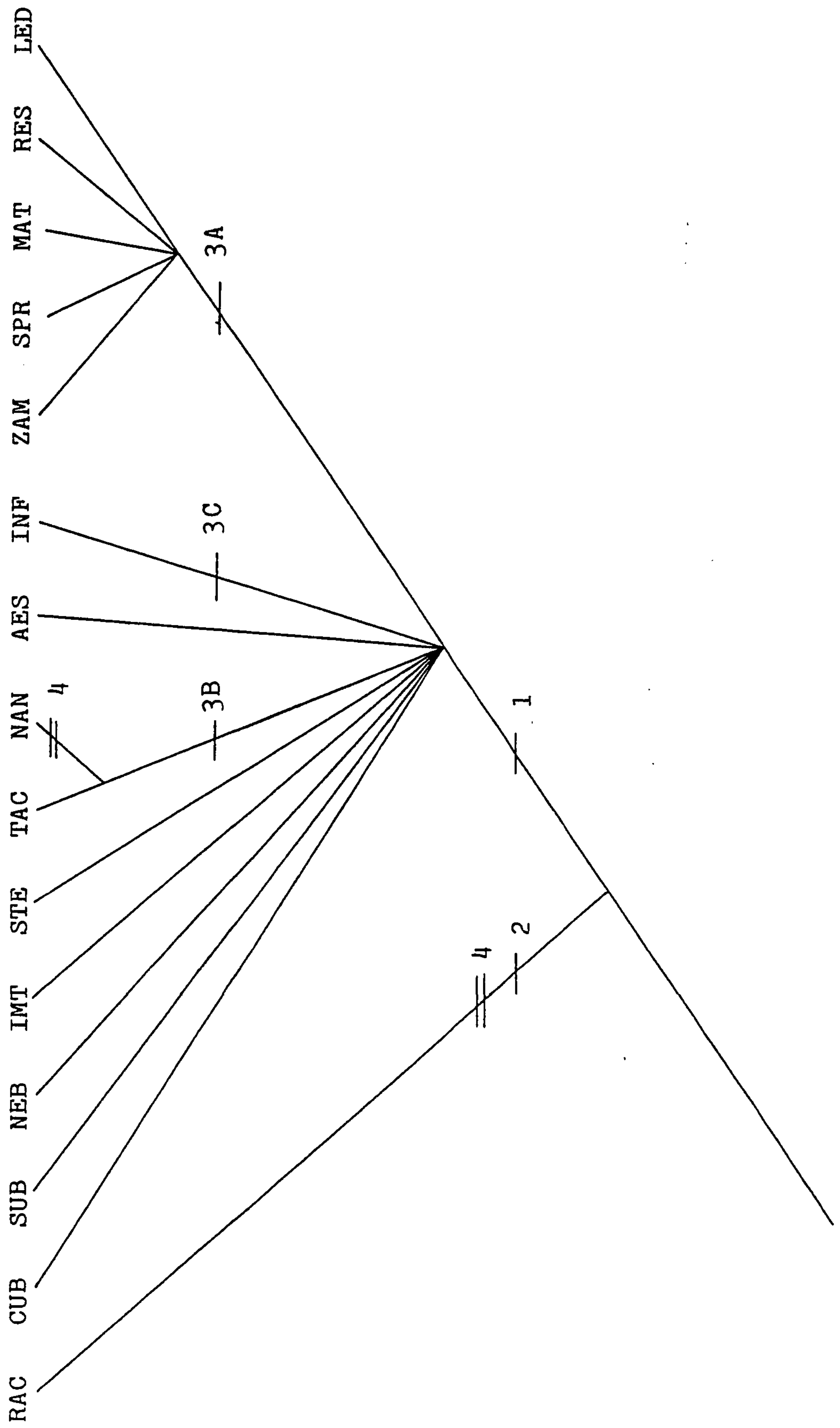
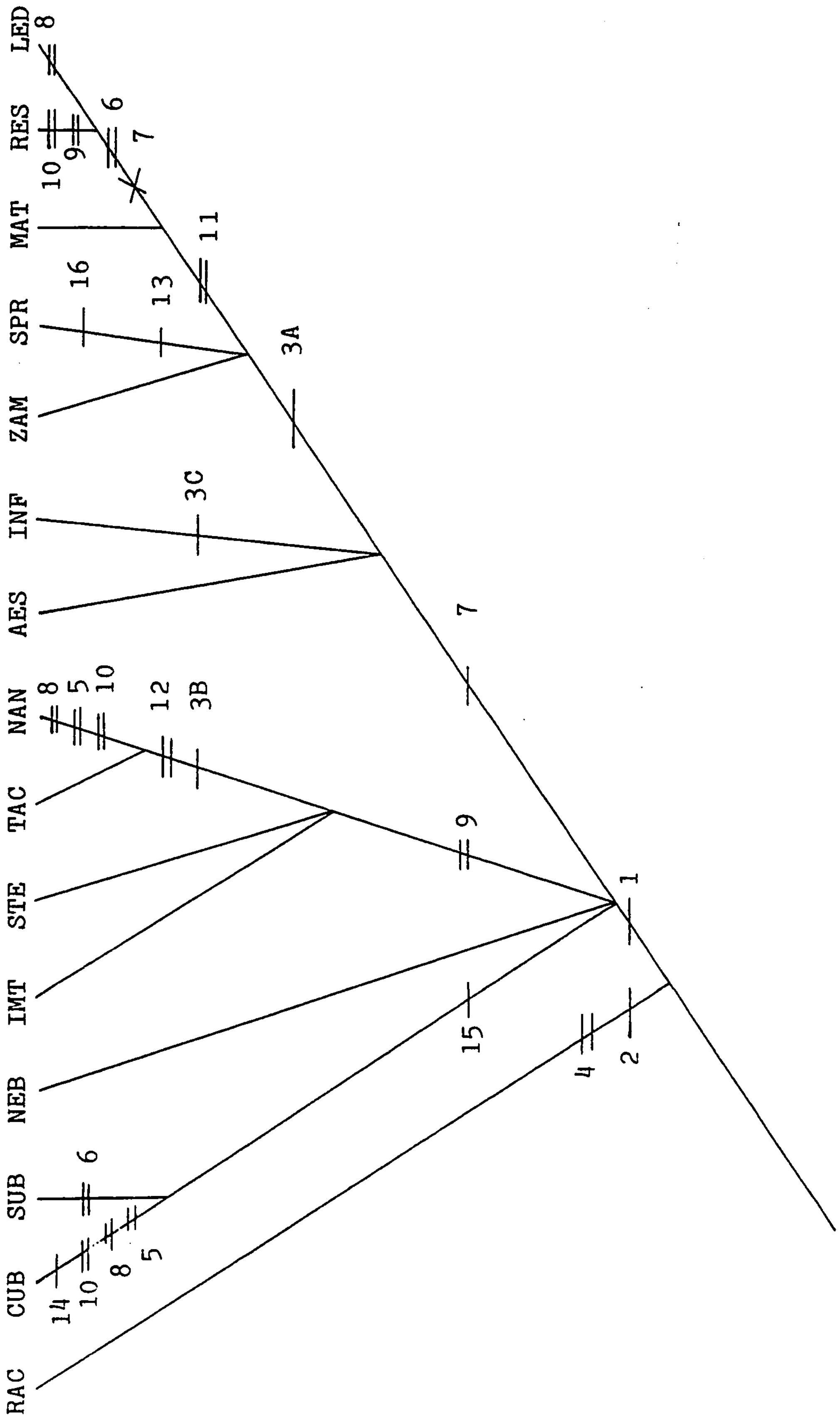

LED
RES
MAT
SPR
ZAM
INF
AES
NAN
TAC
STE
IMT
NEB
SUB
CUB
RAC
3A
3C
4
3B
1
4
2

Fig. 25. Cladogram of Bejaria species (using Table 51). For abbrevisions see Table 50.


RAC
CUB
SUB
NEB
IMT
STE
TAC
NAN
AES
INF
ZAM
SPR
MAT
RES
LED
14
10
8
5
6
15
4
2
1
9
12
3B
8
5
10
7
3C
3A
13
16
11
10
9
6
7
8

tendency for the species to have the derived state. For instance, a single collection of *Bejaria aestuans* has glabrous filaments, a character state found elsewhere only in *B. cubensis*. Since there is a clear tendency in *B. aestuans* to have tomentose filaments I have scored this species as tomentose.

A cladogram is often used to produce a classification. To some extent I did so here. Two sections of the genus are recognized, section *Racemosae* and section *Bejaria*. However no subsectional classification is proposed as there is a great amount of paralellism in the phylogenetic analysis and a great amount of variation found within some species.

Bejaria aestuans, as well as other species, have no autapomorphies (uniqely derived character states). Normally this condition suggests that more study of the taxon needs to be made in order to find autapomorphies. But, in my opinion, *B. aestuans* is the living ancestral species for much of the genus. This species is very widespread, and extremely variable. Many species recognized in this treatment appear to be derived from a species identical with or closely resembling *B. aestuans*. For example *B. infundibula* differs from *B. aestuans* by its larger flowers and different flower shape. Although Hennig did not allow for a living ancestral species, there is no reason to believe that a widespread and variable species such as *B. aestuans* could not be the living ancestral type for many *Bejaria* species.

BIOGEOGRAPHY AND DISTRIBUTION

Bejaria ranges from Central Mexico to South America, with two species found outside this range (Figs. 26-28). In South America it extends east to Guyana and south to Bolivia. Of the two species found outside this range, *B. racemosa* is found in the SE United States (Fig. 26) and *B. cubensis* is found in W Cuba (Fig. 26).

The limits of distribution in *Bejaria* species sometimes coincide with the limits of other taxa or with geological depressions. For example *B. aestuans* (Fig. 27) reaches its southern limit in S Bolivia, an important boundary in *Calceolaria* (Molau, 1981). However the northern limit of *B. aestuans*, in Durango, Mexico, doesn't appear to be important in other taxa.

Both *B. resinosa* (Fig. 28C) and *B. mathewsii* (Fig. 28B) range south to the Huancabamba divide in Peru. The Huancabamba divide is both an important biogeographic barrier and a geological depression. Many species of *Calceolaria* (Molau, 1981) and *Fuchsia* (Berry, 1982) are found only north or only south of this divide. In the north the distribution of *B. resinosa* ends at the Táchira depression in Venezuela.

Bejaria sprucei (Fig. 28A) is interesting because its distribution almost perfectly matches the extent of the

Fig. 26. Distribution of *B*. *racemosa* and *B*. *cubensis*. Circles *B*. *racemosa*, triangles *B*. *cubensis*.

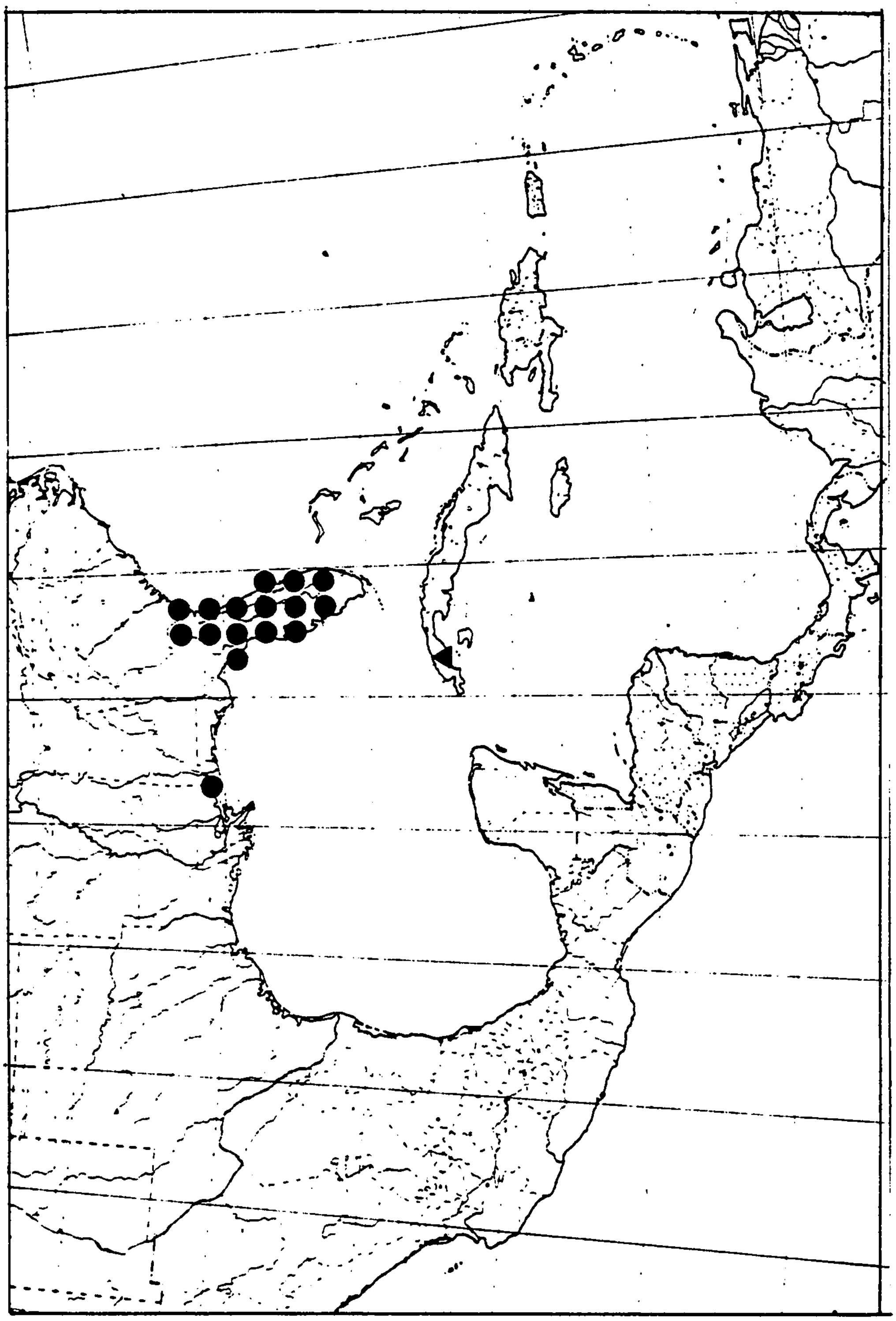


Fig. 27. Distribution of *B. infundibula* and *B. aestuans*. Circles *B. aestuans*, squares *B. infundibula*.

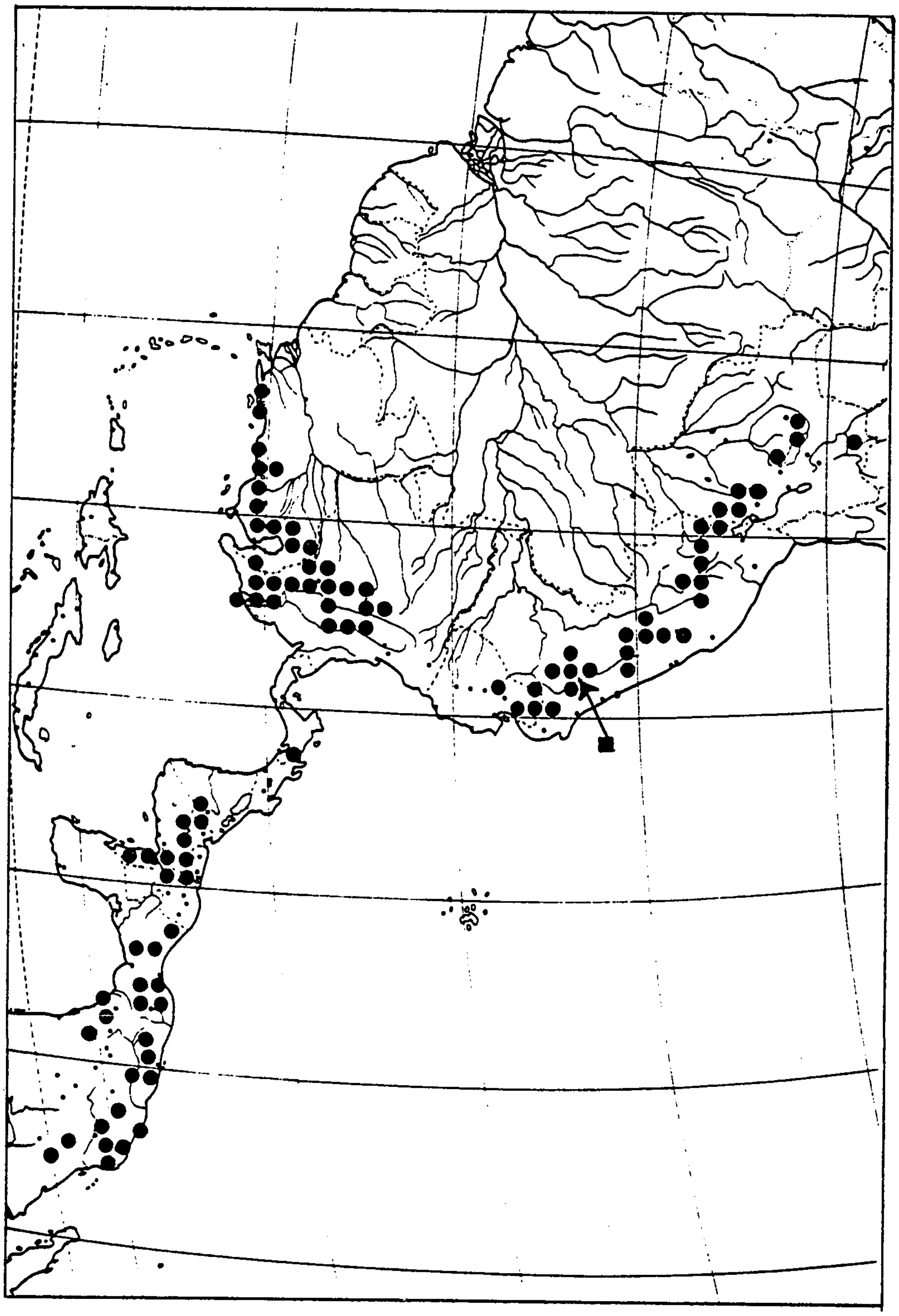
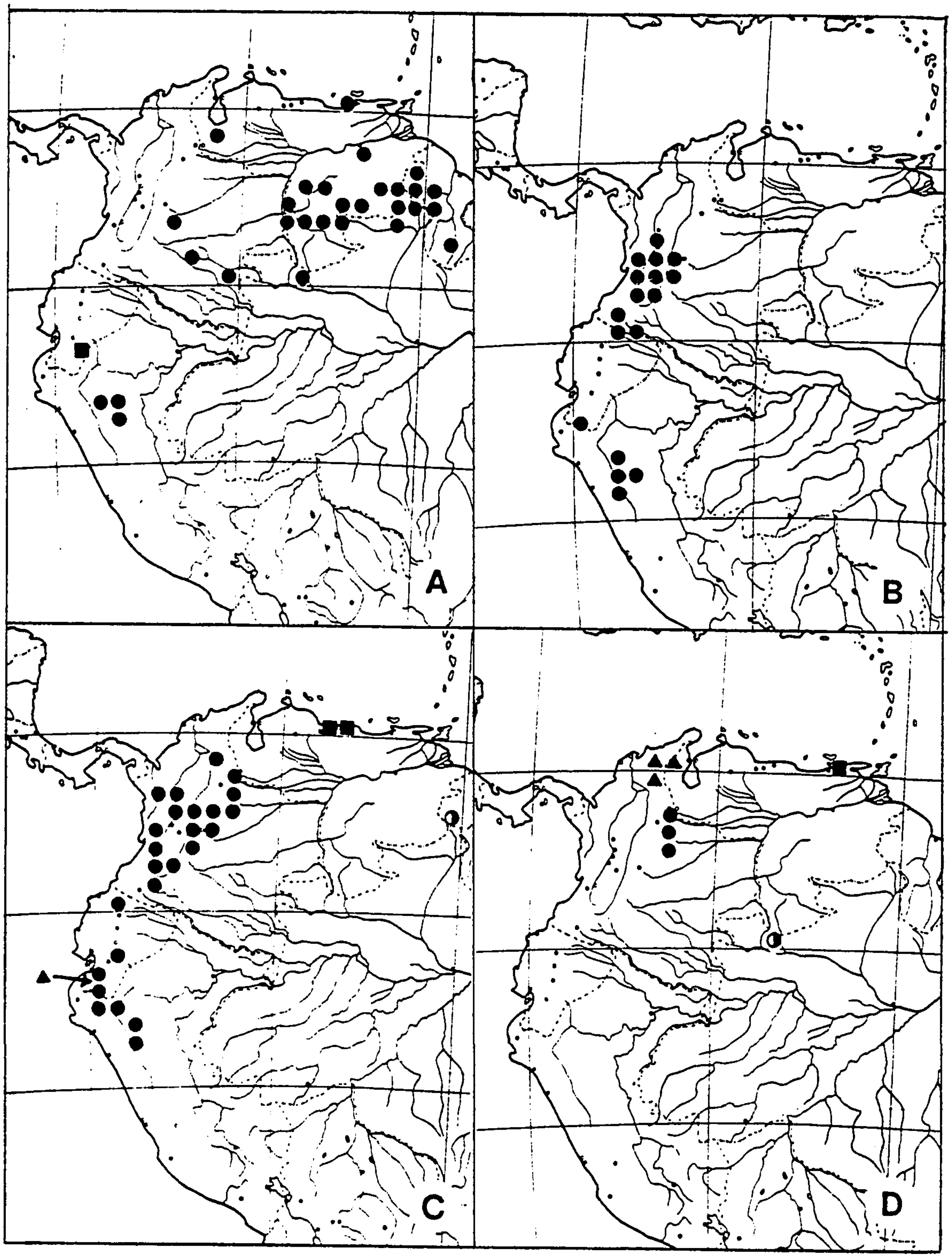


Fig. 28. Distribution of Bejaria species. Fig. A. Distribution of B. sprucei and B. zamorae. Circles B. sprucei, squares B. zamorae. Fig. B. Distribution of B. mathewsii. Fig. C. Distribution of B. resinosa, B. ledifolia, B. subsessilis, and B. imthurnii. Solid circles B. resinosa, squares B. ledifolia, triangles B. subsessilis, half-circles B. imthurnii. Fig. D. Distribution of B. tachirensis, B. steyermarkii, B. nana and B. neblinensis. Solid circles B. tachirensis, squares B. steyermarkii, triangles B. nana, half-circles B. neblinensis.


A
B
C
D

Guayana Highland with one disjunct colony near Tarapoto, Peru and a few collections from Táchira and Anzoátegui, Venezuela. Between these two disjunct centers of *B. sprucei* is found *B. zamorae* (Fig. 28A) (a sister species of *B. sprucei*) at Zamorae, Ecuador.

Many species are local endemics including: *B. nana* (Fig. 28D) endemic to the Sierra de Perijá, *B. steyermarkii* (Fig. 28D) endemic to Cerro Turumiquire, *B. neblinensis* (Fig. 28D) endemic to Cerro Neblina, Venezuela, *B. imthurnii* (Fig. 28C) endemic to Cerro Roraima and nearby mountain tops, and *B. infundibula* (Fig. 27) endemic to Amazonas, Peru.

The species distribution in northern and central Ecuador is interesting because three species (*B. aestuans*, *B. mathewsii*, and *B. sprucei*) are found both north and south of this region but not within and a fourth species (*B. resinosa*) is found north and south of this region with only one collection from within. The absence of *Bejaria* from this region is all the more striking because of the frequency of the genus in southern Ecuador and Colombia. The boundaries of this disjunction coincide closely with the boundaries of the volcanic region of Ecuador. Although volcanic activity would appear to have influenced the absence of *Bejaria* from this region, the presence of *Bejaria* on the slopes of volcanoes in Nariño, Colombia and Pichincha, Ecuador would suggest otherwise.

Biogeographic analyses in connection with phylogenetic analyses have been very useful in clarifying past geological events (Nelson & Platnick, 1981). Within *Bejaria* the presence of a number of widespread and putatively ancestral species make any biogeographic analysis difficult. However, certain hypotheses can be tested. Fedchenko and Basilevskaja (1928) proposed that *Bejaria* originated in the Appalachian region of SE United States. From this area it was proposed that two routes of migration occurred, one going through Mexico and Central America to South America and Cuba, the second going into Florida. An alternative migration route would go through Florida to Cuba and through Mexico and Central America to South America. In order to test these hypotheses I have undertaken a biogeographic analysis.

Following the methods of biogeographic analysis in Nelson and Platnick (1981) I have taken the species cladogram (Fig. 25) and grouped the Mexican, Central and South American taxa into one group, while retaining the two outlying groups, *B. racemosa* and *B. cubensis*. The result of this grouping is a cladogram with only three groups (Fig. 29A). This cladogram shows the phyletic relationship of these three groups, *B. cubensis* is a sister group of the Mexican, Central American, and South American group and not the sister group of *B. racemosa*. Using the methods of vicariance biogeography long-distance dispersal is assumed not to be important. Therefore the terminal taxa (*B. racemosa*, *B. cubensis*, and remaining

Fig. 29. Cladogram and Area cladograms for Bejaria. Fig. A. Reduced cladogram of Bejaria taxa. RAC= B. racemosa, CUB= B. cubensis, OTH= all other Bejaria species. Fig. B. Area cladogram drawn from Fig. A. FLA= Florida and SE US, CUB= Cuba, SCA= South & Central American and Mexico. Fig. C. Proposed migrational relationships of Bejaria species (Fedchenko & Basilevskaja, 1928). Fig. D. An Alternative hypothesis for relationships for Cuba, Florida, and Central and South America.

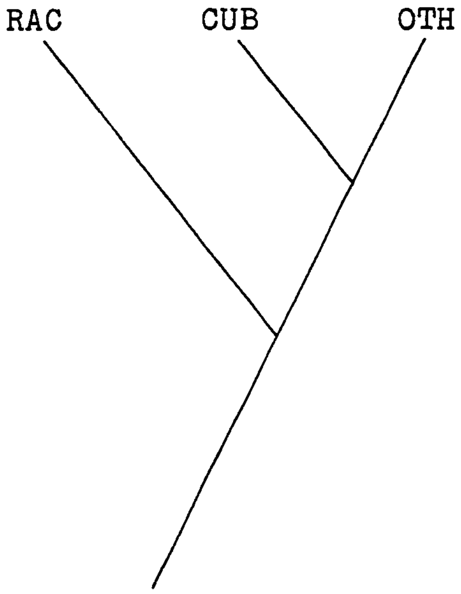


Fig. 29A

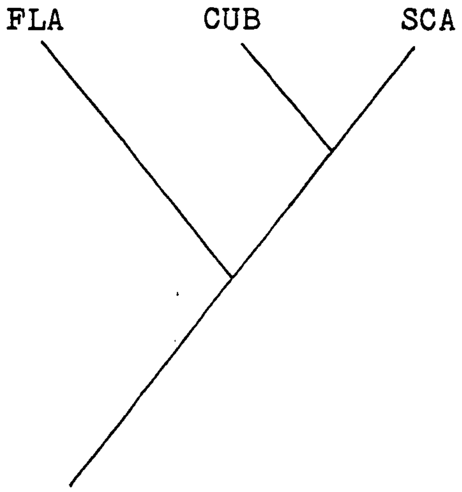


Fig. 29B

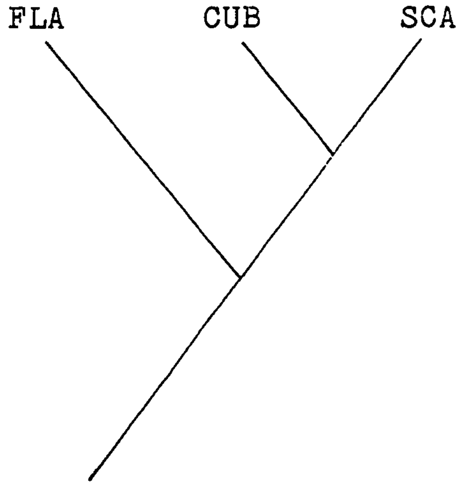


Fig. 29C

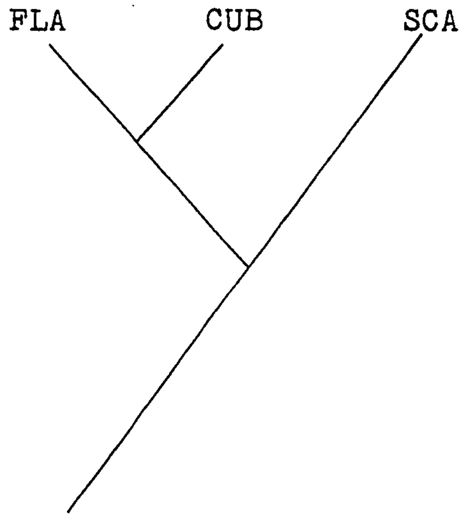


Fig. 29D

members of *Bejaria*) can be replaced with their geographic location. The resulting cladogram (Fig. 29B known as an area cladogram) will show a phyletic relationship of the geographic locations. In *Bejaria*, the area cladogram indicates that western Cuba is biogeographically and probably geologically more closely related to Mexico, Central America and South America, than it is to Florida. Comparing this cladogram with the proposal by Fedchenko and Basilevskaja (1928) (Fig. 29B, drawn as a branching diagram) it can be seen that they agree. The alternative hypothesis, with Cuba and Florida related to each other (Fig. 29D) is falsified, this migration route would require that *B. cubensis* and *B. racemosa* have a common ancestor which differs from the ancestor of the other taxa, but the area cladogram produced here suggests that the Cuban *Bejaria* species shares a common ancestor with the Mexican, Central American, and South American taxa (as proposed by Fedchenko and Basilveskaja (1928), and not with the Florida taxon. The Fedchenko and Basilevskaja proposal although not falsified, is not proven either but a similar relationship between Cuba and Central America was noted and discussed by Rosen (1975).

SPECIES CONCEPT

I believe in a conservative concept of a species such as that of Cronquist (1978) "Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means." I have lumped together many formerly recognized groups because they are not consistently distinct (e.g. the varieties of B. glauca) or because they represent the ends of a cline (i.e. B. mexicana).

Floral characters are more consistently useful than pubescence types, which were used as specific characters in past classifications. The floral shape and the relative lengths of the petals and stamens have obvious importance to pollination. They probably represent reproductive isolating mechanisms and therefore the groups they delimit may represent "biological species".

No subspecific taxa are recognized in this treatment. Some populations of B. aestuans may be sufficiently distinct to be accorded varietal or subspecific rank but the usefulness of recognizing these groups is dubious as they would be almost impossible to identify using a key because they are recognizable only through a combination of a number of characters.

SYSTEMATIC TREATMENT

Bejaria Mutis ex Linneaus, Mant. pl. 152, 242. 1771 (as Befaria); Linné fil., Suppl. pl. 247. 1782 (as

Befaria); Jussieu, Gen. pl. 159. 1789 (as Befaria); Ventenat, Description des plantes nouvelles et peu connues. t. 51. 1801; Bonpland in Humboldt & Bonpland, Pl. aequinoct. 2: 118. 1809 (as Befaria); Kunth in Humboldt, Bonpland & Kunth, Nov. gen. sp. 3: 290. 1819 (as Befaria); G. Don, Gen. hist. 3: 849. 1834; Poeppig & Endlicher, Nov. gen. sp. pl. 1: 24-25. 1836 (as Befaria); A. P. De Candolle, Prodr. 7: 731-732. 1839; Walpers, Annales botanices systematicae 2: 1123. 1852 (as Befaria); Weddell, Chloris andina 2: 182-183. 1860; Hooker in Bentham & Hooker, Gen. pl. 2: 599. 1876 (as Befaria); Hemsley, Biol. Centr.-amer., Bot. 2: 282. 1881; Paxton & Lindley, Paxton's Fl. Gard. 2: 141. 1883; Drude in Engler & Prantl, Nat. Pflanzenfam. IV(1): 34. 1889; Small, Flora of southeastern United States, p. 992. 1903; Standley, Trees & Shrubs of Mexico, Contr. U.S. Natl. Herb. 23(4): 1091. 1924 (as Befaria); Fedchenko & Basilevskaja, Revisio generia Bejaria Vent., Bot. Mater. Gerb. Glavn. Bot. Sada SSSR 6: 37-45. 1926; Fedchenko & Basilevskaja, Revision of the genus Bejaria Mutis, Bot. Gaz. (Crawfordsville) 85: 299-322. 1928; Mansfeld & Sleumer, Revision der Gattung Befaria Mutis, Notizbl. Bot. Gart. Berlin-Dahlem 12: 235-276. 1935; Camp, Bull. Torrey Bot. Club 68: 100-111. 1941 (as Befaria); Pittier et al., Catalogo de la Flora Venezolana 2: 265-274. 1947. Macbride, Fl. Peru, Field Mus. Nat. Hist., Bot. ser. 13(part V, no. 1): 126-133. 1959; Wood, J. Arnold Arb. 42: 10-80. 1961; Standley & L. O. Williams, Flora of Guatemala, Fieldiana: Bot. 24(VIII): 88-127. 1966 (as _Befaria_); Soukup, Biota 9(73): 224-239. 1972; Maguire et al., Mem. New York Bot. Gard. 28: 140-141. 1978 (as _Befaria_); Wilbur & Luteyn, Flora of Panama, Ann. Missouri Bot. Gard. 65(2): 37-40. 1978 (as _Befaria_); Steyermark & Huber, Flora del Avila, p. 238. 1978 (as _Befaria_); Camargo, Catalogo Ilustrado de las Plantas de Cundinamarca, 7: 20-24. 1979. Type species. _Bejaria aestuans_ Linnaeus. Named in honor of Jose Bejar an eighteenth century professor of botany at Cadiz, Spain.

Acunna Ruiz & Pavon, Fl. peruv. prodr. 69, t. 12. 1794. Type species. _Acunna oblonga_ Ruiz & Pavon. Dedicated to Pedro de Acuña y Malvar, minister of the Indies, who recomended Ruiz and Pavon to the Spanish king for the botanical expedition to Peru.

Jurgensenia von Turczaninov, Bull. Soc. Imp. Naturalistes Moscou 20(1): 151. 1847. Type. _Jurgensenia mexicana_ von Turczaninov. Jurgensen was a collector in Mexico from 1840-1845 who collected for Galeotti, after Galeotti returned to Europe.

Heptacarpis Conzatti, Anales de Hospital General 2(5): 5-7. 1940, illegitimate name (Art. 36.1). Type. *Heptacarpis salmonicolor* Conzatti.

Erect or prostrate, evergreen, terrestrial *shrubs* or *trees*; bark thin or thick, fissured or sometimes deeply fissured, often fibrous. *Leaves* alternate, simple, estipulate, brochidodromous, coriaceous or chartaceous, flat or longitudinally curled; margin entire, rarely slightly crenate, usually slightly revolute; abaxial surface usually glaucous. *Inflorescence* terminal, axillary, or both, racemose, sometimes paniculate, eperulate or often encircled at the base by a series of bracts, the smallest usually lanceolate or triangular, the largest leaf-like or approaching the size and shape of the floral bracts; rachis usually thickest at the base; floral bract solitary at base of each pedicel, the proximal often leaf-like in size and shape, the distal smaller and narrower, margins entire; pedicels subterete or sometimes flattened near the base, thickest near base, bibracteolate; bracteoles chartaceous or coriaceous, articulate with pedicels, caducous or persistant, smaller than the floral bracts, usually inserted on the lower ½ of the pedicel, sometimes just below the calyx, margin entire. *Flowers*: calyx continuous with the pedicel, campanulate, 5-7(-11)-lobed, quincuncial or usually with 3 lobes fully outside, 2 lobes fully inside, and 2 lobes

½-inside and ½-outside; tube crateriform; lobes erect or spreading, sometimes curved inward, dissimilar in size and shape; corolla bell-shaped, trumpet-shaped, tube-shaped, cup-shaped, or funnel-shaped; petals free, 5-7(-9), quincuncial, or with 3 fully outside, 2 fully inside, and 2 ½-inside and ½-outside, spreading or imbricate at anthesis; stamens 10-14(-18), subequal or rarely long and short stamens alternating, subequal to corolla or long exserted (1.2-1.5x petal length); filaments filiform, usually flattened in cross-section, usually tomentose on basal 1/3, thickest near base; anthers subequal, each theca dehiscing by a terminal or subterminal cleft; ovary superior, 5-7-locular, short depressed cylindric or depressed ellipsoid, with a low nectariferous disk surrounding the ovary at base, glabrous or rarely long pilose; style terete, filiform, straight or curved, subequal to the corolla or exserted, sometimes apparently elongating after anthesis, glabrous; stigma capitate or 7-lobed. Fruit a 5-7-locular, woody capsule, globose, apically depressed, brown to black; seeds oblong, 0.5-2 mm long, testa long-celled.

A neotropical and subtropical genus of 15 species found in Florida, Cuba, and central Mexico south to Bolivia and east to Guyana.

NOTES ON KEYS, TERMS, AND ABBREVIATIONS

In the following artificial key to sections and species adjacent species in the ultimate couplets of the key do not always imply a close relationship. The characters in the keys were recorded from herbarium material and material preserved in a variety of fluids (FAA, formalin, ethanol, isopropyl alcohol). There appears to be no noticeable shrinkage upon drying, therefore measurements should apply to both fresh and dried material. Colors given are based on personal observations in the field, herbarium labels, and for bark and twig colors, on dried material. Unless otherwise stated, rachis, pedicel, filament, and style measurements were made at or near the base of the organ; petals and calyx lobes are adaxially glabrous; leaf, bract, calyx lobe lengths, and calyx diameter were measured at their widest points. Stamen length includes both the filament and anther but the overall length is nearly equal to the filament length because the filament is attached near the distal portion of the anther and the anther is not prolonged.

The terms I employ are those found in Radford et al. (1974), except for the following. I use the term longitudinally curled to refer to curling of the whole leaf and reserve the term revolute and involute for the margin. Pubescence types are defined as: tomentose, presence of unicellular or multicellular uniseriate hairs; hispid, presence of multicellular multiseriate hairs; glandular-hispid, presence of multicellular multiseriate capitate hairs.

In the distribution maps I have used the degree square method in which one dot represents the presence of a species in a degree-square. "Specimens examined" indicates that all collections seen are cited; "Representative specimens examined" indicates that only a portion of the specimens seen are cited. All specimens examined in this study, however, are cited in the LIST OF EXSICCATAE, and all specimens cited have been seen unless indicated by "n.v." immediately following the citation.

Photographs have been cited by negative number preceeded by the herbarium acronym or photographer's initials. Thus F neg. 1040 = negative from Field Museum of Natural History, J. Francis MacBride type photo collection.

I use the herbarium acronyms found in Holmgren et al. (1981).

Key to the Sections and Species of *Bejaria*.

1. Leaves chartaceous, midveins not noticeably prominent on abaxial leaf surface; inflorescence appearing stalked because of marked reduction in leaf size

immediately below the inflorescence, racemose or paniculate; capsules septacidal and slightly loculicidal at apex; Florida. (sect. Racemosae.)

1. B. racemosa, p. 201

1. Leaves coriaceous, midveins noticeably prominent on abaxial leaf surface; inflorescence not appearing stalked, leaves usually not markedly reduced in size below the inflorescence, racemose, rarely paniculate; capsules setacidal. (sect. Bejaria).

  2. Filaments glabrous; leaves 3.5-6 cm long, linear, longitudinally curled; W Cuba.

  2. B. cubensis, p.210

  2. Filaments tomentose, rarely glabrous; leaves not long, linear, and longitudinally curled in same species (or if so less than 2 cm long).

    3. Petals 12 mm long or shorter.

      4. Petioles 2.5 mm long or shorter; leaves 2.5 cm long or shorter; corolla cup-shaped.

        5. Pedicels 1-4.5 mm long, raceme appearing spike-like; leaves longitudinally curled, abaxially glandular-hispid; petals 5-11 mm long; Sierra de Perijá, Colombia & Venezuela. 14. B. nana, p.329

        5. Pedicels 6.5-14 mm long, racemes not appearing spike-like; leaves flat or slightly longitudinally curled, abaxially glabrous; petals 11-12 mm long; Páramo de

Tamá, Colombia & Venezuela; Sierra de Cocuy, Colombia.

13. _B_. _tachirensis_, p.322

4. Petioles usually longer than 2.5 mm; leaves usually longer than 2.5 cm; corolla spreading or bell-shaped, or tube-shaped.

6. Stamens long exserted (more than 1.2x petal length); pedicels 0.3-0.6(-0.8) mm diam.; corolla tube-shaped or sometimes slightly spreading distally, 5-7-merous; Guayana Highland region (Cordillera de Macarena, Colombia to Kaiteur Plateau, Guyana) and San Martín Dept., Peru.

6. _B_. _sprucei_, p. 259

6. Stamens not long exserted (less than 1.2x petal length); pedicels (0.4-)0.6-1.2 mm diam.; corolla spreading, bell-shaped, or trumpet-shaped, 7-merous (rarely 5-merous); Andes from Venezuela to Bolivia and in Mexico and Central America.

4. _B_. _aestuans_, p.218

3. Petals longer than 12 mm.

7. Longest calyx lobes 3.4 mm long or longer.

8. Petioles less than 3.5 mm long; leaves less than 3.5 cm long (-3.9 mm in _B. subsessilis_).

9. Corolla spreading or bell-shaped, pink;

leaf apex usually acute or obtuse.

10. Leaf bases obtuse of truncate; pedicels 16.5-26 mm long; petals 24-37 mm long; Loja Prov., Ecuador.

15. B. *subsessilis*, p.335

10. Leaf bases cuneate; pedicels 4-17 mm long; petals 15-27 mm long; Cerro Roraima. 10. B. *imthurnii*, p. 313

9. Corolla tube-shaped, usually red; leaf apex usually acute to acuminate.

11. Petals 13-23 mm long; leaves longitudinally curled; Coastal Cordillera, Venezuela.

9. B. *ledifolia*, p.309

11. Petals 20-40 mm long; leaves usually not longitudinally curled; Andes from W Venezuela to N Peru.

8. B. *resinosa*, p.284

8. Petioles usually longer than 3.5 mm; leaves usually longer than 3.5 mm.

12. Corolla tube-shaped, not distally spreading; stamens usually slightly exserted; central Colombia to N Peru.

7. B. *mathewsii*, p.272

12. Corolla spreading, or funnel-shaped (distally spreading); stamens not exserted.

13. Corolla spreading; Mexico & Colombia.

4. *B*. *aestuans*, p.218

13. Corolla funnel-shaped; N Peru.

3. *B*. *infundibula*, p.214

7. Longest calyx lobes usually shorter than 3.4 mm.

14. Corolla tube-shaped (sometimes distally spreading); pedicels thin, 0.2-0.6(-0.8) mm diam. or thinner; corolla 5-7-merous.

15. Stamens long-exserted (more than 1.2x petal length); corolla 5-7-merous; Guayana Highland and San Martín Dept., Peru. 6. *B*. *sprucei*, p.259

15. Stamens subequal to corolla or slightly exserted (less than 1.2x petals length); corolla 7-merous; E Ecuador.

5. *B*. *zamorae*, p.256

14. Corolla spreading or bell-shaped, trumpet-shaped, or funnel-shaped, pedicels thick (0.4-)0.6-1.2 mm diam. or thicker; corolla (6-)7(-8)-merous.

16. Corolla funnel-shaped or trumpet-shaped.

17. Petals 30-39 mm long; longest calyx lobes 2.8-3.9 mm long; N. Peru.

3. *B*. *infundibula*, p.214

17. Petals shorter than 30 mm; longest calyx lobes shorter than 2.8 mm; widespread. 4. _B_. _aestuans_, p.218

16. Corolla spreading or bell-shaped.

18. Leaf bases obtuse or truncate; petals 24-37 mm long; rachis 3.5-7.6 cm long; pedicels 16.5-26 mm long; twigs hispid; Loja Prov., Ecuador.

15. _B_. _subsessilis_, p.335

18. Leaf bases cuneate; petals 14-27 mm long; rachis 0.6-4.3 cm long; pedicels 4-20 mm long; twigs hispid, glandular-hispid, or glabrous; Venezuela & N Brazil.

19. Petals 15-27 mm long; leaves 1.2-2.8 x 0.5-1.4 cm, usually obovate or elliptic, apex usually acute to obtuse; Cerro Roraima and vicinity.

10. _B_. _imthurnii_, p.313

19. Petals 14-17.5 mm long; leaves 1-1.8 x 0.2-0.6 cm, lanceolate to elliptic, apex acuminate or cuspidate, sometimes acute.

20. Pedicels 13-20 mm long; rachis 3.8 cm long; leaf surfaces glandular-hispid; Cerro

Neblina, Territorio Federal
Amazonas, Venezuela & N
Brazil.
12. _B_. _neblinensis_, p.320

20\. Pedicels 3.5-7.5 mm long;
rachis 0.6-1.8 cm long; leaves
glabrous; Cerro Turumiquire,
Sucre Dept., Venezuela.
11. _B_. _steyermarkii_, p.317

Bejaria section _Racemosae_ Fedchenko & Basilevskaja. Type species. _Bejaria_ _racemosa_ Ventenat.

Section _Racemosae_ is easily distinguished by the chartaceous leaves without a prominent abaxial midvein, the terminal, sometimes branched inflorescence which appears stalked because of the marked reduction in leaf size immediately below the inflorescence, and the distinctive leaf anatomy (see MORPHOLOGY: Leaves).

Only _B_. _racemosa_ belongs in this section. This species is endemic to SE United States. I have collected _B_. _racemosa_ from a number of localities in Georgia and Florida.

1\. **Bejaria racemosa** Ventenat, Description des plantes nouvelles et peu connues, t. 51. 1802. Type. Cultivated at Cels, France from seed collected by A.

Michaux in the United States (western Florida) and sent from Charleston (South Carolina), Ventenat s.n. (lectotype, G, photo NY neg. 11686). The lectotype is here designated, the specimen at G has a hand written description matching the protologue and the specimen is in the Ventenat herbarium. Fig. 30A & B.

Bejaria paniculata Michaux, Flora boreali-americana, 1: 280. 1803, "Befaria". Type. United States. Florida: without precise locality or date, A. Michaux s.n. The label of a specimen in the Michaux herbarium at P n.v. (IDC microfiche of Michaux herbarium fiche # 63, column 6, row 2) has the locality "southern Georgia and Florida", whereas a specimen at B-WILLD, n.v. (photos, B neg. 4360, IDC microfiche of Willdenow herbarium specimen # 9128) has a label which matches the protologue locality "Florida, arenosus". The Paris specimen probably represents the lectotype because it is the Michaux herbarium, but since neither specimen has been seen I am not designating a lectotype at this time. Other Michaux specimens exist at BM and P-2 sheets (IDC microfiche of Michaux herbarium fiche # 63, column 4, row 2 & column 5, row 2).

Bejaria floridana Gandoger, Bull. Soc. Bot. France 65: 56. 1918. Type. United States. Florida:

Polk Co., 11 May 1894 (fl), Ohlinger 569 (lectotype, LY, photo NY neg. 11688; isolectotypes, F, FLAS, MIN). This collection is here selected from among the cited specimens as the lectotype because it is the only specimen in Gandoger's herbarium (at LY) with his annotation as *B. floridana*.

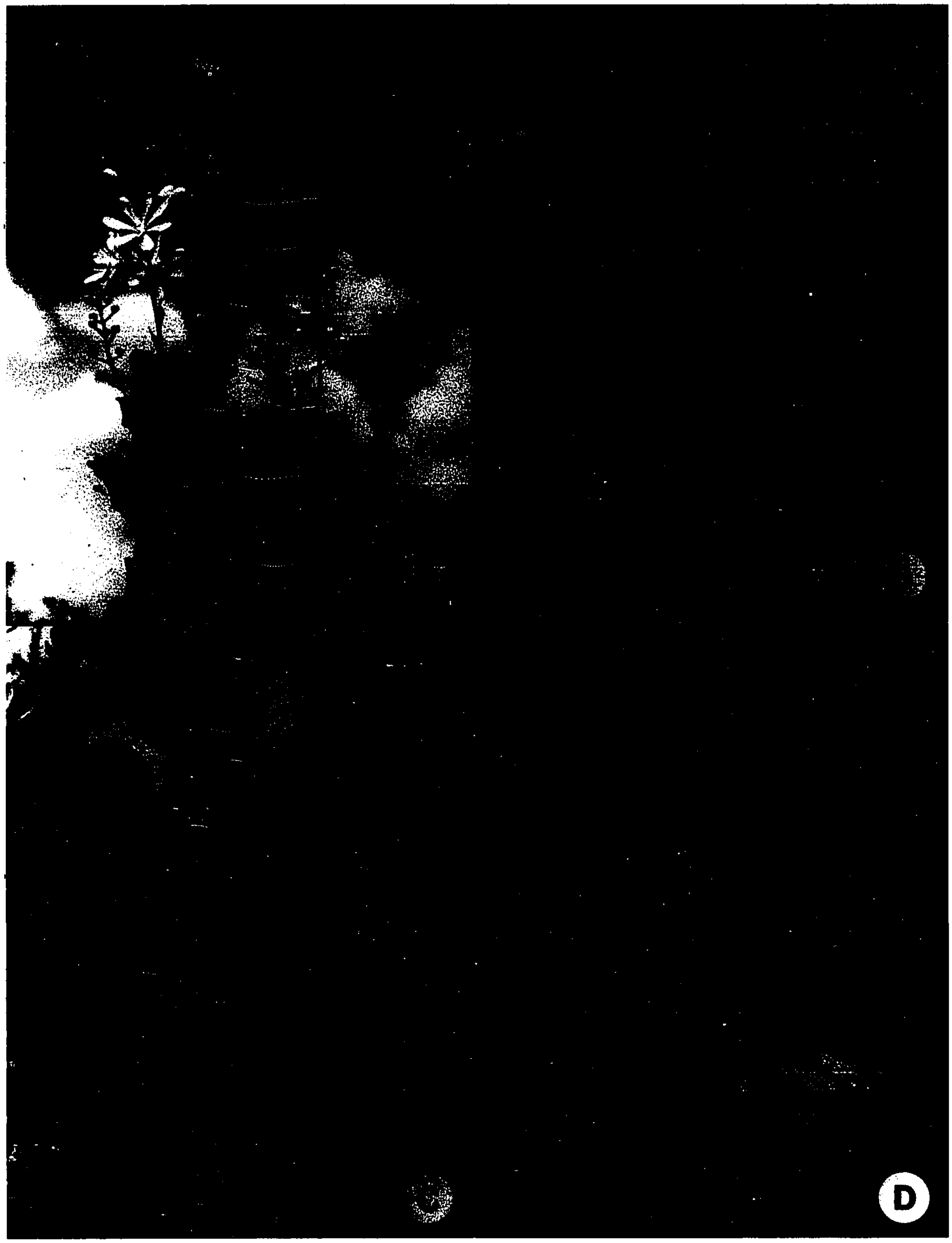
Shrub to 3 m tall; older branches fibrous, often hispid, bark red-brown to gray-brown, usually glaucous; twigs subterete, red-brown or gray-brown, hispid, rarely glabrous or tomentose, sometimes glaucous. Leaves chartaceous, flat, elliptic, obovate, or less commonly ovate or lanceolate, 1.8-5.2 x 0.6-2.5 cm, apex acute, obtuse, or rounded, sometimes mucronulate, base cuneate or rarely rounded, margin glabrous, revolute, both surfaces and midveins glabrous or reddish-tomentose when young; petiole slightly flattened in cross-section, 1.2-1.4 mm long and 0.7-1.2 mm diam., glabrous or sometimes hispid or tomentose. Inflorescence a terminal raceme or sometimes a panicle, appearing stalked because of noticeable reduction in leaf size below raceme, 3-23-flowered; rachis 2-16 cm long and 0.5-1.7 mm in diam., brown to dark purple-brown, rarely glaucous, tomentose and hispid; floral bracts elliptic to lanceolate or ovate, rarely oblanceolate, flat, 3.4-17 x 0.5-6.7 mm, apex acute to acuminate, base cuneate to attenuate, occasionally truncate, margin glabrous, flat or slightly involute, both surfaces usually reddish-tomentose; pedicel ascending or inclined, 4.5-15 mm long and 0.5-1 mm in diam., usually tomentose or glabrous; bracteoles inserted in apical 1/3 of pedicel, often immediately below calyx, lanceolate, oblanceolate, or oblong, flat, 1.8-3.8 x 0.4-1.1 mm, apex acuminate to acute, base truncate, cuneate, attenuate, or rarely rounded, margin glabrous, occasionally ciliolate, rarely erose-ciliolate, often slightly involute, both surfaces glabrous or slightly tomentose. Flowers 7-merous; calyx 3.2-5.2 mm long and 3-9 mm diam.; tube 1.2-2.4 mm long and 1.9-4.9 mm diam., green or tan, occasionally tomentose; lobes ovate to widely depressed ovate, rarely widely obovate, 1.5-2.9 x 1.5-2.9 mm, longest lobe 1.9-2.9 mm, apex acute, obtuse, or rounded, margin erose, glabrous or usually ciliolate, abaxial surface often tomentose; corolla spreading; petals spreading to reflexed, spatulate, white, pink, or white with pink, 18-33 x 3.5-8 mm, apex obtuse to rounded, base attenuate, margin entire or undulate, glabrous, lamina distally tomentose; stamens included, 15-26 mm long; filaments 0.5-0.8 mm diam., tomentose; anthers 1.3-2.4 mm long and 0.9-1.1 mm in diam.; ovary glabrous; style included, 13-23 long and 0.5-1.1 mm in diam.; stigma 7-lobed, 0.5-1 mm long and 0.7-2.4 mm in diam. Capsules depressed obloid, 4-6.6 mm long and 6.3-11 mm in diam., brown to black, valves separating from pericarp; seeds oblong 1.3-1.8 mm long and

0.3-0.4 mm in diam.

Distribution. (Fig. 25). Bejaria racemosa is endemic to low pine flatwoods and shrub oak-saw palmeto areas of SE Georgia, S Alabama, and Florida, United States of America. It flowers from April to June and bears fruit from June to October.

Representative specimens examined. UNITED STATES. Georgia: Camden Co., US Hwy. 17, S of Woodbine, 26 Jun 1967 (fl), Bozeman 10457 (BM, BR, C, E, GA, GH, MICH, MIN, NCU, NY, TEX, U, UC, USF, WIS); Glynn Co., Crooked Creek State Park, 10 Jun 1980 (bud), Clemants & A. Miller 1583 (NY); Glynn Co., S of Brunswick, 21 Jun 1969 (fl), Godfrey 68578 (FLAS, NCU, MO, MSC, UC); Camden Co., Little Satilla River, E of Waverly, 0.8 mi SW of Camden-Glynn Co. line, 26 Jun 1952 (fl, fr), Hardin & Duncan 13791 (BH, FLAS, GA, GEO, GH, MICH, NCU, TEX, UC, USF, WIS). Alabama: Mobile, 1826, Cozzens s.n. (NY). Florida: Clay Co., 15 mi. S of Route 218 on Route 21A, 0.5 mi. E of Route 21, 10 Jun 1980 (fl), Clemants & A. Miller 1594 (NY); Alachua Co., Gainesville, N side 23rd Ave., betw. 12th and 14th Streets, 12 Jun 1980 (fl), Clemants & A. Miller 1604 (NY); Lake Co., Ocala National Forest, ½ mi. W of Route 19, 4.5 mi. S of route 40, 12 Jun 1980, Clemants & A. Miller 1616 (NY); Indian River-Oseola Co. line, 0.2 mi N of route 60, 0.4 mi E of Florida Turnpike at Yeehaw Junction, 13 Jun 1980 (fl), Clemants & A. Miller 1627 (NY); Glades Co., State rd. 29, ca. 2 mi NE of LaBelle, 17 Jun 1980 (fl), Clemants & A. Miller 1637 (NY); Lee Co., Florida rd. 78, ca. 5 mi. W of Alva, 17 Jun 1980 (fl), Clemants & A. Miller 1647 (NY); DeSoto Co., just S of Hardee Co. line, on US 17, 18 Jun 1980 (fl), Clemants & A. Miller 1658 (NY); Jacksonville, 16 Jun 1894 (fl), 1 Nov 1894 (fr), Curtiss 4922 (BH, CAS, E, F, G-BOISS, GA-2 sheets, GH, HBG, K, MIN, MSC, NY, UC, US, W); Hernando Co., US 75, ½ mi. N of Pasco Co., ca. 10 mi. NW of Dade City, 18 Jun 1967 (fl, fr), D'Arcy 1645 (C, FLAS, GH, LL); Taylor Co., along US Hwy. 98, ca. 2.5 mi. NW of Steinhatchee river, 28 Jun 1959 (fl, fr), Dress & Read 7787 (BH, BR, E, W, WIS); Palm Beach Co., Delray Beach golf course, 10 Jun 1945, Fox 525 (DUD, FLAS, GEO, GH, LL, MSC, MO, NCU, NY, US); Lee Co., Meyers, Jul-Aug 1900 (fl, fr), Hitchcock 193 (CU, F, GH, LY, MIN, MO, NY); Lake Co., nr. Eutis, 16-31 May 1894 (fl, fr), Nash 803 (A, BH-2 sheets, E, F, G, G-BOISS, GH, K, MICH, MIN, MSC, MO, NY, UC); Pinellas Co., ca. 1 mi SE of Sug Harbor on Weedon Island, 19 May 1961, Ray et al. 10946 (BM, GH, LL, NCU, USF); Johns Co., St. Augustine, Jun-Jul 1875, Reynolds s.n. (F, MICH-3 sheets, MO, NY-4 sheets, UC, US); Florida, without locality, 1842-1849, Rugel 201 (BM, F, MO, US); Lee Co., nr. Ft. Meyers, 4 Apr 1916, J. P. Standley 131 (A, F, GH, MO, NY, US); Clay Co., ca. 7 mi. NNE of Lawtey, along new US 301, 1.1 mi. S of intersection with Fla 218, 22 Jun 1963, Ward & Ward 3503 (BM, FLAS, GH, NCU, USF).

Fig. 30. A-B. *Bejaria racemosa*. A. *Clemants & Miller 1627*. B. *Clemants & Miller 1594*. C-D. *Bejaria infundibula*. C. *Luteyn & Lebrón-Luteyn 5516*. D. *Clemants & Fernández 2007*. (Figs. A-B by Abigail Miller, Fig. C by Luteyn, Fig. D by Clemants).


D

Common names and uses: Tar-flower, Fly weed. The flowers are sometimes used for fly paper in Florida.

Bejaria racemosa is a distinctive species with no close relatives. It is characterized by spreading or reflexed petals, noticeably reduced leaves below the inflorescence causing the inflorescence to appear stalked, chartaceous leaves without noticeable midveins beneath, and short petioles. A number of character states are not found elsewhere in *Bejaria*. These include the "stalked inflorescence", the chartaceous leaves which have stomata on both surfaces and which lack a mucilaginous epidermis and distinct midveins beneath. This set of unique characters makes *B. racemosa* worthy of sectional rank.

Copeland (1943), in his study of the floral anatomy, examined only *Bejaria racemosa*, upon which he based his conclusions for the genus. Because *B. racemosa* has such distinctive leaf anatomy, any conclusions from floral anatomy based only on studies of *B. racemosa* may not be true for the entire genus.

Bejaria Mutis ex L. section *Bejaria*. Type species *Bejaria aestuans* Linnaeus.

Bejaria section *Bejaria* is distinguished from section *Racemosae* by the coriaceous leaves with prominent abaxial midveins, terminal and often axillary, rarely branched inflorescences which never appear stalked in the manner of B. racemosa, and the distinctive leaf anatomy (see MORPHOLOGY: Leaves).

Fourteen species are placed in the section. I have collected eight of these species, the other six are local endemics.

2. **Bejaria cubensis** Grisebach, Cat. pl. Cub. 52. 1866, "Befaria". Type. Cuba. Pinar del Río: Piñales, 1863 (fl, fr), C. Wright 2200 (holotype, GOET, photo NY neg 11687; isotypes, BUF, G-BOIS, G-DC, GH, L, LE, MO, NY, P, S, US, W, photo, microfiche of NY herbarium 760/B12 & 760/C1).

Shrub to 2.5 m tall; bark of older branches fibrous, usually glandular hispid, rarely also tomentose, bark reddish-orange to red or brown, glaucous; twigs bluntly angled, densely reddish glandular-hispid and tomentose, rusty-red or brownish-red. Leaves coriaceous, longitudinally curled, linear, 3.5-6 x 0.2-0.5 cm, apex acuminate, rarely mucronate, base narrowly cuneate, margin glandular-ciliate, both surfaces glabrous, midveins and base of lamina tomentose and glandular-hispid, glabrate; petiole flattened in cross-section, 1.3-2 mm long and 0.8-1.1 mm diam., glabrous or glandular-hispid, often indistinguishable due to decurrent lamina. Inflorescence a terminal raceme, 7-15-flowered; rachis 3-10.8 cm long and 1.2-2.2 mm diam., reddish-orange, red, or dark red, glandular-hispid and tomentose; floral bracts linear, commonly longitudinally curled, 15-50 x 0.5-3 mm, apex narrowly acuminate, base narrowly cuneate, margin glandular-hispid, revolute, both surfaces glabrous, midveins and base of lamina tomentose and glandular-hispid, glabrate; pedicel ascending to divergent, 12-30 mm long and 0.5-1 mm diam., densely tomentose and glandular-hispid; bracteoles inserted in basal ½ of pedicel, linear or narrowly lanceolate, flat, 3.3-6.3 x 0.2-0.5 mm, apex narrowly acuminate, base narrowly cuneate, margin glandular-ciliate and occasionally also ciliolate, usually involute, both surfaces tomentose. Flowers 7-merous; calyx campanulate, 2.8-3.7 mm long and 5.1-7.7 mm diam.; tube 1.3-2.3 mm long and 2.3-3.5 mm diam., dark purple to black, glandular-hispid; lobes ovate to widely ovate, 1.6-3.4 x 1.1-2.2 mm, longest lobes 2.5-3.4 mm, apex acute or caudate, margin entire or dentate, ciliate, glandular-ciliate, or sometimes ciliolate, abaxial surfaces glabrous, rarely glandular-hispid; corolla bell-shaped; petals spreading or imbricate, oblanceolate, dark purple, 16-24 x 2.6-4.2 mm, apex obtuse, base cuneate or rarely attenuate, margin entire or distally crenate, glabrous, lamina glabrous; stamens subequal to the corolla, 19-26 mm long; filaments 0.3-0.7 mm diam., glabrous; anther 1.4-2.6 mm long and 1.2 mm diam., glabrous; ovary glabrous; style exserted, 29-37 mm long and 0.3-0.5 mm diam.; stigma 7-lobed, 1.0-1.2 mm long and in diam. Capsule depressed obloid, 4.5-5.0 mm long and 5.8-7.2 mm diam., dark brown to black, valves separating from pericarp; seeds oblong, 0.8-1.0 mm long and 0.3-0.4 mm diam.

Distribution. (Fig. 26). *Bejaria cubensis* is endemic to the pinelands of Pinar del Río, Cuba at 200-250 m alt. (although the locality for Wright *s.n.* (MO) is "Cuba Oriental". It flowers primarily from January to May (September), and bears fruit from March to July.

Specimens examined. CUBA. Pinar del Río: Cerro de Cabras, 19 May 1951 (fr), Alain 1847 (US); Sierra de Cabra, Guane rd., 9-11 Sep 1910 (fl, fr), Britton *et al.* 7203 (F, NY-2 sheets, US); Sierra de Cabra, 6 Mar 1911 (fl, fr), Britton *et al.* 9782 (NY; US); Lagunillas, at Río San Sebastian, 12 May 1922 (fl, fr), Ekman 13812 (F, K, MICH, NY, S, US); Sitio del Infierno, 14 Jun 1923 (fl), Ekman 16714 (G-DEL, NY, S); nr. Cerro de Cabras, 5 Aug 1912 (fl), León 3396 (NY); Piñales, 16 Apr 1930 (fl), León 14328 (NY, US); Cerro de Cabras, Jan 1939 (fl), León & Victorin 18736 (GH, US); Luis Lazo, 12 Jul 1905 (fr), O'Donovan 5353 (NY, UC); mts. nr. El Guamá, 9 Mar 1900 (fl, fr), Palmer & Riley 204 (US), 205 (NY); 13 Mar 1900 (fl), Palmer & Riley 310 (NY); Pinar de Río, 200-250 m, 19 May 1933 (fl, fr), Rutten-Pekelharing 430 (U); Consolación del Sur, 1914, Van Herman s.n. (NY). Location unknown: "Cuba Oriental", 1859, 1860, C. Wright s.n. (MO).

Common names. Cuba: Napoleōn del pinar and Clavellina (Leōn & Alain, 1957, p. 94).

Bejaria cubensis is easily distinguished by its linear revolute leaves and glabrous filaments, a combination not found elsewhere in the genus. Revolute leaves are found in B. ledifolia, B. nana, and scattered populations of other species; linear revolute leaves are very rare, smaller linear revolute leaves are only found in a few populations of B. resinosa near Bogotá. Glabrous filaments are only found in one population of B. aestuans from Chiapas, Mexico.

Fedchenko and Basilevskaja (1928) stated that B. cubensis probably originated in Central America. On the other hand, Mansfeld and Sleumer (1935) and Camp (1941), while stating how isolated the species was, believed its nearest relative to be B. ledifolia from near Caracas, Venezuela. While the curled leaves of B. cubensis and B. ledifolia are similar, the flowers are very different. Bejaria cubensis has spreading or bell-shaped corollas (vs. tube-shaped corollas in B. ledifolia) and shorter calyx lobes (1.6-3.4 mm long vs. (2.4-)3.7-5(-5.7) mm long in B. ledifolia). I agree that B. cubensis is isolated geographically and morphologically. The closest relative appears to be B. aestuans from Central America and Mexico.

Befaria cubensis and *B. aestuans* share a similar spreading flower and, in the one instance, glabrous filaments, but *B. aestuans* doesn't have the linear revolute leaves. This pattern of a western Cuba and Central America connection has also been shown in a number of groups both animal and plant (see Rosen, 1975).

A photo showing the flower of *B. cubensis* can be found in León and Alain (1957, p. 95), and one showing the habit in Marie-Victorin and Léon (1942, p. 204).

3. **Bejaria infundibula** Clemants, sp. nov. Type. Peru. Amazonas: Prov. Chachapoyas, ca. 5 km SW of Chachapoyas on rd. to Bagua, 2420 m, 11 Jun 1982 (fl), *Clemants & Fernández 2007* (holotype, NY; isotype, USM and duplicates to be distributed).

Fig. 30C & D.

Bejaria infundibula Clemants; corollis magnis 3-3.9 cm longis infundibuliformibus a congeneris differt.

Shrub to 3 m tall; older branches fissured, densely glandular-hispid or glabrous, bark gray and brown; twigs subterete, brownish-gray to black, mostly glandular-hispid, sometimes tomentose. *Leaves* coriaceous, flat, elliptic to widely elliptic, 2.7-4.6 x 1.4-2.7 cm, apex obtuse, bluntly mucronulate, base cuneate, obtuse, or truncate, margin glabrous, flat or slightly revolute, adaxial surface sparcely hispid, abaxial surface tomentose, usually glandular-hispid especially along midvein, rarely glabrous; petiole semiterete, flattened abaxially, 3.5-6 mm long and 1.2-1.7 mm diam., glandular-hispid, rarely tomentose or glabrous. Inflorescence terminal, axillary, or both, racemose, 9-13-flowered; rachis 3-15 cm long and 1.4-2.8 mm diam., orange to brown, densely glandular-hispid, often tomentose, rarely glabrous; floral bracts lanceolate to ovate, flat, 6-7.7(-30) x 1.2-2.8 mm, apex acute to obtuse, base cuneate or obtuse, margin glabrous or revolute, both surfaces glandular-hispid, sometimes tomentose, rarely glabrous; pedicel ascending, 13-46 mm long and 0.5-1 mm diam., glandular-hispid, tomentose, or rarely glabrous; bracteoles inserted in basal ½ of pedicel, lanceolate or oblong, flat, 1.3-4.7 x 0.4-1 mm, apex acute to acuminate, margin glandular-ciliate, flat or slightly involute, both surfaces glandular-hispid, tomentose, or rarely glabrous. Flowers 7(-8)-merous; calyx 4.9-5.8 mm long and 7.2-10 mm diam.; tube 1.9-3.1 mm long and 4-6.4 mm diam., brown or brown with maroon edges, glandular-hispid; lobes ovate to widely ovate or triangular, 1.8-3.9 x 1.8-3.9 mm, longest lobe 2.8-3.9 mm, apex acute to obtuse, margin entire, glabrous, glandular-ciliate, or rarely ciliolate, abaxial surface glandular-hispid or tomentose; corolla funnel-shaped; petals imbricate, spreading distally, spatulate, white, pink, dark magenta, or purple, 30-39 x 8-13 mm, apex obtuse, base attenuate, margin undulate, glabrous, lamina distally slightly tomentose; stamens included or subequal to corolla, 26-41 mm long; filaments 0.4-0.8 mm diam., tomentose; anther 2.3-3.5 mm long and 1-1.4 mm diam., glabrous; ovary glabrous; style slightly to long exserted, 33-46 mm long and 0.5-0.7 mm diam.; stigma capitate, slightly lobed, 1.2-1.5 mm long and 2.3-2.7 mm diam. Capsules depressed obloid, 5-6 mm long and 9-10 mm diam., brown, valves not separating from pericarp; seeds oblong, 1.1-1.9 mm long and 0.3-0.4 mm in diam.

Distribution. (Fig. 27). *Bejaria infundibula* is endemic to open shrublands of Amazonas, Peru, at 1500-3000 m alt. It flowers from August to March, and bears fruit from Febuary to March.

Specimens examined. PERU. without locality: Lobb s.n. (W); Lobb 277 (CGE). Amazonas: Prov. Bongara betw. Río Utcubamba and Shipasbamba, 4 km from engineering camp, 1520 m, 2 Feb 1964 (fl, fr), Hutchison & Wright 3951 (F, G, GH, K, L, LE, M, MICH, NY, UC, US); Prov. Chachapoyas, km 504-506, ca. 5 km N of Chachapoyas, 2150 m, 11 May 1978 (fl, fr), Luteyn & Lebrón-Luteyn 5516 (NY); Prov. Chachapoyas, Chachapoyas-Rodriguez de Mendoza road, km 546-549 W of Molinopampa, 2300-2360 m, 11 Mar 1978 (fl, fr), Luteyn & Lebrón-Luteyn 5534 (NY); Prov. Chachapoyas, without precise locality or date, Mathews s.n. (BM, BR, CGE, E, G-BOIS, K-2 sheets), 1835, *Mathews s.n.* (GH); Taulea, 1835, *Mathews 1424* (BM, CGE, E-2 sheets, FI, G-2 sheets, OXF, S); 1836, *Mathews 114H* (K); Prov. Chachapoyas, Yambrasbamba, without date, *Mathews 1425* (CGE-3sheets, E, OXF-2 sheets); 1840, *Mathews 3040* (BM, CGE, G-DC-2 sheets, K, OXF, S); ridge SE of Cocamar, 2000-2200 m, 24-26 Jun 1948 (fl), *Pennell 15593* (GH); Chachapoyas-Boca Negra, 6/8 (6 Aug?) 1962 (fl), *Soukup 4923* (US); mts. nr. Chachapoyas, 2700 m, 18 Jan 1930 (fl), *Ll. Williams 7552* (F, NY); between Chachapoyas and Celendín, 2000-3000 m, 17 Dec 1936 (fl), *Woytkowski s.n.* (F); Leimebamba, 2300 m, 27 Nov. 1962 (fr), *Woytkowski 7686* (G, MO, US). Cajamarca: Prov. Cutervo, 10 km NE of Socota, 3200 m, 10 Dec 1938 (fl), *Stork & Horton 10125* (A, F, G-DEL, K, UC).

Common names: Peru: Matamoscas, Mupa sacha (Amazonas).

Befaria infundibula is characterized by long funnel-shaped corollas, elliptic or widely elliptic leaves, and medium length calyx lobes. It differs from *B. mathewsii* and *B. resinosa* by corolla shape (tube-shaped in *B. mathewsii* and *B. resinosa*), stamen length (shorter than or equal to the corolla vs. usually exserted in *B. resinosa* and *B. mathewsii*), and calyx lobe length (longest lobes 2.8-3.9 mm long vs. 3.4-5.6 mm in *B. mathewsii* and 3.8-7.5 mm long in *B. resinosa*). It also differs from *B. resinosa* in leaf size (27-46 mm long vs.

1-25 mm long in *B. resinosa*).

Bejaria infundibula is a close relative of *B. aestuans* and difficult to separate from it. The trumpet-shaped corollas of some *B. aestuans* populations from the Antioquia and Mérida regions appear similar to the funnel-shaped corollas of *B. infundibula* but they are smaller. Flowers as large as those of *B. infundibula* are found in *B. aestuans* from Mexico but these populations have spreading petals. Elliptic leaves are found throughout the range of *B. aestuans* but rarely are they widely elliptic. So, in general, *B. infundibula* can be separated from *B. aestuans* by longer petals (30-39 mm long vs. (8.5-)12-27.5(-45) mm long in *B. aestuans*), longer stamens (26-41 mm long vs. (9-)13-27(-43) mm long in *B. aestuans*), and widely elliptic leaves.

4. **Bejaria aestuans** Linnaeus, Mant. pl. 242. 1771, "Befaria". Type. Mutis plate without number at Madrid Herbarium, n.v. (Madrid slide #1840!). See the Orthography and Typography chapter for a discussion of the typification and application of *B. aestuans*.

Fig. 31A-D, Fig. 32.

Acunna oblonga Ruiz & Pavon, Syst. veg. fl. peruv. chil. 123. 1798; *Bejaria oblonga* (Ruiz & Pavon) Persoon, Syn. pl. 2: 3. 1806, "Befaria". Type. Peru. Churupallano, 1779, *Ruiz & Pavon s.n.*

(lectotype, MA, photo NY neg 11677 & 11677a). Another specimen exists at P but lacks a collection number and is therefore not cited as a isolectotype. Mansfeld and Sleumer (1935) cite Tafalla 204 (MA) as the type, but considering the species was named by Ruiz and Pavon, one of their sheets should be used as the type if it exists. The specimen at MA is here selected as the lectotype, because it has a very thorough description attached.

Acunna lanceolata Ruiz & Pavon, Syst. veg. fl. peruv. chil. 124. 1798; Bejaria lanceolata (Ruiz & Pavon) G. Don, Gen. hist. 3: 849. 1834. Type. Peru. Huânuco: Pillao, 1787, Ruiz & Pavon s.n. (lectotype, G-BOIS; isolectotype, BM). This specimen is here selected as the lectotype since it has a label with good locality information in Pavon's handwriting. Other syntypes exist at G, K, MA, P, US, and W, but they generally do not have as much locality information or data.

Bejaria glauca Bonpland in Humboldt & Bonpland, Pl. aequinoct. 2: 118, t. 117. 1813, "Befaria". Type. Venezuela. Distrito Federal: Silla de Avila, Bonpland 644 (lectotype, B-WILLD n.v., photo B neg. 3449, F neg. 18283, IDC microfiche of Willdenow herbarium #9124; isolectotypes, H, P, P-HBK, n.v., photo, IDC microfiche of H.B.K. herbarium, fiche 62, column 5, row 2). The lectotype was selected by Mansfeld and Sleumer (1935).

Bejaria coarctata Bonpland in Humboldt & Bonpland, Pl. aequinoct. 2: 125, t. 121. 1813, "Befaria"; Bejaria glauca var. coarctata (Humboldt & Bonpland) Mansfeld & Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 253. 1935, "Befaria". Type. Peru. Cajamarca: Páramo de Yanaguanga, 1900-3100 m, Bonpland s.n. (lectotype, P, n.v., photo, IDC microfiche of H.B.K. herbarium fiche 63, column 6, row 2; isolectotype B, photo B. neg. 4362, B+, n.v., photo F neg 18282, IDC microfiche of Willdenow herbarium #9126). The lectotype is selected here. A second collection at P lacks collection data.

Bejaria mexicana Bentham, Pl. hartw. 15. 1819, "Befaria". Type. México. Jalisco: Bolaños, 1837, Hartweg 92 (holotype, K, n.v., photo MICH neg. 702; isotypes, B+, n.v., CGE-2 sheets, E, FI, G, G-BOIS, GH, L, LD, LE, NY, OXF, P, W 2-sheets, frag. F, photo F neg. 18288, microfiche of NY herbarium #760/B11).

Bejaria hispida Poeppig & Endlicher, Nov. gen. sp. pl. 1: 24-25. 1836, "Befaria". Type. Peru.

Huánuco: Cuesta de Carpis, betw. Acomayo and Chinchao, Apr 1831, Poeppig s.n. (lectotype, W, photo NY neg. 11684; isolectotype, G-BOISS). Lectotypified by Mansfeld and Sleumer (1935).

Bejaria laevis Bentham, Pl. hartw. 65. 1840, "Befaria". Type. México. Oaxaca: betw. Talea and Totontepec, Jun-Jul 1839, Hartweg 478 (holotype, K, photo NY neg 11707; isotypes, B+, n.v., CGE-2 sheets, E, FI, G, G-BOISS, K, L, LD, LE, OXF, P, W-2 sheets, photo F neg. 18286, microfiche of NY herbarium #760/B10).

Bejaria discolor Bentham, Pl. hartw. 65. 1840, "Befaria". Type. México. Oaxaca: Talea, Jul 1839, Hartweg 479 (holotype, K, n.v.; isotypes, B+, n.v., CGE-2 sheets, E, FI, G, G-BOIS, K, L, LD, LE, OXF, P, W-2 sheets, frag. F; photo F neg. 28912, microfiche of NY herbarium #760/B6).

Bejaria glabra Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9(6): 543. 1842. Type. México. Oaxaca: Chinantla, nr. Villa Alta, 1060-1970 m, Apr 1840 (fl), Galeotti 1811 (lecotype, BR, in Martens herb., photo NY neg 11689; isolectotypes, BR, G, K, LE, P, W). The lectotype is here selected.

Bejaria floribunda Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9(6): 543. 1842. Type. México. Oaxaca: betw. Villa Alta and Taneze, 1210 m, Nov 1840, Galeotti 1812 (lectotype, BR, photo NY neg 11690; isolectotypes, BR-3 sheets, G, K, LE, P, UC, W-2 sheets, photo, microfiche of NY herbarium #760/B7). Lectotype selected here.

Bejaria parviflora Bentham, Pl. hartw. 143. 1845, "Befaria". Type. Ecuador. Loja: mts. nr. Loja, 1842, Hartweg 795 (holotype, K, n.v.; isotypes, B+, n.v., BR, CGE-2 sheets, E, FI, G-BOISS, K, LD, LE, OXF, P, W-2 sheets, frag. ex P at F, photo F neg. 18289, microfiche of NY herbarium #760/C7).

Jurgensenia mexicana von Turczaninov, Bull. Soc. Imp. Naturalistes Moscou 20(1): 151. 1847. Type. México. Oaxaca: Sierra San Pedro Nolasco, Talea etc., 1843-1844, Jurgensen 562 (holotype, KW?, n.v.; isotypes, FI, G, G-BOISS, K, OXF, frag. F). I have seen no specimen annotated by von Turczaninov, presumably the type is at Kiev.

Bejaria pallens J. Rémy, Ann. Sci. Nat. Bot. sér. 3, 8: 229. 1847. Type. Bolivia. La Paz: Chulumani, d'Orbigny 404 (holotype, P, photo NY neg. 11679; isotype, W).

Bejaria *denticulata* J. Rémy, Ann. Sci. Nat. Bot. sér. 3, 8: 230. 1847. Type. Bolivia. La Paz: Mt. Visachal, *d'Orbigny* *480* (holotype, P, photo F neg. 38278; isotypes, W, frag. F ex P.)

Bejaria *lindeniana* Hérincq, Rev. Hort., sér. 3, 4: 183. 1850. Type. Venezuela. Mérida: betw. Caracas and Mérida, 1820 m, 1843, *Linden* *387* (lecotype, G-DC, photo NY neg. 11696; isolectotypes, BR, CGE, FI, G-DC, G-BOISS, K, LG, OXF, P, US, W-2 sheets, frag. F). Lectotypified here.

Bejaria *drymifolia* Linden ex Hérincq, Rev. Hort., sér. 3, 4: 185. 1850. Type. Colombia. Norte de Santander: Chinacotá, 1830 m, Feb 1847, *Funck* *&* *Schlim* *1456* (lectotype, P, photo NY neg. 11680; isolectotypes, BR, CGE, G, G-BOIS-2 sheets, G-DC, LD, LE, W, frag. F). Lectotypified here.

Bejaria *decora* Drake del Castillo, J. Bot. (Morot) 3: 77. 1889, "Befaria". Type. Ecuador. Loja: Chonta-cruz, E of Loja, *Poortman* *116* (holotype, P?, n.v.). Mansfeld and Sleumer (1935) placed *B*. *decora* in synonomy with *B*. *glauca* var. *coarctata* based on the protologue; they did not see the type. I have not been able to find the type either and I agree with them in placing the name in synonomy here.

Bejaria parvifolia Rusby, Bull. New York Bot. Gard. 8: 110. 1912, "Befaria". Type. Bolivia. La Paz: nr. Apolo, 1760 m, 25 Jul 1902, R. S. Williams 1473 (holotype, NY, photo NY neg. 11692).

Bejaria ghiesbreghtiana Planchon ex Fedchenko & Basilevskaja, Bot. Mater. Gerb. Glavn. Bot. Sada SSSR 6: 38. 1926. Type. México. Oaxaca: without precise locality, 1842-1843, Ghiesbreght s.n. (holotype, LE, photo NY neg. 11711). A number of Ghiesbreght specimens exist with the number 31, which Mansfeld and Sleumer (1935) cite as isotypes. Unfortunately the LE specimen lacks this collection number. Therefore they are not cited as isoltypes.

Bejaria antioquiae Fedchenko & Basilevskaja, Bot. Mater. Gerb. Glavn. Bot. Sada SSSR 6: 40. 1926. Type. Colombia. Antioquia: betw. Yolombó and Cauca, 1500-2000 m, 18 Sep 1884, Lehman 212 (holotype, LE, photo NY neg. 11710; isotypes, F, G-BOISS, K).

Bejaria subserrata Fedchenko & Basilevskaja, Bot. Mater. Gerb. Glavn. Bot. Sada SSSR 6: 41. 1926.

Type. Colombia. Santander: Piedecuesta, 1515-1820 m, Jan 1847 (fl), Funck & Schlim 1331 (holotype, LE, photo NY neg. 11709; isotypes, G, G-DC, LD, P, W, frag. ex P at F).

Bejaria boliviensis Fedchenko & Basilevsakaja, Bot. Mater. Gerb. Glavn. Bot. Sada SSSR 6: 42. 1926. Type. Bolivia. 1500-2000 mi. in the interior, lat. 15-18°S, without date, Bridges 177 (lecototype, LE, photo NY neg. 11708). Fedchenko and Basilevskaja (1926) cite Bridges s.n. and Cummings s.n. as types. I have sected the Bridges as the lectotype because it has more complete label data.

Bejaria glauca var. tomentella Mansfeld & Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 255. 1935, "Befaria". Type. Peru. Cuzco: Forantoy valley, Lucmayoc, 2150 m, Herrera 1727 (holotype, B+, n.v.). Lectotype. Peru. Dept. Cusco: "Pillahuata", Cerro Cusilluyoc, 2700-2900 m, 3-6 May 1925 (fl), Pennell 14085 (lectotype, S, photo, NY neg. 11687; isolectotype, GH, K, NY, US). I have chosen Pennell 14085 (S) as the neotype because it matches the protologue and is annotated by Sleumer as "typisch".

Bejaria glauca var. setosa Mansfeld & Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 256. 1935, "Befaria". Type. Bolivia. La Paz: Larecaja, Cerro Vacani, nr. Ananea, 2500 m, May-Jun 1860, Mandon 563 (holotype, B+, n.v.; lectotype, NY, photo NY neg. 11683, microfiche of NY hebarium #760/C3; isolectotypes, F, G, G-BOISS, G-DC, GH, K, S, W-2 sheets, photo NY neg. 9621). The lectotype is here designated.

Bejaria glauca var. glandulosa Mansfeld & Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 257. 1935, "Befaria". Type. Peru. Huánuco: Macora and Pillao, Chinchao, Tafalla 204 (holotype, MA, photo NY neg. 11685; isotype B+, n.v.).

Heptacarpus salmonicolor Conzatti, Anales de Hospital General 2(5): 5-7. 1940, illegitmate name (Art. 36.1). Type. México. Oaxaca: Dist. Ixtlán, nr. Cacalotepec, Sierra de Ixtlán, 900 m, 10 Oct 1939 (fl), C. Conzatti 6000 (coll. by M. Gómez & V. Conzatti) (holotype, Conzatti herb., n.v.; isotype, ECON, photo NY neg. 11691). A copy of the description is at ECON.

Bejaria hintonii Camp, Bull. Torrey Bot. Club 68: 108. 1941, "Befaria". Type. México. Guerrero:

Dist. Galena, Piedra Ancha, 2800 m, 3 May 1939 (fl), Hinton 14237 (holotype, NY; photo NY neg. 9783, microfiche of NY herbarium #760/B9 isotypes, F, GH, LL, MO, photo, NY neg. 9615).

Bejaria guatemalensis Camp, Bull. Torrey Bot. Club 68: 110. 1941, "Befaria". Type. Guatemala. Zacapa: Sierra de Las Minas, below Finca Alejandria, 1700-2000 m, 12 Oct 1939 (fl), Steyermark 29783 (holotype, F, photos, F neg. 52520, NY neg. 9616; isotype, frag. NY).

Shrub or tree 1-15 m tall; older branches smooth or fissured, glabrous, tomentose, hispid, or glandular-hispid, gray or dark brown; twigs subterete, smooth or fissured, often fibrous, bark gray or brown, glabrous, hispid, or glandular-hispid. Leaves coriaceous, flat, rarely longitudinally curled, elliptic to narrowly elliptic, sometimes lanceolate or oblanceolate, rarely ovate, (0.8-)1.5-8(-12.5) x (0.1-)0.7-2.5(-3.2) cm, apex obtuse, acute, rarely retuse or acuminate, often mucronate, base cuneate, rarely obtuse, margin sometimes slightly crenate, glabrous, ciliate, or glandular-ciliate, sometimes revolute, both surfaces and midvein glabrous, tomentose, hispid or glandular-hispid; petiole slightly flattened in cross-section, (1-)3-12 mm long and 0.7-2.1 mm diam., glabrous, tomentose, hispid or glandular-hispid.

Inflorescence terminal, axillary, or commonly both, racemose, 5-14(-25)-flowered; rachis (0.5-)1.8-18 cm long and (0.7-)1-3.3 mm diam., brown, tan, maroon or orangish-brown, glabrous, tomentose, hispid or glandular-hispid; floral bracts narrowly elliptic to lanceolate or oblanceolate, flat, (0.9-)1.8-15(-30) x (0.4-)0.6-3.6(-8.4) mm, apex acute to obtuse, sometimes acuminate, base cuneate or truncate, margin glabrous, ciliolate, ciliate, or glandular-ciliate, sometimes revolute, both surfaces and midvein glabrous, tomentose, hispid or glandular-hispid; pedicels ascending or divergent, (3-)9-45 mm long and (0.4-)0.6-1.2 mm diam., glabrous, tomentose, hispid or glandular-hispid; bracteoles usually inserted in basal ½ of pedicel, narrowly oblong, lanceolate, or narrowly elliptic, flat, (0.8-)1.3-3.8(-5.2) x 0.2-1(-1.5) mm, apex acute to acuminate, sometimes obtuse, base cuneate or truncate, margin glabrous, ciliolate, ciliate, or glandular-ciliate, sometimes revolute or involute, both surfaces glabrous, tomentose, hispid or glandular-hispid. Flowers (5-)7(-11)-merous; calyx 2.6-6.1 mm long and 4-11 mm diam.; tube 0.5-3 mm long and 2.5-5.6 mm diam., brown, red, green, tan, or orangish-brown, glabrous, tomentose, hispid or glandular-hispid; lobes ovate to depressed ovate, (0.8-)1.4-3.7(-4.6) x 1.2-3.5(-4.7) mm, longest lobe (0.9-)2.3-3.7(-4.6), apex obtuse to acute, often mucronate, margin entire, erose, or dentate, ciliolate, ciliate, or glandular-ciliate, abaxial surface glabrous, tomentose, hispid, or glandular-hispid; corolla bell-shaped, spreading, or narrowly funnel-shaped (distally spreading); petals spreading or imbricate, oblanceolate, rarely elliptic, pink to white, sometimes red, (8.5-)12-27.5(-45) x 2.4-8.8 mm, apex obtuse, base cuneate, margin entire or undulate, glabrous, lamina sometimes distally tomentose; stamens subequal to corolla or slightly exserted (very rarely more than 1.2x length of petals), (9-)13-27(-43) mm long; filaments (0.2-)0.4-1.4 mm diam., tomentose, very rarely glabrous; anther 1.2-2.9(-3.9) mm long and 0.5-1.6(-2) mm diam., glabrous or proximally tomentose; ovary glabrous or rarely pilose; style subequal to corolla or exserted, 6.7-39(-49.5) mm long and 0.4-1.3 mm diam.; stigma capitate or 7-lobed, 0.6-1.9 mm long and 0.7-3.5 mm diam. _Capsule_ depressed obloid, 4-8 mm long and 6.2-15 mm diam., brown, valves not separating from pericarp; seeds oblong, 1.2-2 mm long and 0.3-0.6 mm diam.

Distribution. (Fig. 27). _Bejaria_ _aestuans_ has the broadest distribution of all the _Bejaria_ species. It ranges from S Durango, Mexico to S Bolivia and across the Coastal Cordillera of Venezuela to Sucre State, Venezuela. It is infrequent in Central America and apparently absent from N Ecuador. Within this broad distribution _B._ _aestuans_ grows in a wide range of habitats from the pine woods and cloud forest of Mexico and Central America to the cloud forests, dry montane forest, shrub paramos, grasslands and roadsides of South America. It grows at (300-)1000-3000(-3500) m alt. where it flowers and bears fruit throughout the year.

Representative specimens examined. MEXICO. Chiapas: Mt. Ovando, 1250-2370 m, Jul 1938, *Matuda* *2589* (A-2 sheets, DUD, K, LL, MEXU, MICH-2 sheets, NA, NY, UC, US-3 sheets); mts. E of Fenix, May-Jun 1925 (fl), *Purpus* *10285* (B, G, G-DEL, LE, M, NY, UC). Durango: Los Corrallitos, 2090 m, 27 Nov 1970 (fl), *Soule* *2198* (MO). Guerrero: 36 km NE of Pueblo El Gallo, rd. to Filo del Caballo, 2150-2350 m, 13 Nov 1973 (fl), *Breedlove* *36165* (CAS, DUKE, MEXU, MICH, MO); Dist. Mina, Laguna, 2050 m, 12 Jan 1936 (fl), *Hinton* *9935* (A, BM, F, G-DEL, K, LL, MO, NY, US); Dist. Galeana, Pie de la Cuesta-Toro Muerto, 2600 m, 21 Jan 1938, *Hinton* *11221* (K, NY); 14 km W of Mazarlan, 5 Dec 1942, *Martínez* *s.n.* (F, NY-2 sheets, US); Dist. Mina, Petlacala, 1880 m, 15 Dec 1937 (fl), *Mexía* *8956* (BH, CAS, F, G-2 sheets, G-DEL, GH, K, LL, MO, NY, U, UC, US); Mpio. Chichihualco, Cruz de Ocote, 25 km WSW of Camotla, 2000 m, 3 Dec 1963 (fl), *Rzedowski* *18090* (DUD, MEXU, MICH, MSC, TEX). Hildalgo: trail to Nohoalco, ca. 4 mi. from Zacualtipân, nr. Tianguistengo, 1880 m, 19 Mar 1947, *Moore* *2318* (BH-2 sheets, BM, GH, MICH, UC); Cerro de Tutotepec, 1790 m, 19 Mar 1946, *Sharp* *46194* (GH, MEXU).

Jalisco: summit rd. to Talpa de Allende, from rd. to Mascota, 1610 m, 27 Nov 1968 (fl), *Boutin & Brandt 2595* (CAS, MEXU); Mpio. Ayutla, La Platanillera, 11 km SW of La Iglesias, 1850 m, 25 Jan 1979 (fl), *Guízar & Niembro 1850* (MEXU); Sierra de la Campana, rd. to Mascota, 7-8 mi NW of Los Volcanes, 1900-2000 m, 23-25 Oct 1952 (fl), *McVaugh 13799* (MICH-2 sheets); mts. nr Guadalajara, 24 Sep 1891 (fl, fr), *Pringle 5339* (MEXU); Cerro "La Piedrera", 9 km W of Tesistán, 1700 m, 20 Jan 1974, *Villarreal 5936* (MICH). Nayarit: Mpio. Aponeta, 4 mi. E of La Ciénaga, ca. 5 mi. NW of Mesa del Nayar, 29 Jul 1970, *Norris & Taranto 14245* (MEXU, MICH). Oaxaca: Yelagago, Villa Alta, 1700 m, 9 Jun 1961, *Halberg s.n.* (CAS, F, LL, MEXU); Dist. Miahuatlán, Campamento San Mateo, 14 km E of San Jerónimo, 1900 m, 23 Oct 1980 (fl), *R. Hernández M. 5174* (MEXU); Choapán, Jun 1842, *Liebman 8592* (A, C-3 sheets, F, H, HBG, L, MICH, NY, US-3 sheets); Dist. Mixe, nr. San Lucas Camotlán, 1380 m, 5 Mar 1979 (fl), *Lipp 80* (NY); Dist. Choapán, trail Yaveo-Santa María, 900 m, 7 Apr 1938, *Mexía 9276* (BH, CAS, F, G, G-DEL, GH, K, MO, NY, U, UC); Cerro Cuasimulco, nr. San Pedro Yolox, 2700 m, 24 Jun 1939, *Schultes 677* (ECON, GH, NA, NY); Dist. Choapán, nr. Santiago Yaveo, 900 m, 15 May 1939, *Schultes & Reko 939* (ECON, NA, NY). Puebla: nr. Zacapoaxtla, 1850 m, 8 Apr 1971 (fl), *Ern 608* (B); nr. Huauchinango, 1360 m, 24 Mar 1945, *Sharp 45323* (GH, MEXU); Mpio. Hueytamalco, Limonateno, 1000 m, 12 Mar 1970 (fl), *Ventura 1076* (DUD, F, LL, MO, MICH, NY, US). Sinaloa: Mpio. Concordia, Sindicatura Danuco, El Carriso, *González Ortega 319* (MEXU); Sierra de Chabarria, 1921, *González Ortega 4073* (US). Veracruz: Cerro monte de Oro, 300 m, 20 Jun 1972 (fl), *Dorantes et al. 857* (F, GH, MEXU); rd. to Rancho Nuevo, Huayacocotla, 1900 m, 11 Feb 1972 (fr), *R. Hernândez M. 1471* (F, GH, MEXU); below Atzalan, 1670 m, 12 Mar 1946, *Sharp 46151* (GH, MEXU); Mpio. Yecuatla, Paz de Enriquez, 1650 m, 27 Apr 1971, *Ventura 3512* (DUD, MICH, TEX); Mpio. Jalacingo, Ocotepec, 1835 m, 1 Mar 1972, *Ventura 5012* (CAS, MICH, TEX); Mpio. Tlapacoyan, El El Paraíso, 250 m, 12 May 1976 (fl), *Ventura 12779* (CAS, MICH, MEXU, NY).

GUATEMALA. Zacapa: Sierra de Las Minas, along Río Repollal, 2100-2400 m, 12-12 Jan 1942 (fl), *Steyermark 42578* (F, NY, US).

BELIZE. Cayo: Thousand Foot Falls, nr. Pine Ridge, 7 Sep 1972 (fl), *Dwyer & Pippen 10139* (AAU, F-2 sheets); Augustin, Mt. Pine Ridge, 6670 m, 9 Dec 1959 (fl), *Hunt 228* (BM, LL, US).

HONDURAS. Camayagua: nr. El Achote, above Siguatepeque, 1350 m, 13 Jul 1936 (fl), *Yuncker et al. 5823* (F, G-DEL, GH, K, MO, S, U). Cortés: betw. Cofradía & Cusuco, 200-1300 m, 26 May 1956 (bud), *Molina 7295* (F, US). Distrito Central: 48 km NW of Tegucigalpa, 1250 m, 13 Jan 1971 (fl), *Harmon & Fuentes 6374* (MO). El Paraîso: 31 km S of El Zamorano, rd. to Mandaste, 1360 m, 3 Jul

1970 (fl), Davidse & Pohl 2252 (AAU, MO, NY); Manzaragua, rd. SW of Güinope, 1400 m, 2 Jun 1951 (fl), Standley 28504 (BM, F, GH, MO-2 sheets, US); Cerros el Zapotillo, rd. betw. Zamorano & Güinope, 4600 ft, 4 Jul 1962 (fl), Webster et al. 11975 (DUKE, F, GH, LL, MICH, MO, S, U, US). Intibucá: Cascada de Yamaranguila, 1800 m, 7 Apr 1956 (st), Molina 6361 (F, GH, US). Morazán: Montaña Grande, betw. Santa Lucía & Valle de Angeles, 1800 m, 26 Sep 1950 (fl), Molina 3300 (F, GH, US); betw. La Piramide & Zambrano, 1500 m, 21 Jul 1962 (fl), Molina 11022 (F, G, NY, US, W); Lepaterique, 1600 m, 11 Aug 1971 (fl), Molina R. & A. R. Molina 26111 (BM, DUKE, F, NY, US); Tegucigalpa, 936 m, 29 Jul 1945 (fl), J. V. Rodríguez 3160 (F, GH, NY); La Montañita, 1700 m, 25 Aug 1946 (fl), L. O. Williams & Molina 10416 (F-2 sheets, GH, LL, LIL, MEXU, MO, UC, US); nr. Rancho Quemado, San Juancito mts., 1900 m, 24 Aug 1952 (fl), L. O. Williams & R. P. Williams 18595 (DUD, F, GH, US).

EL SALVADOR. Santa Ana: Cerro Montecristo, 1970 m, 2 Jan 1959 (fl), Allen & van Severen 7134 (US).

NICARAGUA. Jinotega: Cerro Zamaria, 1400 m, 5 Jul 1975 (fl), Atwood & Neill 108 (MO).

PANAMA. Chiriquí: Cerro Colorado, 1200-1500 m, 18 Aug 1975 (fl, fr), Mori & Dressler 7833 (DUKE, MO, NY).

COLOMBIA. Antioquia: Guarne, 2280 m, 20 Oct 1976 (fl, fr), Boeke & McElroy 210 (E, MO, NY); Mpio. Santa Rosa de Osos, Llanos de Cuivá, 96 km NW of Medellín, 2700 m, 22

Nov 1978 (fl), Callejas et al. 977 (NY); Mpio. Medellín, Alto de Santa Helena, 25 km E of Medellín, 2800 m, 20 Jun 1980 (fl), Callejas & Balslev 1024 (NY); rd. betw. Robles & Guadalupe, 1700 m, 13 May 1944 (fl, fr), Core 694 (NY, US); Alto de La Paloma, E of Sonsón, 2425-2475 m, 25 May 1944 (fl), Core 765 (NY, US); Angostura, 2100 m, 12 Mar 1944 (fl), Fosberg 21622 (NY, S, UC, US); Las Palmas, rd. to Retiro, 2500 m, 27 May 1948 (fl), Gutiérrez V. et al. 5 (US); 3 km W of Boquerón pass, 2200 m, 15 Aug 1955 (fl), Hatheway 1552 (B); Yolombó, 1500-2000 m, Lehmann 7893 (F, K); Medellín-Ríonegro, 2 km W of Santa Elena, 2440 m, 21 Mar 1979 (fl), Luteyn et al. 7014 (COL, NY); Primavera, 1800-2200 m, 22 Sep 1922 (fl), Pennell 10965 (NY). Boyacá: rd. Guateque-Santa María, betw. Santa María and Piedra Campana, 800-1200 m, 10-12 Mar 1960 (fl), García-Barriga 17234 (COL, NY, US); Laguna-Bachira path, 2400 m, 19 Aug 1957 (fl), Grubb et al. 611 (COL, K, US); Santuario de Iguaque, Cañon de Mamarramos, 12 km N of Villa de Leyva, 2980 m, 28 May 1980 (fl), Melampy 938 (NY). Cundinamarca: rd. Mundo Nuevo, 16 km E of La Calera, 4 km on side rd. to La Capilla, 2600 m, 28 Feb 1972 (fl), A. S. Barclay et al. 3210 (COL, US); El Peñon, Hda. "Curiche", betw. Bungue and Murca rivers, 1050-1420 m, 1-3 Aug 1947 (fl), García-Barriga 12455 (COL, US); Fosca-Une, 2100-2430 m, 14 Jul 1962 (fl), García-Barriga 17480 (AAU, COL, US); Quebrada Santa Rosa, Río Blanco Valley, 9 km E of Gutiérrez, 1725 m, 29 Jul 1944 (fl), *Grant 9750* (NY, US, WIS); Zipaquirá & Pacho, 1944, *Huertas & Camargo 1077* (US); Gama, 2400 m, 1 Oct 1965 (fl), *Lombo s.n.* (NY). Magdalena: Cerro Chinchicua, 2600 m, Dec 1944 (fl), *Bro. Apolinar Angel 714* (US); Intendencia Guajira, betw. Pueblo Viejo and Páramo de Macotama, 2140-2600 m, 11 Feb 1959 (fl), *H. Barclay & P. Juajibioy 6881* (COL, MO, US); Sierra Nevada de Santa Marta, Río Donachuí valley, above Cancurúa, 2000 m, 11 Oct 1959 (fl, fr), *Cuatrecasas & Romero-Castañeda 24747* (COL, US); Sierra de Perijá, E of Manaure, Quebrada de Floridablanca, 2700-2800 m, 10 Nov 1959 (fl), *Cuatrecasas & Romero-Castañeda 25166* (COL, US); Sierra Nevada de Santa Marta, betw. Pueblo Bello and San Sebastián, 1360 m, 16 Aug 1946 (fl), *Foster & E. Smith 1506* (A, COL); Cerro Quemado, 2800 m, 1932, *Giacometto 104* (NY, US); Sierra del Líbano, 1970 m, 27 Feb 1898-1899, *H. H. Smith 1406* (A, BM, BR, E, F, G-DC, G-DEL, L, MICH, MO, NY, S, U, US, WIS); Río Yebosimeina valley, 3500-4000 m, 26 May 1977 (fl), *S. White & W. S. Alverson 604* (COL, NY, WIS). Norte de Santander: Páramo de Fontibón, 2600-2750 m, 15 Oct 1941, *Cuatrecasas et al. 12272* (BM, GH, U, US); nr. Sarare, Río Margua valley, betw. Junín and Córdoba, 920-1240 m, 22 Nov 1941 (fl), *Cuatrecasas 13384* (COL, F, US); Mpio. Chitagá, Chucarima, mouth of Río Colorado, 1940 m, 14 Nov 1943 (fl), *Fosberg 19093* (NY, US); Abrego-La María rd., 1500-2150 m, 22-23 May 1969 (fl), *Gárcia-Barriga & R. Jaramillo M. 19922* (COL, NY, US); Jurisdicciones, Cerro de Oroque, 3000-3900 m, 22-27 Jul

1974 (fl), *Gárcia-Barriga & R. Jaramillo M. 20739* (AAU, COL, L, NY, US); Pamplona, 2710 m, Apr 1843 (fl), *Linden 1363* (G, G-BOISS, MPU); Ocaña, Aspasica, 1212 m, Mar 1846-1853 (fl), *Schlim 504* (BM, BR, CGE, G, G-BOISS-2 sheets, G-DC-2 sheets, K, frag. F); Ocaña, 1212 m, Apr 1846-1852 (fl), *Schlim 523* (BM, BR, CGE, G-BOIS, G-DC, K, frag. F). Santander: Lebrija, 300 m, 28 Aug 1948 (fl), *Araque 385* (US); Lago Cachirí, 20 Jul 1965 (fl), *Barkley & Montoya 35299* (COL, GH-2 sheets, NY); Mpio. Charlá, El Taladro path, 50-55 km Duitama-Virolín rd., 2250-2300 m, 6 Dec 1978 (fl), *S. Díaz P. 1622* (COL, NY); above "La Victoria", Quebrada Chiriviti, W of Galén, 2575 m, 5 Sep 1944 (fl), *Fasset 25696* (NY, US); Piedecuesta, 2120-2425 m, Jan 1847 (fl), *Funck & Schlim 1332* (BM, CGE, G, G-BOIS-2 sheets, G-DC, K, LD, MPU-2 sheets, OXF, W, frag. F); Matanza and La Baja, 2120 m, Jan 1847 (fl), *Funck & Schlim 1639* (BR, G, MPU-2 sheets); Río Umpalá, nr. Pescadero, Los Curos, 1200 m, 16 May 1969, *Gárcia-Barriga & R. Jaramillo M. 19654* (COL-2 sheets, L, NY); W slopes, Páramo Rico, 3000-3600 m, 15-19 Jan 1927 (fl), *Killip & Smith 17217* (A, NY, US); nr. Charta, 2000 m, 1-11 Feb 1927 (st), *Killip & Smith 18880* (A, GH, NY, US); nr. El Pórtico, rd. betw. Aratoca and San Gil, 2000 m, 25 Jul 1953 (fl), *Langenheim 3350* (COL, MICH, UC, US-2 sheets); Socorro, Piedecuesta, 1550 m, Nov 1842 (fl), *Linden 766* (BM, F, G, G-BOIS, G-DC, GENT, K, MPU, W-2 sheets); rd. above Río Chicamocha, 60 km NNE of Barbosa, 1700 m, 9 May

1979 (fl), *Luteyn et al. 7614* (COL, NY); *7616* (COL, NY); *7618* (COL, NY); Bucaramanga, 1515 m, May 1948 (fl), *Sandeman 5993* (BM, K, OXF, US). Tolima: El Carmen, Santa Rosa, 500 m, *Lehmann 7526* (F, K-2 sheets). Valle: Salasito, 1900 m, Jul 1930 (fl), *Dryander 346* (US).

VENEZUELA. Anzoátegui: Cerro Peonia, above Santa Cruz, 1800-2000 m, 20 Mar 1945 (fl), *Steyermark 61641* (A, F, NY, US, VEN). Aragua: Colonia Tovar, 1800-2000 m, Dec 1924 (fl), *Allart 329* (A, NY, US, VEN); La Mesa-Trayecto Guamitas, 20 Mar 1951 (fl), *Aristeguieta & Saldivia 560* (VEN); Pico Guacamaya, Parque Nacional Henri Pittier, 7 Oct 1975 (fl), *Wood 306* (NY, VEN). Carabobo: Dtto. Guacara, Hda. Los Aguacates, 800 m, 22 Nov 1980 (fr), *Benitez de Rojas 2868* (NY). Distrito Federal: Pico Avila-Lagunazo trail, 1990-2225 m, Oct 1982 (st), *Clemants 2482* (NY, VEN); nr. Colonia Tovar, 1515-1820 m, 1854-1855 (fl, fr), *Fendler 743* (F, G-BOIS, G-DC, GH, GENT, MO); Galipán, 1270 m, Jan 1846, *Funck & Schlim 159* (BM, G, G-BOIS, LD); *Linden 12* (BM, CGE, G, G-BOIS, G-DC, LG, OXF, W-2 sheets, frag. F); Caracas, Jul-Aug, *Moritz 478* (BM, G-BOIS, G-DC, HBG-2 sheets); headwaters Chichiriviche and Petaquire rivers, 1800-2000 m, 4 Sep 1918 (fl), *Pittier 8133* (US); Cerro Naiguatá, Las Delicias, 1500-1635 m, 15-19 Nov 1963 (fl), *Steyermark 92024* (NY, VEN); Agua Negra, 1400 m, 4 Jan 1940 (fl, fr), *Ll. Williams 12349* (A, F-2 sheets). Guarico: Cerro Platillón, SE of San Juan de Los Morros, 19 Oct 1967 (fl), *Rivero & Esteves s.n.* (VEN).

Lara: Las Sabanetas, above Los Aposentos, W of Humocaro Bajo, 2530 m, 5 Feb 1944 (fl), Steyermark 55302 (A, F, VEN). Lara-Falcón: rd. El Silencio-Portéria, 0-10 km SSW of La Portéria, 560-1360 m, 28 Jun 1979 (fl), Liesner et al. 8312 (NY); Cerro Socopó, 1400-1560 m, 29 Jun 1979 (fl), Liesner et al. 8406 (NY). Mérida: rd. Santa Cruz de Mora-El Molino, before San Isidro Alto, 2300-2400 m, 22 Dec 1972, Badillo 5802 (F, MY); Páramo Mucuchíes, 3640 m, 1922, de Bellard 51 (US); La Carbonero, 2200 m, 20 Mar 1948 (fr), Buza 12 (COL, F, NY, UC); Mpio. La Trampa, summit of rd. to La Trampa, 2270 m, Sep 1982 (fl), Clemants & Dugarte 2415 (MERF, NY, VEN); La Mucuy valley, SE of Tabay, 12 Sep 1982 (fl), Clemants & Díaz 2420 (MERF, NY, VEN); Páramo La Negra, km 599, 14 Sep 1982 (fl), Clemants & Dugarte 2428 (MERF, NY, VEN); Bailadores-Pregonero rd., 5-10 km from La Grita turnoff, 2940-2970 m, 14 Sep 1982 (fl), Clemants & Dugarte 2434 (MERF, NY, VEN); rd. to San José, above Río Chama valley, 2270 m, 17 Sep 1982 (fl), Clemants & Dugarte 2441 (MERF, NY, VEN), 2515-2545 m, Clemants & Dugarte 2443 (MERF, NY, VEN); Páramo de San José, above San José, 17 Sep 1982 (fl), Clemants & Dugarte 2445 (MERF, NY, VEN); Mérida, 1820-1970 m, 1846, Funck & Schlim 874 (BM, G, G-DC, G-BOIS, GH, LD, W, frag. F); Sierra Nevada, 2425 m, Jun 1847 (fl, fr), Funck & Schlim 1600 (BM, BR, G, LD, OXF, W); Funck & Schlim 1604 (G, LD); Tabay, 1800-2000 m, 28 Aug 1930 (fl), Gehriger 363 (A, F, G-DEL, MO, NY, US, VEN); Páramo del Tambor, 2850 m, 25 Aug 1938 (fl), *Hanbury-Tracy* *69* (K, US); Páramo de Pueblo Nuevo, 2000 m, 8 Oct 1921 (fl), *Jahn* *716* (US); Bailadores-La Grita, La Granzonera region, 31 km S of Bailadores, 3050 m, 26 Jan 1978 (fl), *Luteyn* *et* *al.* *5254* (NY); rd. to El Delgadito, 22 km S of Bailadores, 2700 m, 26 Jan 1978 (fl), *Luteyn* *et* *al.* *5270* (NY); Páramo La Negra, 1 km above Portachuelo, 1 Feb 1978 (fl), *Luteyn* *et* *al.* *5386* (NY); Tustas area, Estanques-Páramo del Molino, 32 km S of Estanques, 2550 m, 3 Feb 1978 (fl, fr), *Luteyn* *et* *al.* *5400* (NY); Los Aserruchos, Estanques-Páramo del Molino rd, 49 km S of Estanques, 3 Feb 1978 (fl), *Luteyn* *5411* (NY); nr. La Trampa, 2000 m, 28 Oct 1978 (fl), *Luteyn* *et* *al.* *6065* (NY), *6066* (NY); Los Lagunetas, 18 Nov 1845, *Moritz* *1351* (BM, BR-2 sheets, CAS, CGE, G-BOIS, GH, HBG-2 sheets, K-2 sheets, L, W); Dto. Sucre, Mpio. Estanques, Alto de Las Cruces, Páramo de Quirorá, 3200 m, 23 Apr 1971 (fr), *Rúiz-Terán* *&* *López-Figueiras* *1769* (L, NY); Dtto. Campo Elías, nr. San José, quebrada El Burro, 2300-2500 m, 19 Dec 1971 (fl), *Rúiz-Terán* *&* *López-Palacios* *6590* (NY); Dto. Libertador, Quebrada Los Muchachos, betw. El Toro peak and Los Nevados, 3100 m, 22 Jun 1972 (fl), *Rúiz-Terán* *6859* (NY); Dto. Campo Elías, betw. Pozo Negro and Las Quebraditas, Sierra de La Culata, 3300-2100 m, 30 Oct 1972 (bud), *Rúiz-Terán* *8039* (NY); Dto. Libertador, Páramo de Don Pedro, 20-33 km ESE of El Morro, 2850-3300 m, *Rúiz-Terán* *&* *López-Figueiras* *8638* (NY); Dto. Libertador, Filo de La Vagabunda, betw. El Milago and El Portachuelo, rd. El Morro-Aricagua, 2450-2850 m, 10 Oct 1973, Rúiz-Terán & López Figueiras 9349 (NY); Dto. Libertador, Páramo de Mocaz, 15 km NE of El Morro, 2800-3100 m, 13 Oct 1973 (fl), Rúiz-Terán 9530 (NY); Dto. Miranda, El Chorrerón-Gañada del Ahorcado, 2560-2750 m, 30 May 1975 Rúiz-Terán & Dugarte 12511 (NY); Río Albarregas, Monte Serpa, 5-10 km NE of Mérida, 1675-2135 m, 18 Apr 1944, Steyermark 55935 (A, F, VEN). Miranda: Los Guayabitos, nr. Barrita, 1350 m, Apr 1958 (fl), Aristeguieta 3034 (VEN); Silla de Caracas, betw. Quebrada Los Palos Grandes & Quebrada Pajaritos, 1200-1300 m, 17 Oct 1971 (fr), Morillo & Manara 1722 (NY, VEN); betw. Antímano and Aguas Negras, 900-1500 m, 6-7 Apr 1913 (fl), Pittier 6025 (NY, US); El Cedral de las Ajuntos, nr. Los Teques, 1000-1800 m, 26-28 Apr 1913 (fl), Pittier 6114 (NY, US). Mongas: nr. La Cuchilla, betw. Guanaguana and Guácharo, 1200-1480 m, 21 Apr 1945 (fr), Steyermark 62248 (A, F, VEN). Sucre: Cumaná, 4000 m, Jul 1842 (fl), Funck 85 (G-BOIS, K, LD, OXF, W); Cerro Turumiquire, 2300 m, 8 May 1945 (fl), Steyermark 62679 (A, F, NY, US). Táchira: nr. Palo Grande, 1450 m, 16 Feb 1939 (fl), Alston 7088 (BM, L, NY, S, U, US, USF); rd. San Cristóbal-Táriba-San José de Bolívar, betw. Zumbador & San Isidro, 9 Oct 1967 (fl), Bunting 2549 (MY, VEN); Páramo La Negra, 3015 m, 14 Sep 1982 (fl), Clemants & Dugarte 2427 (MERF, NY, VEN), 2428 (MERF, NY, VEN), 2429 (MERF, NY, VEN); Páramo de Zumbador, El Cobre-San Cristóbal rd., 2640 m, 19 Sep 1982 (fl), *Clemants & Díaz 2447* (MERF, NY, VEN); Hwy 9, 37 km S of Rubio, 6 km N of Delicias, 2000 m, 28 Jan 1978 (fl, fr), *Luteyn et al. 5296* (NY); below Páramo de Zumbador, Zumbador-Quenique rd., 3 km SE of Zumbador, 31 Jan 1978 (fl), *Luteyn et al. 5372* (NY); Zumbador-Michelena rd., 11 km NW of Zumbador, 2750 m, 31 Jan 1978 (fl, fr), *Luteyn et al. 5377* (NY); Dto. Uribante, Ramal betw. Pregonero and Guaraque, 1340-1750 m, 24 Jun 1978, *Rúiz-Terán & Dugarte 15477* (NY); Dto. Jáuregui, Páramo de Duque, 5 km S of El Cedrillo, 3260 m, 6 Oct 1978 (fl), *Rúiz-Terán & Dugarte 15790* (NY); Cerro Las Minas, 18-20 km SE of Santa Ana, 1150-1250 m, 10 Nov 1979 (fl), *Steyermark et al. 119841* (NY); Sierra El Casadero, 13 km N of Rubio, betw. Las Dantes & Las Adjuntas, 12 Nov 1979 (fl), *Steyermark et al. 120065* (NY, VEN). Trujillo: nr. Jajó, toward La Morita, 2400 m, Aug 1958 (fl), *Aristegieta 3404* (US, VEN); betw. Valera and Monte Carmela, 535-1830 m, Aug 1923 (fl), *de Bellard s.n.* (US); Dto. Carache, La Gran Parada, 3 Sep 1975 (fl), *Benitez de Rojas 1910* (MO, MY, VEN); Las Mesa de Esnujaque, 2100 m, 14 Mar 1947 (fl), *Box & Alayon V. 3714* (VEN); Cerro de Baño, NE of Motatarí, 27 Oct 1927, *Christ 67* (NY, VEN); Páramo de Las Rosas, 2800 m, 1 Oct 1912 (fl), *Jahn 109* (US); Santana, 1600 m, 16 Jan 1922 (fl), *Jahn 763* (GH, NY, US, VEN); nr. Escuque, betw. Escuque and La Mesa de San Pedro, 1300-1650 m, 20-23 Feb 1971 (fl), *Steyermark 104631* (L, MO, NY, US); betw. Las

Peña and Agua de Obispo, 28-34 km from Carache, 2100-2400 m, 28 Feb 1971 (fl), Steyermark 104968 (L, VEN). Yaracuy: Sierra de Aroa, 9 km W of San Felipe, 900-1500 m, 5 Apr 1980 (fl), Liesner & González 10081 (NY, VEN). Zulia: Campamento Frontera VI, betw. headwaters Río del Norte & S most branch Río Aricaisa, 2400 m, 23-28 Jul 1974 (fl), Berry 131 (MO, NY, VEN-2 sheets); Sierra de Perija, nr. quebrada of Río Omira-kuná (Tumuriasa), nr. border, 1500-1800 m, 27 Mar 1972 (fl, fr), Steyermark et al. 105708 (F, L, NY, U, US, VEN); Campamento Frontera V, headwaters Río Guasare, 3200 m, 20-23 Jul 1974 (fl), C. W. Wood & Berry 73 (NY, VEN-2 sheets).

ECUADOR. El Oro: betw. Curtincapa and Guagra Uma, 8 mi. NE of Curtincapa, 1500-2895 m, 16 Aug 1943 (fl), Steyermark 53872 (F, K, NY, US). Loja: Pan Am Hwy, 5 km W of Loja, 2300 m, 1 Jan 1981 (bud), Balslev 1335 (AAU, NY); Cerro Villanaco, 2151 m, 15 Jan 1981 (fl), Clemants & Luteyn 1668 (NY), 1670 (NY), 2420 m, 17 Jan 1981 (fl), Clemants & Luteyn 1677 (NY), 2610 m, Clemants & Luteyn 1679 (NY), 31 Jul 1982 (bud), Clemants 2275 (NY, QCA); 176 km E of Loja, rd. to Zamora, 2730 m, 15 Jan 1981 (fl), Clemants & Luteyn 1671 (NY); Nudo de Sabanilla, 13 km S of Yangana, 2210 m, 16 Jan 1981 (fl), Clemants & Luteyn 1672 (NY); 15 km S of Yangana, 2420 m, 16 Jan 1981 (fl), Clemants & Luteyn 1673 (NY), 1674 (NY); S side of Nudo de Huagrauma, 13 km S of Saraguro, 2940 m, 18 Jan 1981 (fl), Clemants & Luteyn 1681 (NY); 12 km S of Saraguro, 2970 m, *Clemants* & *Luteyn* *1682* (NY); N side of Nudo de Huagrauma, 8 km S of Saraguro, 3060 m, 18 Jan 1981 (fl), *Clemants* & *Luteyn* *1684* (NY); Páramo de Saraguro, 19 km N of Saraguro, 2910 m, 18 Jan 1981 (fl), *Clemants* & *Luteyn* *1687* (NY); 6.6 km E of Loja, rd. to Zamora, 2210 m, 17 Aug 1982 (fl), *Clemants* *2345* (NY, QCA); rd. Loja-Zamora, km 9, 2500-2750 m, 31 Dec 1978 (fl), *Luteyn et al. 6549* (NY). Morono-Santiago: Los Tayos, Serra do Condor ridge, 1500 m, 22 Jul 1979 (fl, fr), *Argent* & *Burbidge* *261* (E, L, NY). Zamora-Chinchipe: along Inca trail, Loja-Zamora, 2800-2360 m, 3 Aug 1982 (bud), *Clemants* *2295* (NY, QCA); km 42, rd. to Zamora, 1400 m, 29 Sep 1961 (fl), *Dodson* & *Thien* *844* (MO, WIS).

PERU. Amazonas: ca. 2 km S of Rodríguez de Mendoza, 1730 m, *Clemants* & *Fernandez* *2019* (NY, USM); Yambrasbamba, 1835, *Mathews* *1427* (CGE, E-2 sheets, K); Prov. Chachapoyas, betw. Molinopampa and Rodríguez de Mendoza, 10 km E of Molinopampa, 2400 m, 23 Feb 1977 (fl), *Wasshausen* & *Encarnación* *1006* (NY, US); Prov. Bongará, 3 km S of Pomacocha, E of Shipasbamba, 2400 m, 20 Jun 1962 (fl), *Wurdack* *972* (F, L, NY, US). Ayacucho: 50-54 km NNE of Tambo, 2220-2560 m, 3 Dec 1978 (fl), *Luteyn* & *Lebrón-Luteyn* *6366* (NY). Cajamarca: Prov. Chota, Huambos, 2000 m, 10 Sep 1956, *Soukup* *4490* (US). Cuzco: Prov. Urubamba, Hda. Santa Rita, Aug 1941 (bud), *Dreyfus* *s.n.* (NY); Prov. Urubamba, Machu Picchu mt., 2500-2800 m, 3 Jan 1963, *Iltis et al.* *1081* (CM, DUD, K, MSC, U, WIS-2 sheets); Vilcabamba, Hda. on Río Chinchao, 1820 m, 17-26 Jul 1923 (fr), Macbride 4992 (F); Prov. Quispicanchis, Marcapata valley, 1900 m, 20 Feb 1929 (fl), Weberbauer 7837 (F, GH, NY, U, US, WIS). Huánuco: Prov. Huánuco, Mitotambo, above Mitu, 3000-3100 m, 3 Feb 1950 (fl), Ferreyra 6670 (F, US, USM); Acomayo, betw. Huánuco and Tingo María, 2600-2650 m, 3 Oct 1950 (fl), Ferreyra 8187 (US, USM); Carpiscillo, Tingo María, 1820 m, Jun 1938 (fl), Sandeman 155 (OXF); Chaglia, 6 Mar 1959, Woytkowski 5186 (F, MO); Pillao, 2700 m, 12 Feb 1946, Woytkowski et al 34021 (F, LIL, UC). Junín: Prov. Tarma, nr. Huacapistana, betw. Tarma and San Ramón, 1800-2100 m, 25 Jun 1948 (fl), Ferreyra 3593 (F, LIL, NY, US, USM); Colonia Perene, 680 m, 14-25 Jun 1929, Killip & Smith 24978 (F, NY, US); ca. 60 km E of Tarma, rd. to San Ramón, ca. 11 km below rd. to Huasahuasi, 2000 m, 14 May 1982 (fl), Landrum 4587 (NY); below Tarma, toward Carpapata, rd. to the Chamchamayo valley, 2500 m, Mar 1947, Ochoa 79 (NY, US); rd. Quimire, S of Junín, 900 m, 5 Nov 1962 (fr), J. Schunke V. 6224 (F, US); Yunguy, 1600 m, 14 Jul 1961 (fl), Woytkowski 6577 (GH, MO, US). La Libertad: Prov. Bolívar, Cajamarquilla, 3000 m, 12 Sep 1946 (fl), Infantes V. 3989 (LILLO). San Martín: Prov. Lamas, Ditto. Lamas, trail Lamas-San Antonio, E of Río Chupiseña, 1 Oct 1937 (fr), Belshaw 3494 (BH, DUKE, F, GH, LL, MICH, MO, NY, U, UC, US, WIS); Jepelacio, nr. Moyobamba, 1200-1600 m, Mar 1934 (fl), Klug 3610 (A, F, G-DEL, GH, MO, NY, S, US);

Pasco; Prov. Oxapampa, San Luis, Oxapampa, 1850 m, 20 Sep 1948 (fl), Infantes Vera 1506 (NY). Piura: Prov. Huancabamba, Ditto. Sondor, below Cerro La Viuda, 2170 m, 21 Jul 1975 (fl, fr), Sagástegui A. et al. 8204 (AAU, MO, NY). Puno: Prov. Sandia, nr. Santo Domingo, 1550 m, 2 Mar 1940 (fl), McCarroll 116 (NY); Prov. Sandia, nr. Limbani, 3200-3450 m, 14-16 May 1942, Metcalf 30510 (A, G-DEL, UC, US).

BOLIVIA. Cochabamba: nr. Cochabamba, Espíritu Santo, 1891, Bang 1167 (A, BM, C, CM, E, F-2 sheets, G, G-BOIS, GH, K, LD, LV, LY, M, MICH, MO, NY-2 sheets, UPS, US, W). La Paz: Milluhuaya Noryungas, 1500 m, Dec 1917, Buchtien 714 (E, F, G-DEL, GH, LD, MO, NY, US); Hda. Simaco, rd. to Tipuani, 1400 m, Mar 1920, Buchtien 5512 (E, GH, US); Mapiri, 1515 m, May 1886 (fl, fr), Rusby 2010 (BM, E, F, G-BOIS, GH, K, MICH-2 sheets, MO, NY-3 sheets, US-2 sheets, W, WIS); Yungas, Tushuaya-Chulumani, 1740 m, Sep 1947 (fl), Scolnik 517 (NY); nr. Atten, 1820 m, 18 Aug 1902, R. S. Williams 1455 (BM, K, NY, UC, US). Santa Cruz: El Fuerte de Samaipata, 1900 m, Apr 1960 (fl, fr), Cardenas 5859 (NY, US, WIS). Tarija: rd. betw. Rios and Narváez, 1500 m, 9 Nov 1974 (bud), Hildegard Türpe et al. 5141 (NY).

Local names and uses. Mexico: peosle, jara (Guerrero), flor de mayo (Hidalgo), flor blanca (Jalisco), rosa del monte, madroño (Oaxaca), coyopolin (Puebla), madroño del agua (Sinaloa). Guatemala: azajarillo

Fig. 31. Bejaria aestuans. A. Luteyn et al. 5192. B. Without collector or number, photo of specimen on Baldy Mountain, Belize. C. Luteyn et al. 5386. D. Clemants & Díaz 2420. (Fig. A & C by Luteyn, Fig. B by Richard W. Pippen, Fig. D by Clemants).

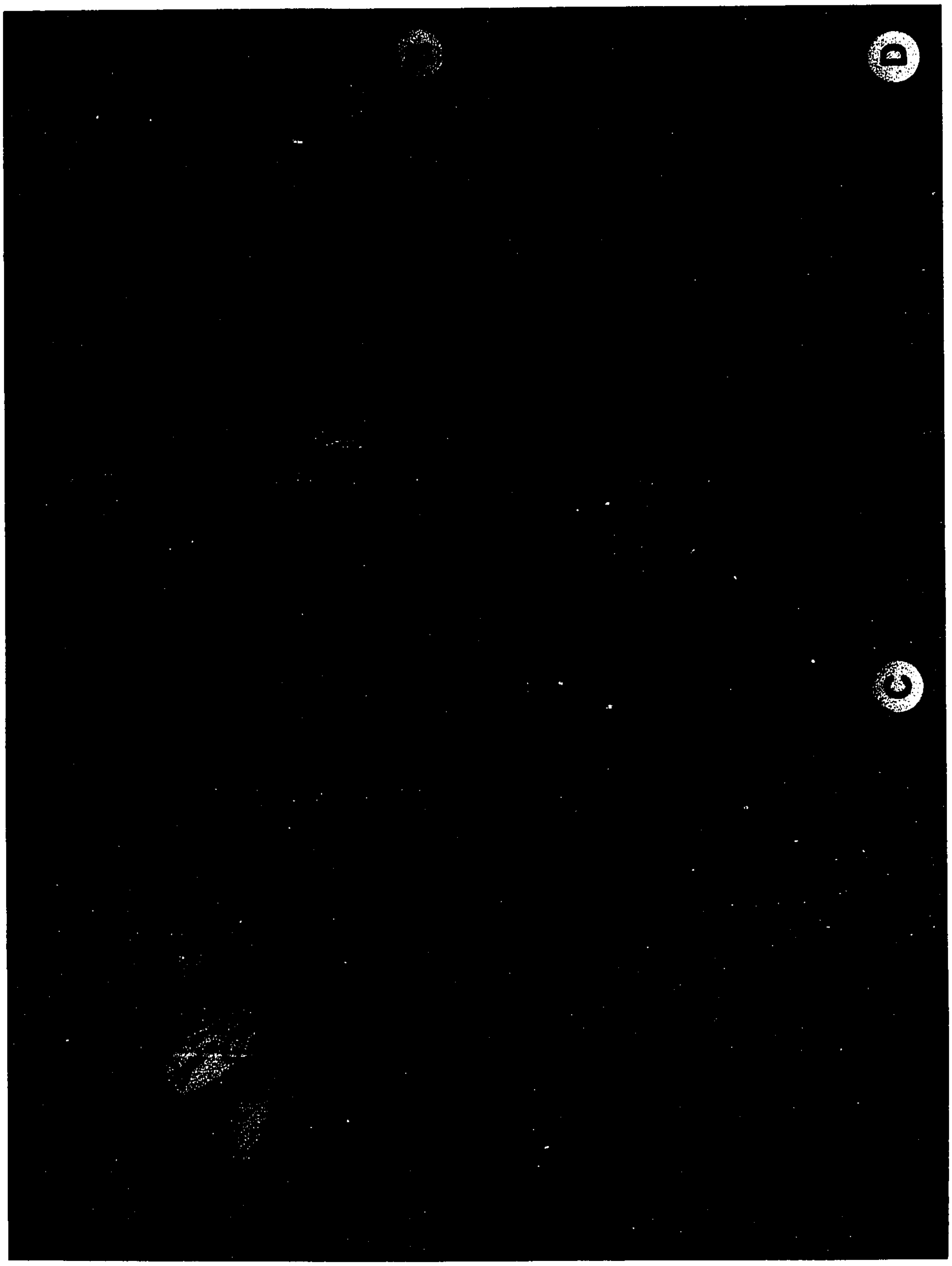
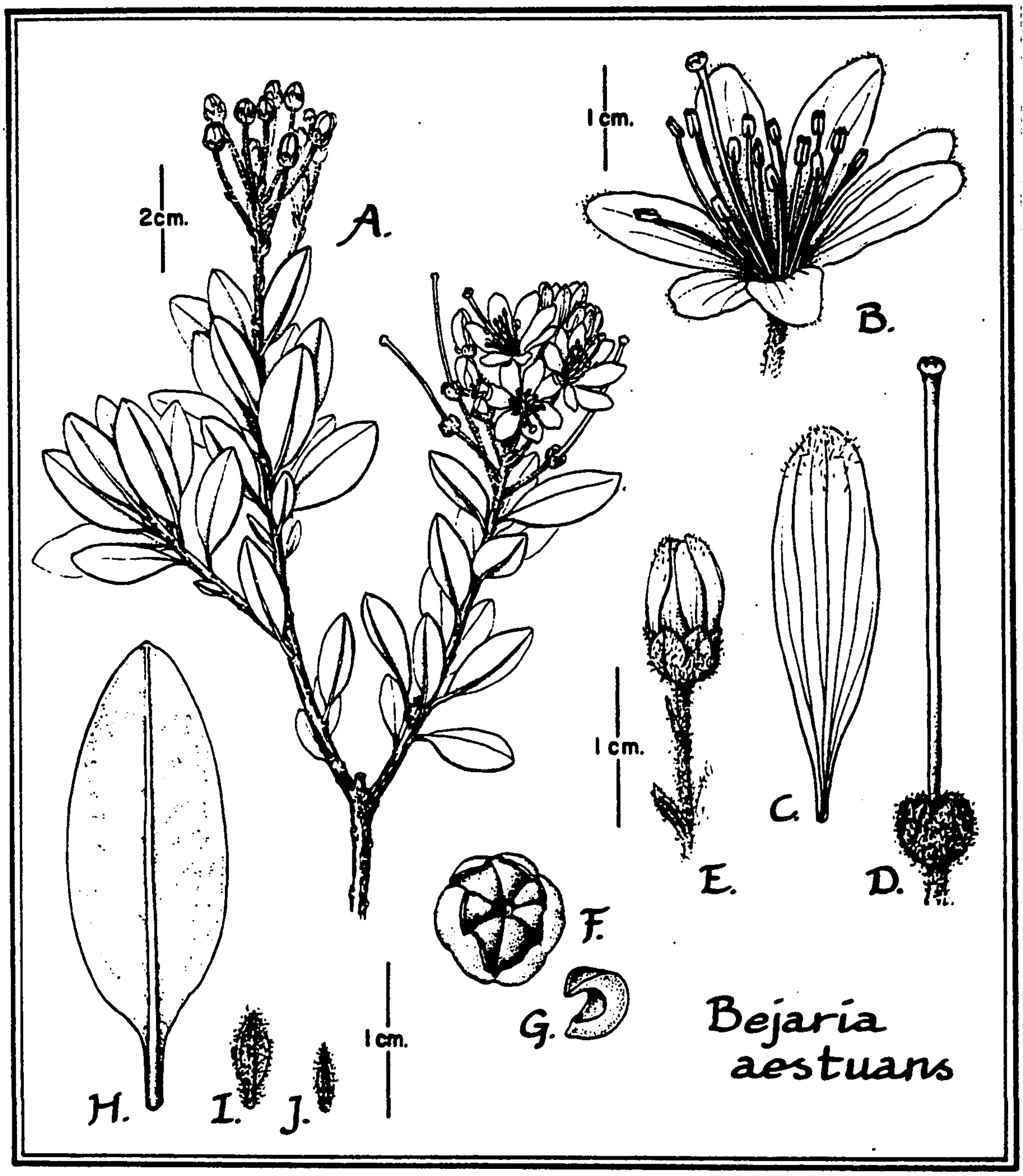


Fig. 32. Drawing of _B_. _aestuans_. A. habit. B. Close-up of flower. C. Petal. D. style. E. Bud. F. Capsule. G. Valve of capsule. H. Leaf. I. Floral Bract. J. Bracteole.


2cm.
A.
1cm.
B.
C.
D.
1cm.
E.
F.
G.
H.
I.
J.
1cm.
Bejaria
aestuans

(Zacapa). Colombia: carbonero, encillo (Antioquia), carbon (Cundinamarca), guinda (Magdalena), clavelito, pegamoscos, pegajosa, pegajoso (Norte de Santander). Venezuela: rosa del Avila (Distrito Federal); paramito clavirosa (Lara); melote, neloso, rose de los Andes, pega-pega, pegosito, pegosita, melotero, curoito, pegasa, flor de María (Mérida); azahar de ángel (Táchira). Ecuador: payama (El Oro). Peru: laurel (Cuzco), andean azalea, palo de acer, and palo acero (Junín), rosa rosa (Huánuco). Bejaria aestuans is used as fuel wood in Mexico, Colombia, and Peru. Woytkowski 6570 (Junin) states "[The] best charcoal [comes] from roots, which are large and thick". The shrub is toxic to cattle in Peru (Junín & Huánuco). In Venezuela it is used to catch flies. Medicinally the crushed leaves are used in Venezuela, (Luteyn et al. 5270) "to heal bone aches". Mexía 4270 (Bolivia) states "[the] fruit [when] eaten produces great discomfort and dizziness, but if [it is] used for some time, [the] person is greatly stimulated".

Bejaria aestuans is a widespread and variable species which is difficult to characterize. It can generally be distinguished by pink or white, spreading or bell-shaped corollas (sometimes red and trumpet-shaped corollas), short calyx lobes (except in some Mexican populations), and long petioles.

Perhaps the most important character of B. aestuans is the floral presentation. The pink spreading or bell-shaped flowers are notably different from the large red tube-shaped flowers of *B. resinosa*, *B. mathewsii*, and *B. ledifolia*, and the small cup-shaped flowers of *B. tachirensis* and *B. nana*. This difference is reflected in pollination. The large tube-shaped flowers are probably hummingbird pollinated (see *B. resinosa* and *B. mathewsii* discussion), whereas the pollinators of *B. tachirensis* and *B. nana* are unknown. The pink spreading or bell-shaped flowers of *B. aestuans* are visited by honey bees (*Apis melifera*) in Ecuador (pers. obs.), and bees (sp. unknown) in Venezuela (pers. obs.). This marked difference in floral type is probably the most important trend in *Bejaria* phylogeny, and probably represents a mechanisim for isolation of species.

Bejaria aestuans represents a large polymorphic species which is probably the ancestor of most of the other species including those with large red tube-shaped flowers (*B. resinosa*, *B. ledifolia*, and *B. mathewsii*), with small cup-shaped flowers (*B. tachirensis* and *B. nana*), with short, subsessile leaves (*B. steyermarkii*, *B. imthurnii*, and *B. neblinensis*), and with large funnel-shaped flowers (*B. infundibula*). Discussion of the differences between *B. aestuans* and these species can be found under the respective species.

Bejaria sprucei is probably the most difficult species to separate from *B. aestuans*. In general, they can be separated by corolla shape (spreading or bell-shaped in *B.*

aestuans vs. tube-shaped in *B. sprucei*), merosity (7-merous in *B. aestuans* vs. 5-7-merous in *B. sprucei*), thickness of the pedicel (0.6-1.2 mm diam. in *B. aestuans* vs. 0.4-0.6 mm diam. in *B. sprucei*), and relative stamen length (less than 1.2x petal length in *B. aestuans* vs. more than 1.6x petal length in *B. sprucei*). The problem is differentiating between the trumpet-shaped populations of *B. aestuans* (from Antioquia and Mérida regions) and *B. sprucei*. Here the corolla shape distinction breaks down, and merosity and pedicel thickness are similar, although relative stamen length is still useful.

Within *B. aestuans* one finds the greatest variation of any *Bejaria* species. But most of the variation is based on hair type (and topography), leaf shape, and to some extent flower size. This variation has resulted in recognition of five species as well as five varieties within *B. glauca* by Mansfeld and Sleumer (all considered synonyms here), and in the recognition by Camp of an additional two species.

Mansfeld and Sleumer (1935) did, however, recognized the similarity between three of their species, *B. laevis*, *B. glauca* (=*B. aestuans*), and *B. discolor*, which they placed in one of their informal groups. These three species differ in leaf shape (*B. laevis* with acuminate leaf apices, *B. discolor* with obtuse leaf apices, *B. glauca* various) and pubescence (*B. laevis* with glabrous pedicels, *B. discolor* with glandular-hispid pedcels, *B.*

glauca with various pedicels). Later, Camp (1941) suggested that *B. laevis* was only a variant of *B. glauca*, and that *B. discolor* represented a collection of hybrid populations (*B. mexicana* x *B. glauca*). The only reason for considering *B. discolor* different from *B. glauca* is the size of the flowers, which are larger than typical *B. glauca*. But connections in flower size between *B. discolor* and *B. glauca* are found in Central America (Guatemala and Honduras) and the distinction therefore breaks down.

Mansfeld and Sleumer (1935), as well as Camp (1941), recognized *B. mexicana*, a large white flowered species in western Mexico. Mansfeld and Sleumer did not place *B. mexicana* in one of their informal groups, but suggested that it was related to *B. glauca* var. *glandulosa* (=*B. aestuans*). Camp suggested that *B. mexicana* was one of the parents of *B. discolor*. *Bejaria mexicana* looks very different with its large white spreading flowers, glandular-hispid abaxial leaf surfaces and small leaves, but *B. discolor* provides a very good intermediate in all characters as do the Central American populations. In addition, populations of *B. mexicana* from Sinaloa and Durango have shorter petals. The overall impression is that *B. mexicana* is the end of a cline starting with the typical *B. aestuans* of South America and passing through *B. discolor*. I do not think *B. discolor* represents a hybrid of recent origin (if at all) because *B. discolor* occurs in eastern Oaxaca, hundreds of kilometers from the nearest populations of *B. mexicana* one of the proposed parents.

Camp named two new species in 1941--*B. hintonii* and *B. guatemalensis*. *Bejaria hintonii* is a very large flowered species with glabrous leaves. It is a slightly larger flowered, glabrous form of the *B. mexicana* part of *B. aestuans* with which it is sympatric. Camp also named *B. guatemalensis* which is simply a hair type variant of *B. aestuans*.

Mansfeld and Sleumer recognized *B. hispid*, a miscellaneous collection of *B. aestuans* and *B. sprucei* specimens, because of the hispid abaxial leaf surfaces. They related *B. hispida* to *B. sprucei*, *B. schomburgkii*, *B. variabilis* (all synonyms of *B. sprucei*) and *B. sandiensis* (a doubious species). But the type is a copiously glandular-hipsid representative of *B. aestuans*.

Five varieties were recognized within *B. glauca* (=*B. aestuans*) by Mansfeld and Sleumer. These varieties were based on hair type (and topography) and racemose vs. corymbose inflorescences. The difficulty in using pubescence as a character is mentioned elsewhere (under *B. sprucei* and *B. resinosa*). In many populations of *B. aestuans* more than one hair type can be found, for instance on Páramo La Negra, Venezuela, I have collected tomentose individuals (*Clemants & Dugarte 2437*), hispid individuals, (*Clemants & Dugarte 2438*), and glandular-hispid individuals (*Clemants & Dugarte 2439*). Only the glandular-hispid individual had any distinguishing characters (trumpet-shaped corolla) and was in slightly more exposed areas. Furthermore in Ecuador on the road to Zamora, I have collected hispid individuals (*Clemants & Luteyn 1671*) at slightly lower elevations than the glandular-hispid individuals (*Clemants 2345*). Again the glandular-hispid individuals were in a more exposed habitat suggesting that the presence of glands is a phenotypic response to desiccation.

Raceomse vs. corymbose inflorescences, which were very important in the classification of Fedchenko and Basilevskaja (1926, 1928), are not found to be very useful within *B. aestuans*. Both racemose and corymbose individuals occur in this species and show no geographic or other morphologic distinctions. Instead, they appear to be different manifestations of the same basic inflorescence type, e.g. a simple raceme.

Although there are distinctly different hair types, this is probably a phenotypic response to the environment as is the inflorescence type. I am therefore lumping all the varieties of *B. glauca* into *B. aestuans* as well as the type of *B. hispida*. Moreover, although the extremes of the Mexican populations are easily recognized, they represent the end points of clines and therefore do not warrant species recognition.

5. **Bejaria zamorae** Clemants, sp. nov. Type. Ecuador. Zamora-Chinchipe: "Oriente", Río Zamora valley, E of Loja, ridge across the river from the village of Zamora, 1970 m, 28 Jun-1 Jul 1944 (fl), *Camp E-28* (holotype, NY; isotype, S).

Bejaria zamorae Clemants; *Bejariae sprucei* affinis sed staminibus non exsertis et floribus heptameris differt, *B. aestuanti* affinis sed corollis tubiformibus et pedicellis tenuibus differt.

Shrub to 5 m tall; older branches slightly fissured, glabrous, bark gray to dark gray; twigs subterete, dark gray or dark brown, glandular-hispid. *Leaves* coriaceous, flat, elliptic to narrowly elliptic, 4.2-7.6 x 1.25-3.1 cm, apex acuminate or cuspidate, base cuneate, rarely obtuse, margin glandular-ciliate, both surfaces and midveins glabrous or adaxial surface and midvein glandular-hispid; petiole subterete, flattened adaxially, 4-7 mm long, 0.9-1.3 mm diam., glandular-hispid. *Inflorescence* a terminal raceme, 9-12-flowered; rachis 2.2-9.2 cm long and 0.8-1.1 mm diam., dark gray or dark brown, glandular-hispid; floral bracts lanceolate, flat, 3-5 x 0.6-0.9 mm, apex acuminate to acute, base cuneate, margin glandular-hispid, sometimes involute, both surfaces glabrous, or abaxial surface glandular-hispid; pedicels ascending, 21-35 mm long and 0.2-0.4 mm diam., glandular-hispid; bracteoles inserted in basal ½ of pedicel, linear to lanceolate, flat, 2.4-3.8 x 0.3-0.4 mm, apex acuminate, base truncate, margin glandular-hispid, involute, both surfaces glabrous or glandular-hispid. Flowers 7-merous; calyx 4.1-4.2 mm long and 4.7-6.9 mm diam.; tube 1.5-2.2 mm long and 2.9-4 mm diam., dark brown to brown, glandular-hispid; lobes widely deltate to shallowly deltate or ovate to widely ovate, 2.2-3 x 1.7-3.3 mm, longest lobes 2.6-3 mm, apex acute, margin entire, glabrous or ciliolate, abaxial surface glandular-hispid, tomentose, or glabrous; corolla tube-shaped; petals imbricate, oblanceolate, pink, 21.5-31 x 4-6.5 mm, apex obtuse, base cuneate, margin undulate, glabrous, lamina distally slightly tomentose; stamens exserted (less than 1.2 x petal length) or subequal to corolla, 24.5-32.5 mm long; filaments 0.2-0.9 mm diam., tomentose; anthers 2.1-2.5 mm long and 0.6-1.3 mm wide, glabrous; ovary glabrous; style exserted, ± 36.5 x 0.6 mm; stigma capitate ±1 x 1.4 mm. Capsules not seen; seeds not seen.

Distribution. (Fig. 28A) Bejaria zamorae is endemic to the montane forest of the Río Zamora valley, Zamora-Chinchipe Prov., Ecuador, at ca. 2000 m alt. Flowering specimens were collected in late June to early July.

Specimens examined. ECUADOR. Santiago-Zamora: "Oriente", Río Zamora valley, E of Loja, ridge across the river from the village of Zamora, 1970 m, 28 Jun-1 Jul 1944 (fl), Camp E-30 (NY).

Bejaria zamorae is characterized by long pink tube-shaped corollas, thin pedicels, long leaves with acuminate or cuspidate apices and long petioles. It appears to be related to B. sprucei and B. aestuans, and may be an intermediate. On the one hand it has the tube-shaped corollas and thin pedicels typical of B. sprucei, and on the other hand it has the subequal or slightly exserted stamens and 7-merous corolla typical of B. aestuans.

It differs from B. sprucei in consistantly 7-merous corollas (5-7-merous in B. sprucei), and at most slightly exserted stamens (less than 1.2x petals length vs. more than 1.6x petal length in B. sprucei). It differs from B. aestuans in pedicel thickness (0.2-0.4 mm diam. vs. 0.6-1.2 mm diam. in B. aestuans), and corolla shape (tube-shaped vs. spreading, bell-shaped, or trumpet-shaped in B. aestuans). The geographic position on the eastern slopes of the Andes also suggests a relationship with B. sprucei which has a disjunct distribution with populations both north and south of the B. zamorae locality. In addition these two species are the only two which are consistently east of the Andes or on the eastern slopes (B. aestuans sometimes occurs on the eastern slopes).

6. **Bejaria sprucei** Meisner in Martius, Fl. bras. 7: 171. 1863. Type. Peru. San Martín: nr. Tarapoto, 1855-1865, Spruce 3994 (lectotype, BR, photo NY neg. 11699; isolectotypes, BM, BR, C, E, G-DC, G-BOISS, GH, GOET, K, LD, LE, MPU, NY, OXF, S-2 sheets, W-3 sheets, frags. F, NY, photo F neg. 760, microfiche of NY herbarium #760/C9). Lectotypified by Mansfeld and Sleumer (1935). Fig. 33 A-D.

Bejaria pallens Remy var. tarapotana Meisner in Martius, Fl. bras. 7: 171. 1863. Type. Peru. San Martín: Tarapoto, 1060 m, Nov 1855, Spruce 4252 (lectotype, BR, photo NY neg. 11698; isolectotypes, K, W, frag. NY). Lectotypified here.

Bejaria guianensis Klotzsch ex N. E. Brown, Trans. Linn. Soc. London, Bot. ser. 2, 6: 46. 1901, "Befaria"; Bejaria guianensis Klotzsch ex Schomburgk, Reisen in Britisch Guiana, 3: 1088. 1848, "Befaria", nomen nudum. Type. Guyana. Richard Schomburgk 1041 (lectotype, B+ n.v., photo F neg. 18285; neolectotype, K, photo NY neg. 11702; isolectotype CBG). Lectotypified by Mansfeld and Sleumer (1935), neolectotype selected here.

Bejaria variabilis A. C. Smith in Gleason, Bull.

Torrey Bot. Club 58: 437. 1931. Type. Venezuela. Territorio Federal Amazonas: Mt. Duida, summit, 1545 m, Aug 1928-Apr 1929 (fl), *Tate* *723* (holotype, NY, photo NY neg. 9790, microfiche of NY herbarium #760/C11; isotype, US).

Bejaria *schomburgkiana* Klotzsch ex Mansfeld and Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 273. 1935, "Befaria"; *Bejaria* *schomburgkiana* Klotsch ex Schomburgk, Reisen in Britisch-Guiana, 3: 1088. 1848, "Befaria", nomen nudum. Type. Guyana. Cerro Roraima, 485 m, Oct 1842, *Richard* *Schomburgk* *871* (holotype, B+, n.v., photo F neg. 18292).

Bejaria *puberula* Klotzsch ex Mansfeld and Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 256. 1935, "Befaria", pro syn.; *Bejaria* *puberula* Klotzsch ex Ule, Bot. Jahrb. Syst. 52(115): 45. 1914, nomen nudum. Type. Venezuela. Bolívar (Roraima): Río Cuquenan, *Ule* *8711* (lectotype B+ n.v.; neolectotype, G, photo NY neg. 11693; isolectotype, U). Lectotypified by Mansfeld and Sleumer (1935), neolectotype selected here.

Shrub or *tree* 0.3-15 m tall; older branches fissured, glabrous, hispid, or glandular-hispid, bark brownish-red, gray, or black and white striped; twigs terete, rusty-red, maroon, or gray, glabrous, tomentose, hispid, or glandular-hispid. Leaves coriaceous, flat or rarely longitudinally curled, elliptic to narrowly elliptic or lanceolate to narrowly lanceolate, sometimes ovate or obovate, 1.5-5.3(-6.6) x 0.2-2.1(-2.9) cm, apex acute to obtuse, sometimes acuminate or rounded, often mucronate, base cuneate, sometimes obtuse, margin glabrous, ciliate or glandular ciliate, flat or sometimes revolute, both surfaces and midveins glabrous, tomentose, hispid or glandular-hispid, the hairs near the leaf apex sometimes forking; petiole subterete, 2-6(-7.5) mm long and 0.6-1.7 mm diam., glabrous, tomentose, hispid, or glandular-hispid. Inflorescence terminal, axillary, or both, racemose, (3-)8-17-flowered; rachis brown, tan, or brownish-orange, (1.8-)2.8-7.4(-12) cm long and 0.6-1.4(-1.7) mm diam., glabrous, tomentose, hispid, or glandular-hispid; floral bracts narrowly elliptic to elliptic or narrowly lanceolate, flat, 1.8-6.9(-13.3) x 0.5-2.8(-3.1) mm, apex acute to acuminate, sometimes obtuse, base cuneate or truncate, margin glabrous, ciliate, glandular-ciliate, or ciliolate, flat or involute, both surfaces tomentose or glabrous, sometimes hispid or glandular-hispid; pedicel 9-29(-33) mm long and 0.3-0.6(-0.8) mm diam., glabrous, tomentose, hispid, or glandular-hispid; bracteoles inserted in basal ½ of pedicel, narrowly elliptic or narrowly oblong to linear, flat, 1-3(-3.3) x 0.2-0.6 mm, apex obtuse or acute, base truncate, margin glabrous, ciliolate, ciliate, or glandular ciliate, involute, both surfaces glabrous, tomentose, hispid, or glandular-hispid. Flowers 5-7-merous; calyx 2.5-4.8 mm long and 3.1-7.1 mm diam.; tube 0.5-2 mm long and 2.4-4 mm diam., brown, orange, or purple, glabrous, tomentose, hispid, or glandular-hispid; lobes widely-ovate to depressed-ovate, sometimes ovate, 0.9-3.2(-4.2) x 1.1-3.3(-3.7) mm, the longest lobes 1.1-3.1(-4.2) mm long, apex obtuse to acute, margin entire, erose, or dentate, glabrous, ciliolate or sometimes glandular-ciliate, abaxial surface glabrous, tomentose, glandular-hispid, or sometimes hispid; corolla tube-shaped; petals imbricate or slightly spreading distally, oblanceolate, pink to dark red, rarely white, 7-28 x 2-7.6(-8.8) mm, apex obtuse, base cuneate, margin glabrous, lamina glabrous or distally slightly tomentose; stamens long exserted (more than 1.2 x petal length), rarely subequal to corolla, (8-)13.5-36.5 mm long; filaments 0.2-0.9 mm diam., tomentose; anther 1-2.6 mm long and 0.6-1.2 mm diam., glabrous; ovary glabrous; style exserted, 18.5-40.5 mm long and 0.7-1.8 mm diam.; stigma capitate, ±0.4 mm long and 0.5-0.8 mm diam. Capsule depressed obloid, 4-4.7 mm long and 5.5-6.8 mm diam., brown, valves not separating from pericarp; seeds narrowly oblong, 0.6-1.5 mm long and 0.2-0.6 mm diam.

Distribution. (Fig. 28A). *Befaria sprucei* exhibits a disjunct distribution similar to that of *B. aestuans*, *B.*

resinosa, and *B. mathewsii*. These species have populations north and south of the volcanic region of Ecuador (see BIOGEOGRAPHY AND DISTRIBUTION). *Bejaria sprucei* is native to the Guayana Highland from the Cordillera de Macarena, Colombia to the Pakaraima Mountains and Kaiteur Plateau, Guyana at 150-2200 m elevation, and to the mountains near Tarapoto, Peru, and in two small populations from Táchira and Anzoátegui; Venezuela. It grows in a variety of habitats including grassland, savannahs, forests, and rarely on exposed rock faces at 750-1500 m alt. It flowers and bears fruit sporadically throughout the year.

Representative sprecimens. COLOMBIA. Meta: Sierra de la Macarena, central mts., 1200 m, 20 Dec 1949 (fl), *Phillipson & Idrobo 1833* (BM, COL, NY, S, US). Vaupés: Circasia, nr. river, 200 m, 9 Oct 1939 (fl), *Cuatrecasas 7152* (COL, F, US); Cerro Chiribiqete, Jan 1944 (fl), *Gutiérrez V. & Schultes 605* (K, NY, US).

VENEZUELA. Terretorio Federal Amazonas: Serranía Parú, Cerro Asisa, 1310 m, 7 May 1973 (bud), *Hoyos & Morillo 40* (VEN); Caño Caname, 100 m, 1 Mar 1980 (fr), *Huber 4915* (NY); Cerro Sipapo, 1500 m, 25 Dec 1948 (fr), *Maguire & Politi 27918* (F, K, NY, S, US); Caño Guaviarito, 1200-1800 m, 4 Feb 1951 (fr), *Maguire et al. 31763* (NY, US); Serranía Yutaje, 1300 m, 9 Feb 1953 (fl), *B. Maguire & C. K. Maguire 35137* (NY, US); Cerro de la Neblina, 1700-2000 m, 30 Dec 1953, *Maguire 37010* (NY, US); Cerro Yaví, 2200 m, 1-3 Mar 1947 (fl), *Phelps & C. B. Hitchcock 41* (originally *130*) (NY, VEN); Cerro Duida, Savanna Hills, 1025-1200 m, 2 Sep 1944 (fl), *Steyermark 58269* (A, F, VEN); Cerro Yapacana, 125-400 m, 3 May 1970 (fl), *Steyermark & Bunting* 103065 (F, NY-2 sheets, US, VEN); Cerro Autana, 1230-1240 m, 20-22 Sep 1971 (fl), *Steyermark 105129* (MO, MY, NY, US, VEN); Sierra Parima, 795-830 m, 18 Apr-23 May 1973, *Steyermark 107437* (MO, U, VEN); Cerro Marahuaca, 2450 m, 9-10 Feb 1982 (fl, fr), *Steyermark et al. 126352* (NY, VEN). Anzoátegui: Dist. Libertad, Ridges and tops of Montanas Negras, serranía de Turimiquire, 2000-2350 m, 28 Nov 1981 (fr), *Davidse & González 19498* (NY); Dist. Freites, betw. San Durrial & Los Pajaritas, 1200-1400 m, 1 Dec 1981 (fl), *Davidse & González 19800* (NY). Bolívar: Cerro Sarisariñama, 6 Jan 1942 (fl), *Cardona 377* (US, VEN); Cerro Acopán, 2200 m, Oct 1947 (fr), *Cardona 2301* (MO, US, VEN); Gran Sabanna, 247 km S of El Dorado, 1100 m, 3 Oct 1982 (fl), *Clemants & Delascio 2479* (NY, VEN); *2480* (NY, VEN); La Gran Sabanna, 141 kms S of El Dorado, nr. Río Aponguas, 1515 m, 3 Oct 1982 (fl), *Clemants & Delascio 2481* (NY, VEN); Uaipan-tepuí, 1200 m, 1 Mar 1967 (fl), *Koyama & Agostini 7348* (NY-2 sheets, VEN); Gran Savanna, km 132.5 S of El Dorado, 1370 m, 16 Nov 1978 (fl), *Luteyn et al. 6275* (NY); km 146 S of El Dorado, 1280 m, 17 Nov 1978 (fl), *Luteyn et al. 6283* (NY); Cerro Bolívar, 1200 m, 1 Dec 1951, *Maguire 32665* (NY, US);

Ilu-tepuí, 1000 m, 25 Mar 1952 (fl), Maguire 33598 (originally 33548) (NY, US); Ptari-tepuí, 1500-2000 m, 17 Dec 1952 (fr), Maguire & Wurdack 33911 (NY, US); Soropan-tepuí, 1800 m, 18 Dec 1952 (fl), Maguire & Wurdack 33941 (NY, US); Cerro Pitón, 400 m, 5 Sep 1962 (fl), Maguire et al. 53636 (MY, NY, VEN); Kavanayén, 1100-1200 m, 8 Aug 1970, H. E. Moore, Jr. et al. 9611 (BH, VEN); nr. Arabupu, 4200 ft, 19 Jan 1939 (fl), Pinkus 276 (F, G-DEL, GH, NA, NY, US); Uaramapa-tepuí, 1200 m, 9 Mar 1962 (fl, fr), 9 Mar 1962, Steyermark & Aristeguieta 61 (F, NY, VEN); Chimantá Massif, central section, 2120 m, 12 Feb 1955 (fl, fr), Steyermark & Wurdack 802 (F, MY, NY-2 sheets, US, VEN); Chimantá Massif, Abúcapa-tepuí, 2125-2300 m, 13 Apr 1953, Steyermark 74866 (US, VEN); Chimantá Massif, Chimantá-tepuí (Torono-tepuí), 1700 m, 21 May 1953, Steyermark 75514 (F, NY-2 sheets, US, VEN); Chimantá Massif, Apácara-tepuí, 2450-2500 m, 21-22 Jun 1953 (fl), Steyermark, 75947 (F, NY, US, VEN); Sierra Ichún, 625-725 m, 27 Dec 1961 (fr), Steyermark 90261 (F, NY, US, VEN); Auyan-tepuí, 1690 m, 2 May 1964 (fr), Steyermark 93215 (K, L, NY-2 sheets, US, VEN); Meseta del Jaua, Cerro Jaua, 1850-1920 m, 4 Mar 1974, Steyermark et al. 109775 (NY, VEN); Cerro Akurimá, Gran Savanna, Feb 1946 (fl), Tamayo 2751 (F, US, VEN); Chimantá Massif, Churi-tepuí, 2200 m, 26 Jan 1953 (fl), Wurdack 24245 (NY, US). Tachira: E of Páramo La Negra, betw. Sabana Grande & Páramo La Negra, 2800-3000 m, 29 Aug 1966 (fl), Steyermark

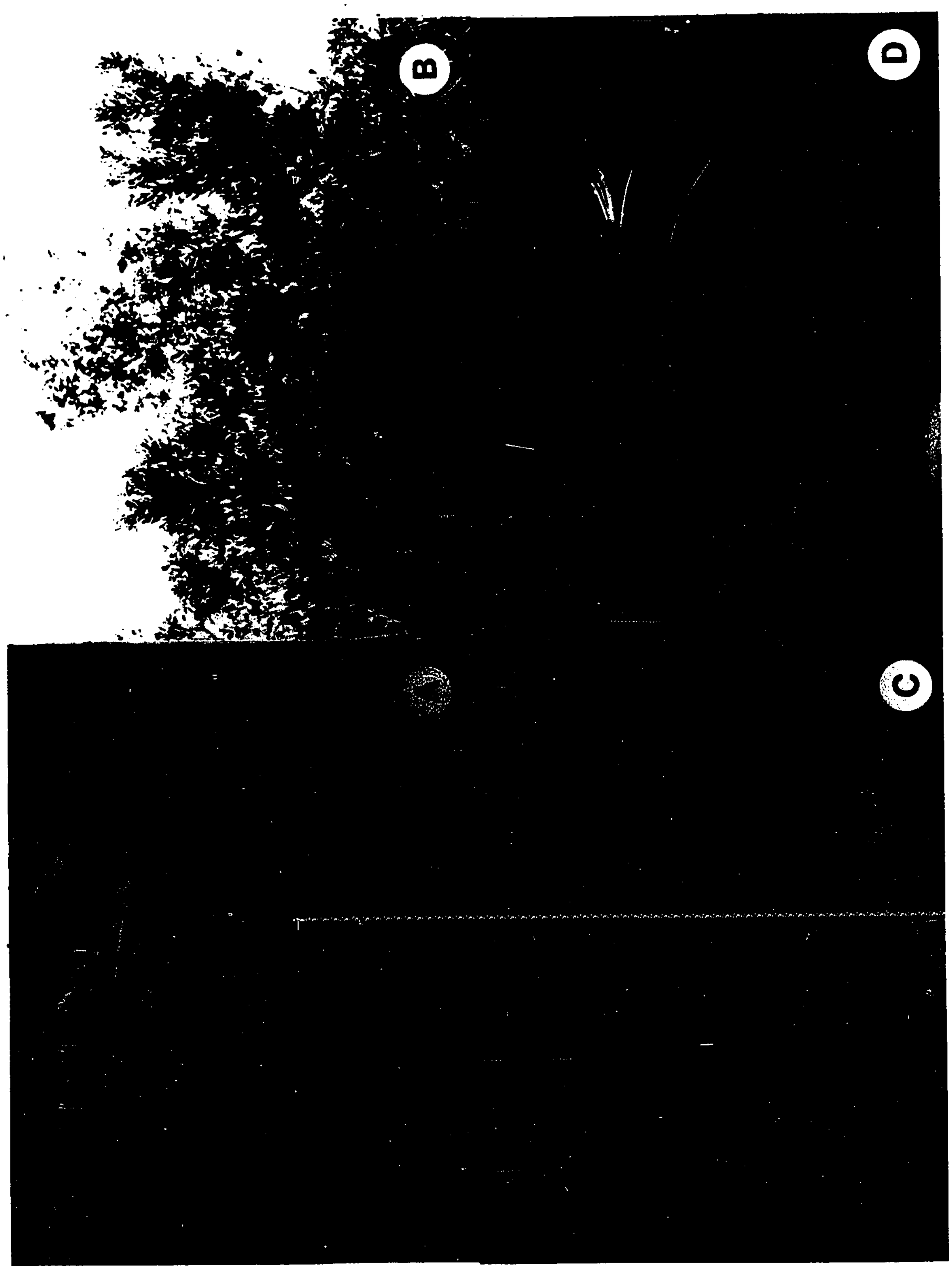
& Rabe 96856 (K, L, NY, US, VEN).

GUYANA. Between Cerro Perai & Río Uaiparú, 900 m, 22 Oct 1946 (fl), *Cardona 1865* (US, VEN); Kaieteur Falls, 1400 ft, 13 Mar 1962 (fl), *Cowan & Soderstrom 2168a* (F, NY, US, VEN); Mure-mure creek, 1400 ft, 15-16 Mar 1962 (fl), *Cowan & Soderstrom 2187* (US); Mt. Latipú, 15 km N of Kamarang, 900 m, 22 Aug 1977 (bud), *P. J. Maas et al. 2620* (U); Pakaraima Mts., Mt. Aymato, 1150 m, 15 Oct 1981 (fl, fr), *P. J. Maas et al. 5706* (NY); Upper Mazaruni River, Imbaimadai Savannas, 550 m, 22 Oct 1951 (fl, fr), *Maguire & Fanshawe 32183* (NY, US); Samwarakna-tipu (Holi-tepu), 1100 m, 9 Nov 1951 (fl, fr), *Maguire & Fanshawe 32473* (NY, US); Upper Mazaruni river, Kataima, 550 m, 17 Nov 1951 (fr), *Maguire & Fanshawe 32641* (NY, US); Pakaraima Mts., Mt. Ayanganna, 1100 m, 7 Feb 1955 (fl), *Maguire et al. 40603a* (NY); Kopinang Savanna, Kopinang Falls, 818 m, 29 Aug 1961 (fl), *Maguire et al. 45987a* (NY); Chimapu Falls, 1212 m, 9 Sep 1961 (fl), *Maguire et al. 46156* (K, NY, US, VEN); Roraima, 1842-1843, *Richard Schomburgk 577* (G); *673* (BM, F, G-2 sheets, OXF, W-2 sheets); *1065* (F, G, K, W, frag. F, photo F neg. 31954); Upper Mazaruni River, Karow tipu, 950 m, 30 Sep-2 Oct 1960, *S. S. Tillett & C. L. Tillett 45570* (NY).

BRAZIL. Territory Roraima: Serra Tepequem, 1500 m, 16 Feb 1967 (fr), *Prance et al. 4429* (COL, F, L, M, NY, S, US).

PERU. Loreto: Campo de Cerro de Escaler, 1000 m, Nov

Fig. 33. _Bejaria sprucei_. A. Inflorescence, _Luteyn et al. 6275_. B. Habit, _Clemants & Delascio 2479_. C. Inflorescence, _Clemants & Delascio 2481_. D. Flower, _Clemants & Fernández 2000_. (Fig. A by Luteyn, Fig. B-D by Clemants).


B
D
C

1902, Ule 6388 (G-DEL, HBG). San Martín: Prov. Moyobamba, Savanna on Cerro de Morro, NNE of Calzada, 900-1000 m, 17 Apr, 1970 (fl), Chrostowski 70-184 (WIS); Prov. Rioja, Jepelacio, 9 Jun 1982 (fl), Clemants & R. Fernández 2000 (NY, USM); 1100-1200 m, Oct-Nov 1933 (fl, fr), Klug 3251 (A, F, G-DEL, GH, K, MO, NY, S, US); Jesús del Monte, 2700 ft, Aug 1938 (fl), Sandeman 151 (OXF); Tarapoto, 750 m, 10 Dec 1929 (fr), Ll. Williams 5976 (F, NY); San Rogue, 1350-1500 m, 4 Feb 1930 (fl, fr), Ll. Williams 7658 (F, NY); Río Negro, 1000 m, 14 Jan 1961 (fl), Woytkowski 6191 (MO, US).

Local names. Candelaria (Peru); Itu-kuyó-kuyén (Gran Savanna, pemón dialect).

Bejaria sprucei is a variable and taxonomically difficult species characterized by tube-shaped corollas, long exserted stamens (more than 1.2x petal length), short calyx lobes, 5- or 6-merous flowers, and thin pedicels (less than 0.6 mm diam.). Particularly stiking is the tube-shaped corollas and exserted stamens which probably are a selection for an unknown pollinator. I have collected two visitors to flowers of this species, an oil collecting bee (Centris flavifrons Friese) and a large wasp (Scolia sp.?). It is this stiking suite of characters which suggest that it is a species different from the closely allied B. aestuans.

Befaria sprucei can be separated, with difficulty, from B. aestuans by the tube-shaped corollas (vs.

spreading, bell-shaped, or trumpet-shaped in *B. aestuans*), thin pedicels (0.4-0.6 mm in diam. vs. 0.6-1.2 mm in diam in *B. aestuans*), 5- or 6-merous (rarely 5-merous in *B. aestuans* and not always consistent in *B. sprucei*), and the long exserted stamens (not evident in immature specimens). No single character can be used but taken in combination these species can be separated.

Another closely related species, *B. zamorae*, known only from three specimens, can be separated by a numnber of characters (Table 52) including its 7-merous flowers, only slightly exserted stamens, acuminate or caudate leaf apices (vs. acute or obtuse in *B. sprucei*) and slightly larger flowers and leaves. Again only a combination of characters can consistently separate these species.

Much of the difficulty in defining *B. sprucei* results from its morphological variation which has also resulted in the previous publication and recognition of six synonyms: two from Peru and four from the Guayana Highland. The Peruvian populations differ only slightly from the Guayana Highland ones. They have 5-merous flowers vs. (5-)6(-7)-merous flowers (Guayana Highland) and slightly shorter flowers. In addition, forked hairs are present on the abaxial surface of many Peruvian individuals, but these hairs are also found in a few Guayana Highland individuals.

Befaria sprucei exhibits a variety of hair types, which, although consistent on an individual, are often

Table 52. Morphological comparison of *B. zamorae* and *B. sprucei*.

	B. sprucei	*B. zamorae*
Height (m)	0.3-15	less than 5
Leaf size (mm)	15-53(-66) x 2-21(-29)	42-76 x 12.5-31
Leaf apex	acute to obtuse	acuminate to cuspidate
Pedicel length (mm)	9-29(-33)	21-35
Pedicel diam. (mm)	0.3-0.6(-0.8)	0.2-0.4
Calyx lobe length (mm)	1.1-3.1(-4.2)	2.6-3
Petal length	7-28	21.5-31
No. of locules	5-6(-7)	7
Elevation (m)	200-2500	2000

variable in a population. Four synonyms of *B. sprucei* are based on hair type (e.g. *B. guayanensis* with glandular-hispid pedicles and glabrous leaves, *B. schomburgkiana* with glandular-hispid pedicels with glandular-hispid and tomentose leaves, *B. puberula* with hispid pedicels, and *B. variablis* with variable pubescence), but vestiture is variable in a population. In the Gran Savanna, specimens which are morphologically identical except for hair type would have been placed in different species in past treatments of *Bejaria*. Compare, for example, *Clemants & Delascio 2479* with glanduar-hispid hairs and *Clemants & Delascio 2480* with eglandular-hispid hairs. I concur with A. C. Smith (1931) that "...too much emphasis has doubless been placed upon pubescence as a specific character..." and therefore hair type variants are not recongnized as species in this revision.

In lumping the Peruvian and Guayana Highland populations and the various hair type variants, I bring together most of the species Mansfeld and Sleumer (1935) placed in their fourth informal species complex. This group, (not given official rank) included *B. sprucei*, *B. schomburgkiana*, *and B. variabilis* as well as *B. hispida* (here placed in *B. aestuans* and *B. sprucei*) and *B. sandiensis*, a species of unknown position.

7. **Bejaria mathewsii** Fielding & Gardner, Sert. pl. 1. t. 69. 1844. Type. Peru. Amazonas: Chachapoyas,

Mathews 1426 (lectotype, K, photo A neg. 1038, NY neg. 11704; isolectotypes, CGE, E-2 sheets, G, K, OXF-4 sheets, P, S, photo NY neg. 11705). Lectotypified by Mansfeld and Sleumer (1935), though one of the specimens at OXF probably represents a better type because it appears to be the specimen used for the plate.

Bejaria phillyriaefolia Bentham, Pl. hartw. 225. 1846, "Befaria". Type. Colombia. Cauca: Andes of Popayán, 1820-3330 m, Oct 1843 (fl), Hartweg 1231 (holotype, K, photo NY neg. 11706; isotypes, B+ n.v., CGE, E, G, G-BOIS, K, LD, LE, OXF, P, W-2 sheets, frag. F, photo F neg. 18290).

Bejaria popayana Fedchenko & Basilevskaja, Bot. Mater. Gerb. Glavn. Bot. Sada SSSR 6:44. 1926. Type. Colombia. Cauca: Popayán, Karsten s.n. (holotype, LE, photo NY neg. 11713).

Bejaria corymbosa Fedchenko & Basilevskaja, Bot. Mater. Gerb. Glavn. Bot. Sada SSSR 6:44. 1926. Type. Colombia. Nariño: Pasto, Venta Menes, Karsten s.n. (holotype, LE, photo NY neg. 11712; isotype, W).

Bejaria mathewsii f. pulcherrima Mansfeld & Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem. 12: 259. 1935, "Befaria". Type. Peru. Amazonas: Prov. Luya, betw. Vilaya and Conila, 3200 m, Jun 1915 (fl), Weberbauer 7144 (holotype, B+, n.v.; lectotype, F, photo NY neg. 9607; isolectotype, GH). I have chosen the specimen at F as the lectotype because it is more complete then the specimen at GH.

Shrub or tree 1.5-8 m tall; older branches fissured, glabrous or tomentose, bark dark brown; twigs subterete, dark brown, rusty-red, or grayish-orange, usually tomentose and hispid. Leaves coriaceous, flat, narrowly elliptic to elliptic, occasionally lanceolate to ovate, (1.9-)2.8-5.8(-7.2) x 0.6-2 cm, apex acute to obtuse, sometimes acuminate, sometimes mucronate, base cuneate, rarely obtuse, margin glabrous, both surfaces and midveins usually glabrous, sometimes tomentose, rarely hispid or glandular-hispid; petiole flattened adaxially; (1.5-)3-7(-10.5) mm long and 0.6-1.7(-2.2) mm diam., usually tomentose or glabrous, rarely hispid or glandular-hispid. Inflorescence of terminal or usually terminal and axillary racemes, 6-12(-21)-flowered; rachis 2-7.5(-11) cm long and 0.9-2.9 mm diam., gray, tan, brown, or orange, tomentose, rarely also hispid or glandular-hispid; floral bracts narrowly elliptic to lanceolate, rarely ovate, flat, 0.45-27 x 0.9-6.2(-10) mm, apex acuminate or acute, rarely obtuse, base cuneate or truncate, margin usually ciliate, sometimes glabrous or glandular ciliate, revolute, both surfaces usually tomentose, sometimes glabrous, rarely glandular-hispid; pedicels ascending, 7-28 mm long and 0.6-1.5(-1.7) mm diam., tomentose, rarely hispid or glandular-hispid; bracteoles inserted in basal ½ of pedicel, narrowly elliptic to lanceolate, sometimes elliptic to ovate, flat, 1.3-4.8 x 0.4-1.9 mm apex acute to acuminate, rarely obtuse, base cuneate or truncate, margin glabrous, often ciliolate, rarely glandular-ciliate, often slightly invlolute, both surfaces tomentose or glabrous. Flowers 7-merous; calyx 3.9-7.9 mm long and 5-15 mm diam.; tube 0.5-2.8 mm long and 2.7-6 mm diam., rusty-red, brown, or gray, glabrous or tomentose, rarely glandular-hispid; lobes widely to very widely ovate, sometimes ovate, widely depressed ovate, widely elliptic, or deltate, 2.7-5.6 x 2-4.9 mm, the longest lobes (3.1-)3.4-5.6 mm, apex acute to obtuse, rarely mucronate, margin erose, ciliolate or ciliate, abaxial surface tomentose or glabrous, rarely glandular-hispid; corolla tube-shaped; petals imbricate, oblanceolate or elliptic, pink to red, sometimes white, (15.5-)18.5-35.5 x (3.3-)4.4-10(-12.5) mm, apex obtuse, base cuneate, margin entire or undulate, glabrous, often lamina distally slightly tomentose; stamens usually slightly exserted, sometimes subequal to corolla or long exserted, (15.5-)19-35.5(-48.5) mm long; filaments 0.4-1.6 mm diam., tomentose; anthers 1.9-4 mm long and 0.8-1.7 mm diam., glabrous or slightly tomentose; ovary glabrous; style exserted, 20.5-53 mm long and 0.4-1.2 mm diam.; stigma lobed, 0.7-1.9 mm long and 1.2-2.5 mm diam. Capsules depressed transversely ellipsoid, 4.5-6 mm long and 8.4-11.8 mm diam., dark brown, valves separating from pericarp; seeds oblong, 1.2-1.7(-2.6) mm long and 0.2-0.6 mm diam.

Distribution. (Fig. 28B). Bejaria mathewsii grows in montane forests, and shrub páramos of central and southern Colombia, extreme southern Ecuador and northern Peru at (1350-)1500-3200(-3900) m alt. This disjunct distribution is similar to the distribution of B. aestuans, B. resinosa, and B. sprucei and is discussed under BIOGEOGRAPHY AND DISTRIBUTION. It flowers and bears fruit throughout the year.

Representative specimens examined. COLOMBIA. Antioquia: Alto de la Honda, 6 km W of Sonsón, 2600 m, 19 Mar 1949 (fl), Scolnick et al. 19An301 (F, MICH, S, US). Caldas: San Félix, Jul 1943 (fl), Tomás 1868 (US). Cauca: Trail Silvia-Pitayó, summit, 3000 m, 17 Nov 1943 (bud), Core 49 (NY, US); valley of Río Cofre, Alto de San Pedro, 3100-3140 m, 14 Oct 1961 (fl), Cuatrecasas & Willard 26468 (COL, US); Río Vinagre, Puracé, 3000 m, Sep 1936 (fl), Dryander 1830 (US); Páramo del Peñon, nr. Jambaló, 3100 m, 22 Oct 1968, Espinal T. 3108 (COL); "Chisquío", 21 km NE of Tambo, 1700-1900 m, 30 Sep 1954 (fl), Fernández P.

2726 (COL, NY); region of Malvazá, nr. town of Gabriel López, 3000-3100 m, 9 Oct 1954 (fl, fr), Fernández P. 2826 (COL); Finca El Salado, Río Machete, 25 km N of Popayán, 1750-1800 m, 19 Mar 1943 (fl), Fosberg 20313 (GH, NY, S, US); Munchinque National Park, El Planchón, 2500 m, 15 May 1979 (fl), Lobo 78 (COL); Puracé National park, nr. Pilimbalá, 3150-3230 m, 3 Mar 1979 (fl), Luteyn & Lebrón-Luteyn 6895 (COL, NY); "Las Guacas", Morales, 1500-1600 m, 4-5 Jun 1922 (fl), Pennell & Killip 6292 (GH, NY, US); Popayan, Río Blanco, 1800 m, 9 Jul 1939 (fl), Pérez-Arbeláez & Cuatrecasas 5808 (COL, F, US); San Antonio, 1700 m, Dec 1905 (fl), Pittier 748 (BM, NY, US); Popayan, 1820 m, Aug 1939 (fl), Sandeman 116 (BM, K, OXF); El Tambo, 1700 m, 27 Jul 1944 (fl), von Sneidern 4814 (COL, F, LIL, UC). Cundinamarca: Rd. to Fusagasugá, André K773 (F, K, NY); El Tabazo, betw. Subachoque and San Francisco, 1900-2100 m, 26 Jan 1944 (fl), García-Barriga 11035 (COL, LILLO, US). Huila: Ca. 20 km NE of Santa Ana, 2850 m, 23 Feb 1944 (fl), Little 7329 (COL, NY, UC, US); Hda. Pensilvánica, 15 km E of Baraya, 3000 m, 24 Jun 1944 (fl), Little 8136 (COL, NY, US); E of Neiva, 1300-1800 m, 1-8 Aug 1917 (fr), Rusby & Pennell 988 (MO, NY, US). Nariño: Cerro de Puerto, nr. Puerto, 2320 m, 26-30 Jul 1944 (fl), Ewan 15951 (BM, S, US-2 sheets); N slope, Volcán de Cumbal, 2980 m, 11 Sep 1944 (fl), Ewan 16142 (US-2 sheets); Cerro Tablón, above Las Mesas, W slope Volcán Doña Juana, 2700-2800 m, 15 Dec 1944 (fl), Ewan

16580 (BM, US-2 sheets); rd. N of Pasto, km 14 rd. to airport, 2620 m, 24 Jan 1976 (fl), *Luteyn et al. 4991* (AAU, CAS, COL, DUKE, MO, NY); nr. Granja Botana, 3.5 km rd. from entrance, 7 km S of Pasto, 2895 m, 24 Jan 1976 (fl), *Luteyn et al. 5004* (AAU, COL, DUKE, F, MICH, MO, NY); N end of Lago Guamuey, 2880 m, 19 Nov 1958 (fl), *V. D. Miller & B. D. Miller 62* (NY, UC); Mpio. El Tambo, rd. Pasto-Matituy, betw. Las Plazuelas and Matituy, 2700 m, 9 Sep 1062 (bud), *Mora 2355* (COL, US); Mpio. de la Unión, Cerro de La Jacoba, 2300 m, 31 Jul 1977 (fl), *Pinto E. et al. 1745* (COL). Tolima: Betw. Caucho and Río Negro, 10 Feb 1944 (fr), *Little 7190* (COL, NY, US); Murillo, 2000-2300 m, 18 Dec 1917 (fl), *Pennell 3195* (F, GH, MO, NY, US). Valle de Cauca: Hda. de San José, Loma de Barrogán, valley Río Bugalagrande, 2600-2580 m, 15 Mar 1946 (fl), *Cuatrecasas 20032* (A, COL, F, US); Cali, Loma Los Cristales, 1300-1400 m, 25 Dec 1959 (fl, fr), *Cuatrecasas et al. 25681* (COL, US); Saladito, 1500-1700 m, Jan 1933 (fl, fr), *Dryander 181* (M); betw. Carpinterías and Mina de Munchique, 2100-2300 m, 17 Jul 1939 (fl, fr), *Pérez-Arbeláez & Cuatrecasas 6300* (COL, F).

ECUADOR. Loja: Amaluza, 5-10 km ENE, Pasaje del Romillo, 2400-2700 m, 23 Sep 1976 (fl), *Øllgaard & Balslev 9738* (AAU, F, MO, NY).

PERU. Amazonas: Rd. Leimebamba-Balsas, km. 416-414, nr. Pomacocha, 2515-2575 m, 17 Jun 1982 (fl), *Clemants 2046* (NY, USM); Cerros de Calla-Calla, 45 km from Balsas toward Leimebamba, 3100 m, 17 Jun 1964 (fl), *Hutchison & Wright 5726* (C, E, F, G, GH, L, M, MICH, MO, NY, S, UC, US, USM); Cerro de Fraijaco, (Huani-Huni), NE of Tambo de Ventilla, 2800-2900 m, 7 Jul 1948 (fl), *Pennell 15845* (GH, PH); Quebrada Molino, 5 km below Chachapoyas, 2200-2400 m, 5 Jun 1962 (fl), *Wurdack 755* (F, K, NY, UC, US); Cerro Yama-uma, summit, above Taulia, 12-15 km SSE of Molinopampa, 3200-3450 m, 11 Aug 1962 (fl), *Wurdack 1668* (K, NY, US). San Martín: Dist. Huallaga, valley of Río Apisoncho, 30 km above Jucusbamba, *Hamilton & Holligan 2008* (UC); Rioja, Aug 1938 (fl), *Sandeman 14* (OXF).

Common Names: Angucho or Angujo (Cauca).

Befaria mathewsii is characterized by large red tube-shaped corollas, long calyx lobes, often exserted stamens, and long leaves with long petioles. As in *B. resinosa* the large red tube-shaped corollas are part of a hummingbird pollination syndrome. Hummingbirds are reported to visit this species in Colombia (*Luteyn et al. 6895*). This corolla shape is also found in *B. resinosa* and *B. ledifolia*.

Bejaria mathewsii is easily separated from *B. ledifolia* by leaf curling (present in *B. ledifolia*, absent in *B. mathewsii*). It is more difficult, however, to separate *B. mathewsii* from *B. resinosa*. *Bejaria mathewsii* can usually be recognized by leaf shape (elliptic vs. ovate, rarely elliptic in *B. resinosa*), leaf length (usually more than 3 cm vs. usually less than 3 cm in *B.*

Fig. 34. Graph showing the relationship of petiole length and leaf length in *B. mathewsii* & *B. resinosa*.

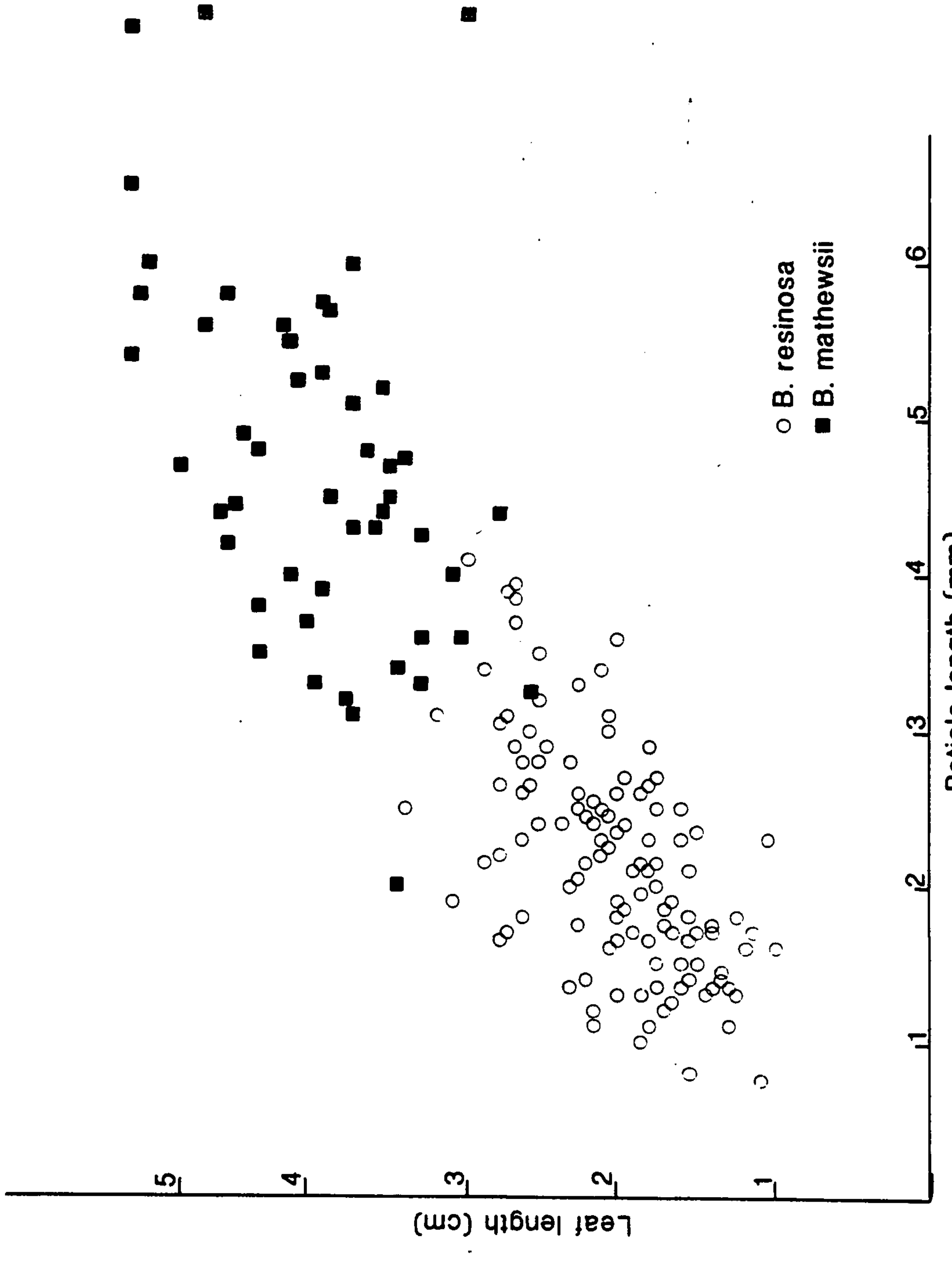
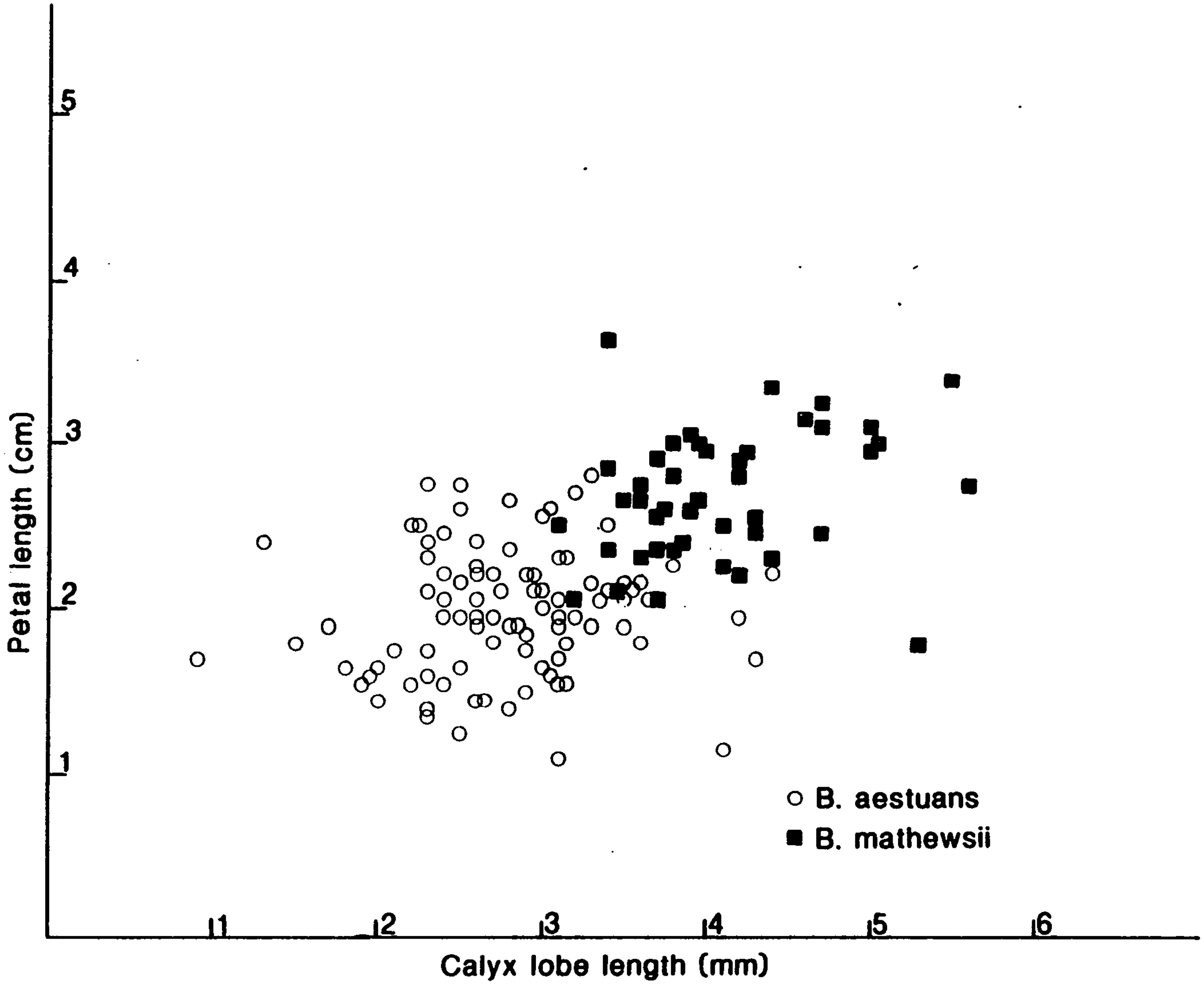

○ B. resinosa
■ B. mathewsii
Petiole length (mm)
1
2
3
4
5
6
Leaf length (cm)
1
2
3
4
5

Fig. 35. Graph showing the relationship of calyx lobe length and petal length in _B_. _mathewsii_ & _B_. _aestuans_.


Petal length (cm)
1
2
3
4
5
Calyx lobe length (mm)
1
2
3
4
5
6
○ B. aestuans
■ B. mathewsii

resinosa), and petiole length (usually more than 3.5 mm vs. less than 3.5 mm in B. resinosa). A comparison of leaf length and petiole length is shown in Fig. 34. It can be seen from this table that there is some intergradation and a need to use a combination of characters to separate these two species. However, the area where this intergradation occurs is small (nr. Popayan) and in most instances there will be no difficulty separating these species.

Bejaria mathewsii can be separated from B. aestuans by corolla shape (tube-shaped vs. spreading, bell-shaped, or if tube-shaped then petals spreading at tip in B. aestuans), calyx lobe length (longest lobe more than 3.1 mm long vs. less than 3.1 mm long in B. aestuans or if more than 3.1 mm long the plants from Mexico) (Fig. 35), and stamen length (usually exserted vs. included in B. aestuans).

Within B. mathewsii there is some morphological variation which can be correlated with geography. The Colombian populations, to which the names B. aestuans and B. phillyriaefolia were applied, are slightly smaller than the Peruvian populations in several morphological aspects. because there is such great overlap I have not separated these populations into separate species.

8. **Bejaria resinosa** Mutis ex Linné filius, Suppl. pl. 246. 1781, "Befaria". Type. Colombia. Without

locality or date, Mutis 55 (lectotype, LINN, n.v., photo IDC microfiche specimen 613.1; isolectotype, S without collection number, n.v., photo IDC microfiche sheet 198, row 1, column 1). Mansfeld and Sleumer (1935) selected Mutis 4640 (B+, n.v., MA, US), as the type because it closely matched a Mutis plate from MA, however they did not validly choose this specimen as the type because they cite both the B and MA specimens. I have chosen the specimen at LINN and S as the lectotype and isolectotype respectively, because Linnaeus presumably had them in his possession when he described the plant. Fig. 36 A-C. Fig. 37.

Bejaria grandiflora Bonpland in Humboldt & Bonpland, Pl. aeqinoct. 2: 122. 1813, "Befaria". Type. Ecuador. Loja: Pâramo de Saraguro, 1799-1804, Humboldt & Bonpland s.n. (lectotype, B+, n.v., photo F neg. 18284). Lectotypified by Mansfeld and Sleumer (1935). Another specimen at P, n.v. (photos NY neg. without number, IDC microfishe sheet 79, row 2, column 7) has not been seen so no neotype is here selected.

Bejaria caxamarcensis Kunth in Humboldt, Bonpland & Kunth, Nov. gen. sp. 3: 294. 1819, "Befaria". Type. Peru. Cajamarca: Cajamarca?, without date, Humboldt & Bonpland s.n. A specimen exists in the

HBK herbarium at P, n.v. (photos F neg. 38217, NY neg. without number, and IDC microfishe sheet 79, row 3, column 3) but I have not seen this specimen so I am not choosing a lectotype at this time. A second specimen collected by Humboldt at B-WILLD (IDC microfiche of Willdenow herbarium #9125) is annotated with the epithet "laxensis" which may be referable to this name. Probable isolectotypes exist at P and a frag. ex P at F. However there is no collection data on either specimen.

Bejaria cinnamomea Lindley, Gardn. Chron. 175. 1848. Type. Peru. Cajamarca: Cajamarca, 2425 m, Lobb 276 (holotype, CGB, photo NY neg. 11700; isotype, K, W).

Bejaria myrtifolia Hérincq, Rev. Hort. sér. 3, 4: 184. 1850, "Befaria". Type. Colombia. Cundinamarca: Bogotá, Zipaquirá, 2800 m, 1842, Linden 773 (lectotype, P, photo NY neg. 11681; isolectotypes, BR, CGE, G, G-BOIS, G-DC, GENT, K, LE, OXF, W-2 sheets, frag. at F). The Paris specimen is here chosen as the lectotype because Hérincq states in the protologue that he had seen Linden specimens at Paris.

Bejaria congesta Fedchenko & Basilevskaja, Bot. Mater.

Gerb. Glavn. Bot. Sada SSSR 6: 28. 1926. Type. Colombia. Norte de Santander: La Baja, nr. Pamplona, 3300 m, 26 Feb? 1846 or Jan 1847, Funck & Schlim 1330 (holotype, LE, photo NY neg. 11715; isotypes, BR, CGE, G, G-DC, LD, P, frag. L, n.v., photo F neg. 28911).

Bejaria aestuans Mutis ex Linnaeus var. macrantha Danguy & Chermezon, Bull. Mus. Hist. Nat. (Paris) 28: 436. 1922, "Befaria". Type. Ecuador. Loja: Loja mts., June, without year, Hartweg 796 (lectotype, P, photo NY neg. 11682; isolectotypes, BM, CGE, G, G-BOIS, E, K-2 sheets, LD, NY, OXF, W-2 sheets, photo, microfiche of NY herbarium #760/C2).

Bejaria albiflora Linden ex Fedtchenko & Basilevskaja, Bot. Mater. Gerb. Glavn. Bot. Sada SSSR 6: 41. 1926, nomen nudum, pro syn. Although this is a nomen nudum, Linden 1351 (F, G, G-BOIS, G-DC, LG, OXF, P, W-2 sheets, frag. F), has the name Befaria albiflora written on the label. Therefore, I suspect that this is the collection on which the name was based.

Bejaria tricolor Linden ex Hérincq, Rev. Hort., sér. 3, 4: 185. 1850; Bejaria grisea Fedchenko & Basilevskaja, Bot. Mater. Gerb. Glavn. Bot. Sada

SSSR 6: 43. 1926. nomen illeg. Type. Colombia. Norte de Santander: Pamplona, 2880 m, Feb 1847, Funck & Schlim 1475 (lectotype of B. tricolor, CGE, photo NY neg. 11701; holotype of B. grisea, LE; isolectotypes, BR, F, G-2 sheets, K, LD, P, W, frag. L, n.v., photos F neg. 28913, A neg. 1040).

Bejaria lehmanniana Fedchenko & Basilevskaja, Bot. Mater. Gerb. Glavn. Bot. Sada SSSR 6: 43. 1926. Type. Ecuador. Loja: Páramo de Saraguro, between Oña and Saraguro, 2800-3000 m, Oct-Jan, Lehmann 4962 (holotype, LE, photo NY neg. 11714; isotype, F, GH, LY, US-2 sheets, photo NY neg. 9609).

Bejaria weberbaueriana Mansfeld & Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 261. 1935, "Befaria". Type. Peru. Cajamarca: Above the Hacienda La Tahoma nr. Hualgayoc, 3100-3400 m, 13 May 1904 (fl), Weberbauer 4014 (holotype, B+, n.v.; lectotype, G, photo F neg. 28917; isotype, frag. F). The lectotype is here selected.

Bejaria peruviana Mansfeld & Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 268. 1935, "Befaria". Type. Peru. Cajamarca: Prov. Jáen, E side of cordillera E of Huancabamba, 2800-3000 m, 8 Apr 1912, Weberbauer 6106 (holotype, B+, n.v.; lectotype, US, photo NY neg. 11228; isolectotypes, F, GH, photo, NY neg. 9604). The US specimen is in better condition and more complete than the others, I have therefore chosen it as the lectotype.

Bejaria dryanderae Mansfeld & Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem 12: 268. 1935, "Befaria". Type. Colombia. Valle: Páramo de Farallones, 3200 m, 1 Oct 1933 (fl), Dryander 1367 (holotype, B+, n.v.). I have seen no isotypes nor have I seen Stuebel 321b (B+), a paratype probably lost at Berlin. The other paratype, Smith 1406 (A, BM, E, F, G-DC, G-DEL, MICH, MO, NY, WIS, US), is not the same entity. Therefore I am choosing the following specimen which was collected at the same locality and matches the description given by Mansfeld and Sleumer (1935) as the neotype: Colombia. Valle: Los Farallones, Quebrada de Las Nieves, 3000-3120 m, 31 Jul 1946 (fl, fr), Cuatrecasas 21831 (neotype, A, photo NY neg. 11694; isoneotypes COL, F, US, frag. US).

Shrub or small tree, 0.25-6 m tall; older branches fissured, glabrous, tomentose, hispid, or glandular-hispid; bark dark brown or gray; twigs subterete, brown or gray, often hispid, rarely glandular-hispid. Leaves coriaceous, flat or rarely curled, usually ovate to elliptic, sometimes narrowly elliptic to lanceolate, rarely obovate, orbicular or cordiform, (0.7)1-2.5 x 0.3-1.6 cm, apex acute to acuminate, occasionally obtuse, rarely rounded, usually bluntly mucronate, base obtuse to truncate, sometimes cuneate, rarely cordate, margin glabrous, occasionally ciliate, rarely glandular-ciliate, flat or revolute, both surfaces usually glabrous, sometimes tomentose or hispid, rarely glandular-hispid, midvein usually hispid, sometimes glabrous, tomentose, or glandular-hispid; petiole slightly flattened in cross-section, 0.5-3.5(-4) mm long, 0.7-1.5 mm diam., usually hispid, sometimes glabrous or tomentose, rarely glandular-hispid. Inflorescence terminal, rarely axillary, racemose, (3-)5-12(-22)-flowered; rachis 1-3.6 cm long and 13-24 mm diam., brown or dark brown, tomentose and usually hispid, sometimes glandular-hispid; floral bracts lanceolate to ovate or elliptic, rarely oblanceolate, flat or longitudinally curled, 2.3-12.5 x 0.8-2.5 mm, apex acute to acuminate, base cuneate, margin glabrous, sometimes ciliate, glandular-ciliate, or ciliolate, sometimes revolute or invlolute, adaxial surface glabrous to tomentose, sometimes hispid or glandular-hispid, abaxial surface usually hispid, sometimes glabrous or tomentose, rarely glandular-hispid; pedicels ascending, 10-18 mm long and 0.6-1.6 mm diam., usually hispid, occasionally glandular-hispid, glabrous, or tomentose; bracteoles usually inserted in basal 1/2 of pedicel (often at very base), lanceolate to oblanceolate or oblong, sometimes narrowly elliptic to elliptic, flat, 1.9-6.6 x 0.4-2.1 mm, apex obtuse to acute to acuminate, base truncate, margin usually ciliate, occasionally glandular-ciliate, often involute, both surfaces glabrous or tomentose. Flowers 7-merous; calyx 3.6-9 mm long and 5.2-13.1 mm diam.; tube 1-4 mm long and 2.5-6.5 mm diam., brown or reddish-brown, glabrous, tomentose, hispid, or glandular hispid; lobes ovate, occasionally lanceolate or elliptic, rarely deltoid, 2.8-5.9(-7.5) x 1.5-4.9 mm, longest lobe 3.8-7.5 mm, apex acute to obtuse, occasionally acuminate, rarely caudate or mucronate, margin entire, ciliolate or ciliate, occasionally glandular-ciliate, abaxial surface glabrous, tomentose, hispid, or glandular-hispid; corolla tube-shaped; petals imbricate, oblanceolate, red to purple, occasionally pink or white, (16.5-)20-40 X 4-10 mm, apex obtuse, base cuneate, margin entire or undulate, glabrous or distally ciliate, lamina distally slightly to densely tomentose; stamens subequal to corolla or slightly exserted, (16-)19-47 mm long; filaments 0.4-1.5 mm diam., tomentose; anthers 1.6-3.7 mm long and 0.8-1.9 mm diam., glabrous; ovary glabrous; style exserted, 23-56 mm long and 0.5-1.4 mm diam.; stigma capitate, slightly lobed, 0.6-1.9 mm long and 1.1-3.3 mm diam. Capsules depressed transversely ellipsoid, 5.5-9 mm long and 9.2-11 mm diam., brown, valves not separating from pericarp; seeds oblong, 1.2-1.6

mm long, 0.3-0.7 mm diam.

Distribution. (Fig. 28C). *Bejaria resinosa* is common in the shrub paramos and lower paramos from Páramo de Tamá, Venezuela to southern Colombia, and from Páramo de Castillo, Ecuador to Cerros de Calla-Calla, Peru, at (1750-)2500-3700 m alt. It is rare (one collection) in the northern part of Ecuador the same region that a number of other species are disjunct across (i.e. *B. aestuans*, *B. mathewsii*, and *B. sprucei* see BIOGEOGRAPHY AND DISTRIBUTION). It flowers and bears fruit throughout the year.

Representative specimens examined. COLOMBIA. Antioquia: Mpio. de Santa Rosa de Osos, Llanos de Cuivá, 2700 m, 22 Nov 1978 (fl), *Callejas P. et al. 961* (NY); Páramo de Chaquiro, 3000-3200 m, *Pennell 4274* (GH, MO, NY, US). Arauca: Sierra Nevada de Cocuy, Quebrada El Playón, 3050 m, 10 Jun 1973 (fr), *Cleef 10173* (COL, NY). Boyacá: Betw. Santa Rosa de Viterbo and Cerinza, 2890 m, 9 May 1959 (fl), *H. G. Barclay & Juajibioy 7188* (US); Sierra Nevada de Cocuy, Quebrada de San Paulino nr. Alto Ritacuva, 3650 m, 3 May 1959 (fl), *H. G. Barclay & Juajibioy 7506* (COL, MO, US); Páramo de Hüina betw. Belén and Susacón, 3400 m, 6-9 May 1959, *H. G. Barclay & Juajibioy 7617* (MO, US); Páramo de Guina, Sta. Rosita, E of Quebrada los Colorados, 3300 m, 5 May 1973 (fl), *Cleef 9842* (COL, L, NY); betw. Soatá and Cocuy, Páramo del Alto del Cañutal, 3300-3400 m, 8 Sep 1938, *Cuatrecasas 1185*

(COL, F, U, US); Páramo de Guantivá, Alto de Canutos, 3100-3400 m, 17 Jul 1940 (fl), *Cuatrecasas* & *García Barriga* *9743* (COL, F, US); El Gran Hotel Termales, nr. Paipa, 2577 m, 6 May 1944 (fl), *Ewan* *15638* (BM, G, S, US-2 sheets); Páramo de La Rusia, W slopes, 7-20 km on Duitama-San Gil rd., 2900-3375 m, 8 May 1979 (fl), *Luteyn et al.* *7580* (COL, NY), *7586* (COL, NY); Km 48 Malaga-Duitama rd., 3230 m, 13 May 1979(fl), *Luteyn et al.* *7687* (COL, NY); El Pino, on ridge 12 km NE of Leiva, 2460 m, 19 Jan 1949 (fl), *Mason* *13728* (COL, UC, US); Santuario de Iguaque, above Villa de Leyva, 3100 m, 2 Aug 1979 (fr), *Melampy* *315* (COL, NY); rd. betw. Belén and Susa, 2500 m, 7 Jul 1966, *Schulz* & *Rodríguez P.* *528* (U); nr. Laguna de Tota, Páramo de La Sarna, 3500 m, Apr 1965 (fl), *Uribe Uribe* *5208* (COL, L). Cauca: Headwaters of Río Palo, Quebrada de Santo Domingo, 2950-3150 m, 13 Dec 1944 (fl), *Cuatrecasas* *19254* (A, F, US); Cerro Munchique, 2500 m, 3 Mar 1884, *Lehmann* *3633* (G-BOIS); Páramo de Buena Vista, 3000-3600 m, Jan 1906 (fl), *Pittier* *1081* (US); Puracé, 3700 m, Feb 1938 (fl), *von Sneidern* *1860* (S); El Tambo, 3060 m, 25 Sep 1939 (fl), *von Sneidern* *2482* (G-DEL, S, US). Cundinamarca: Nemocón, 1922, *Ariste-Joseph* *s.n.* (US); Páramo de Guasca, 2970 m, 15 Dec 1938 (fl), *Balls* *B5676* (BM, COL, E, K, UC, US); Páramo de Zipaquirá, betw. Zipaquirá and Pacho, 3100-3200 m, 16 Jun 1940 (fl), *Cuatrecasas* *9534* (COL, F, US); Fusagasugá, nr. "La Aquadita", 1750-2080 m, 15 Apr 1946 (fl), *Duque-Jaramillo*

3247 (COL-2 sheets); hills W of Laguna de Guatavita, 9 km, NNW of Guatavita, 2900-3000 m, *Fosberg* *21348* (NY, US); Páramo de Guasca, 2800 m, 10 Dec 1949 (fl), *García-Barriga* *13386* (COL, LIL, US); Páramo de Chasques, nr. Villapinzón, 3000-3500 m, 23 May 1951 (fl), *García-Barriga* *et* *al.* *13582* (COL, GH, L, US); Cerro Negro, Hato Grande, ridge E of Río Muchindote, 15 km E of Gachetá, 3000 m, 13 Jun 1944 (fl, fr), *Grant* *9428* (NY, US, WIS); Guadalupe, nr. Bogotá, 3100 m, 5 Apr 1947 (fl), *Haught* *5633* (COL, US, VEN); Bogotá, *Holton* *635* (G-BOISS, G-DC, GH-2 sheets, K, NY, PH); Mpio. Fómeque, Páramo de Chingaza, Leticia and nr. La Paila, 3000 m, 21 Jan 1966 (fl), *Huertas* *&* *Camargo* *6404* (COL-2 sheets); Páramo de Sibaté, 3500 m, 19 May 1981 (fl), *Iglesias* *258* (COL); Ubaté, 2600 m, 18 May 1952, *Køie* *5193* (C); canyon at E edge of Chapinero, Bogotá, 2880 m, 6 Jan 1945 (fl, fr), *Little* *&* *Little* *9206* (COL, GH, MICH, NY, UC, US); 17 km from Bogotá on Bogotá-Villavicenio rd., 3050 m, 11 Jan 1976 (fl), *Luteyn* *et* *al*. *4803* (COL, NY); 7-10 km from Guasca on Guasca-Gachetá rd., 2865-3050 m, *Luteyn* *&* *Lebrón-Luteyn* *7726* (COL, NY); Carmen de Carupa, Peña de Sumangá, 3400 m, 18 Feb 1968, *Pinto* *780* (COL); Mpio. Suesca, path to Hato Grande, 7.3 km SE of Caserío, 2900 m, 19 Dec 1963 (fl, fr), *Saravia* *T.* *&* *Torres* *R.* *3136* (COL); Páramo de Guerrero, 20 km Zipaquirá-Pacho rd., 25 Jan 1967 (fl), *Schultes* *et* *al*. *32* (GH, K, US); El Retiro, Bogotá, 2600-2700 m, 7 May 1946 (fl), *Schultes* *7204* (COL, F-3 sheets, GH, K, NY-2 sheets, U, US); Páramo de Guasca, 14 Feb 1951 (fl), *Schultes 11518* (COL-2 sheets, GH, NY, U); Páramo de Sumapáz, 3300 m, 4 Feb 1964 (fl), *L. Uribe Uribe 4649* (COL). Norte de Santander: Páramo de Fontibón, 2600-2750 m, 15 Oct 1941 (fl), *Cuatrecasas et al. 12274* (COL, GH, US); Cerro de Oroque, Jurisdicciones, border of Norte de Santander and Cesar, 3000-3700 m, 22-27 Jul 1974 (fl), *García-Barriga & Jaramillo M. 20698* (COL, NY, US); Alto de las Coronadas, S of Pamplona, 29 Nov 1946 (fl), *de Garganta 1286* (F-2 sheets); Páramo del Hatico, rd. Toledo-Pamplona, 2900 m, 12-13 Mar 1927 (fl), *Killip & Smith 20687* (A, NY, US). Santander: Pamplona, La Baja, 3030 m, 26 Feb 1846 or 1847 (fl), *Funck & Schlim 1329* (BM, BR, G, G-BOISS-2 sheets, G-DC, LD, MPU-2 sheets, W, frag. F); Páramo de las Puentes, above La Baja, 3500-3700 m, 25 Jan 1927 (fl), *Killip & Smith 18213* (A, NY, US); Páramo de Santurbán, W slopes, towards Tona, 3000 m, 18 Feb 1927 (fl), *Killip & Smith 19531* (A, NY, US); 35-33 kms N of Malaga, 2900-2800 m, 12 May 1979, *Luteyn et al. 7681* (COL, NY). Valle: Los Farallones, extreme N of Cerro Alto del Buey, 3500-3600 m, 11 Oct 1944 (fl), *Cuatrecasas 17915* (F, US); Páramo de Bavaya, 3680-3600 m, 16 Mar 1946 (fl), *Cuatrecasas 20063* (A, F, US, frag. US); Cerro Pan de Azúcar, 3700 m, 26 Feb 1969 (fl), *Cuatrecasas et al. 27550* (NY, US).

VENEZUELA. Apure: Betw. Alto de Cruces and Tierra Negra, Páramo Pata de Judío, 3000-3200 m, 19 Jan 1968, *Steyermark et al. 101118* (L). Táchira: Páramo de Tamá, trail to summit, 2500-3200 m, 29 Jan 1978 (fl), Luteyn et al. 5304 (MERF, NY, VEN), 5314 (MERF, NY, VEN), 2900-3200 m, 18 Oct 1978 (fl), Luteyn et al. 5911 (MERF, NY, VEN).

ECUADOR. Azuay/Morona-Santiago: Muletrack Sevilla de Oro-Méndez, Páramo de Castillo, 3250-3500 m, 16 Sep 1976 (fl), Ollgaard & Balslev 9549 (AAU, MO, NY). Azuay: Km 65-67, Cuenca-Loja rd., 3360 m, 27 Jul 1982 (fl), Clemants et al. 2220 (NY, QCA); Río Collay, slopes Huagrarancha, S of El Pan, 2650-3290 m, 6 Jul 1943 (fl), Steyermark 53329 (F, US). El Oro: Betw. Curtincapa and Guagra Uma, 13 km NE of Curtincapa, 2787 m, 16 Aug 1943 (fl), Steyermark 53871 (F, NY, US). Loja: S of Loja, 2350 m, 4 Oct 1955 (fl), Asplund 17931 (L, LD, NY, S, UPS); 12 km E of Loja, rd. to Zamora, 2485 m, 15 Jan 1981 (fl), Clemants & Luteyn 1669 (NY, QCA); Cerro Villanaco, 15 km, W of Loja, 2425 m, 17 Jan 1981 (fl), Clemants & Luteyn 1675 (NY, QCA), 1676 (NY, QCA), 2610 m, Clemants & Luteyn 1680 (NY, QCA); S slope Nudo de Huagrauma, 11 km. S of Saraguro, rd. to Loja, 3030 m, 18 Jan 1981 (fl), Clemants & Luteyn 1683 (NY, QCA); Páramo de Saraguro, 19 kms N of Saraguro, 2910 m, 18 Jan 1981 (fl), Clemants & Luteyn 1685 (NY, QCA); 30 km N of Saraguro, rd. to Cuenca, 2910 m, 18 Jan 1981 (fl), Clemants & Luteyn 1688 (NY, QCA); Cuenca-Loja rd., 26 km, N of Saraguro, 3060 m, 28 Jul 1982 (fl), Clemants et al. 2221 (NY, QCA); SW slopes, Cerro Villanaco, 31 Jul 1982 (fl), Clemants 2274 (NY, QCA); 31.3 km S of Amaluza, rd. to Zumba, 2790 m, 22 Aug 1982 (fl), Clemants 2396 (NY, QCA); 34.7 km S of Amaluza, rd. to Zumba, 2970 m, 22 Aug 1982 (fl), Clemants 2397 (NY, QCA); Cajanuma, 2400 m, 7 May 1946, Espinosa 307 (LOJA); Mt. Chuguirahuas, W of Palmira, 3400 m, 25 Jul 1977 (bud), Hart 977 (US); E of Vilcabamba, 2600-2700 m, 12 May 1978 (fl), Hart 1337 (US); rd. Saraguro-Tenta, 25 Feb 1979 (fl), Jaramillo & Jaramillo 840 (AAU, QCA); ca. 8 km E of Yangana, path to Nubala, 3100 m, 31 Jan 1966 (fl), Knight 35 (WIS-2 sheets); 17 km N of Saraguro, 2865 m, 2 Jan 1979, Luteyn et al. 6677 (NY, QCA); betw. Tambo Cachiyacu, La Entrada, Nudo de Sabannila, 2500-3500 m, 7 Oct 1943 (fl), Steyermark 54407 (A, F, NY, US, frag. US); Cordillera Condor, Nudo de Sabanilla, nr. Tambo Cachiyacu, Río Cachiyacu, 2000-3000 m, 19 Oct 1943 (fl), Steyermark 54810 (A, F, frag. US). Pichincha: Calacalí, 2700 m, 7 Aug 1979 (fl), Holm-Nielsen 18774 (AAU).

PERU. Amazonas: Prov. Bagua, Cordillera Colán, E of La Peca, 3120 m, 25 Aug 1978 (fl), Barbour 3151 (MO, NY); Prov. Chachapoyas, rd. Leimebamba-Balsas, km 416-414, nr. Pomacochas, 2515-2575 m, 17 Jun 1982 (st.), Clemants 2045 (NY, USM); rd. Leimebamba-Balsas, km. 410, 3100 m, 14 Oct 1964 (fl), Hutchison & Wright 6919 (F, K, M, MICH, MO, NY, UC, US, USM); Prov. Chachapoyas, without locality, 1836, Mathews s.n. (CGE, E, G, G-BOIS, GH-2 sheets, K); Taulia, Jul, Mathews 1423 (K, OXF). Cajamarca: nr. Huancabamba Talleneo, Las Huringas, 3500 m, 20 Feb 1981 (fl), Davis & Turner 703 (ECON, NY). La Libertad: Prov. Huamachuco, Munmalca, Hda. Cochabamba, 3200 m, 26 Jun 1958 (fl), López & Sagástegui 2814 (US). Piura: Prov. Huancabamba, Dist. Sóndor, below La Viuda, 2300 m, 21 Jul 1975 (fl), Sagástegui A. et al. 8216 (AAU, BM, MO, NY); Cordillera Chinguela (Sapalache-El Cármen), 2900 m, 15 Sep 1981 (fl), Sagástegui A. et al. 10228 (NY).

Common names and uses. Venezuela: pegajosa (Táchira). Colombia: pegamosca or pegamosco, matamosca, carbonero, azalea del monte, and pegapega (Cundinamarca), angucha, angucho, and angujo (Cauca, Cundinamarca, and Valle). Ecuador: payama, payana (Azuay, El Oro, and Loja); Peru: pegapega (Cajamarca) and purun rosa (La Libertad). It is used in Colombia (Cundinamarca) for fly paper (Haught 5633), hence the names matamosca and pegamosca (fly killer and fly sticker). In Ecuador (Azuay) and Peru (Cajamarca) it is used medicinally: in Ecuador "for wounds [and], sprains cook the leaves and put the crude crushed leaves over the wound, also used as a purgative... for heart attacks cook the flowers and drink the infusion" (Steyermark 53329), where as in Peru it is "considered the strongest medicine for respiratory ailments. Cooked and mixed with miel de palo" (Davis & Turner 703).

The type of B. resinosa is not the specimen suggested by Mansfeld and Sleumer (1935). They cited Mutis 4640 as the type, stating "Mutis 4640 entspricht der Abbildung von Mutis am meisten und ist als Typus anzusehen ..." (Mutis 4640 corresponds to the picture by Mutis most and is

Fig. 36. A-C. *Bejaria resinosa*. A. Flowers, *Luteyn et al. 7687*. B. Habit, *Clemants 2396*. C. Inflorescence, *Clemants et al. 2221*. D. Inflorescence, *Bejaria imthurnii*, *Clemants & Delascio 2453*. (Fig. A by Luteyn, Fig. B-D by Clemants).

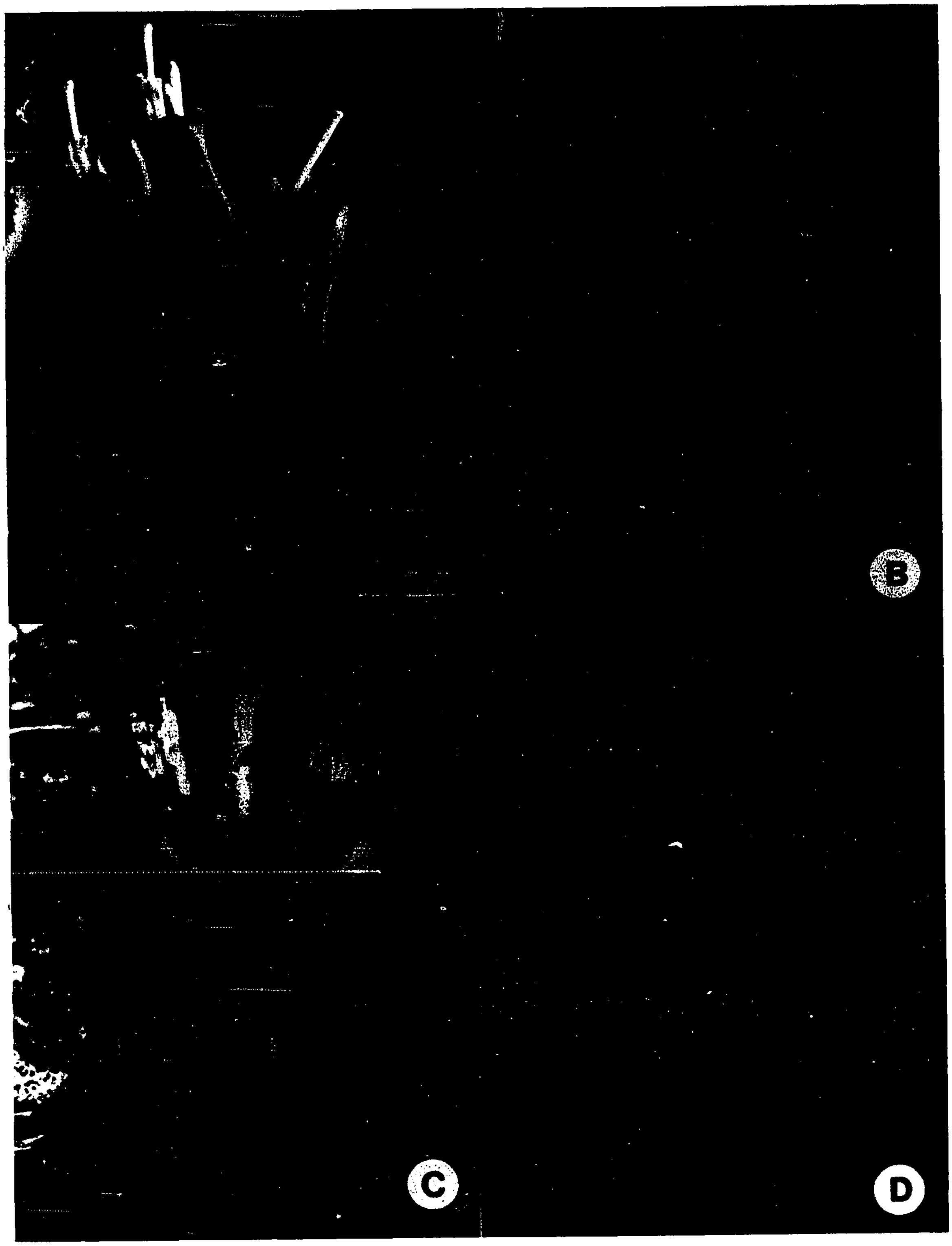
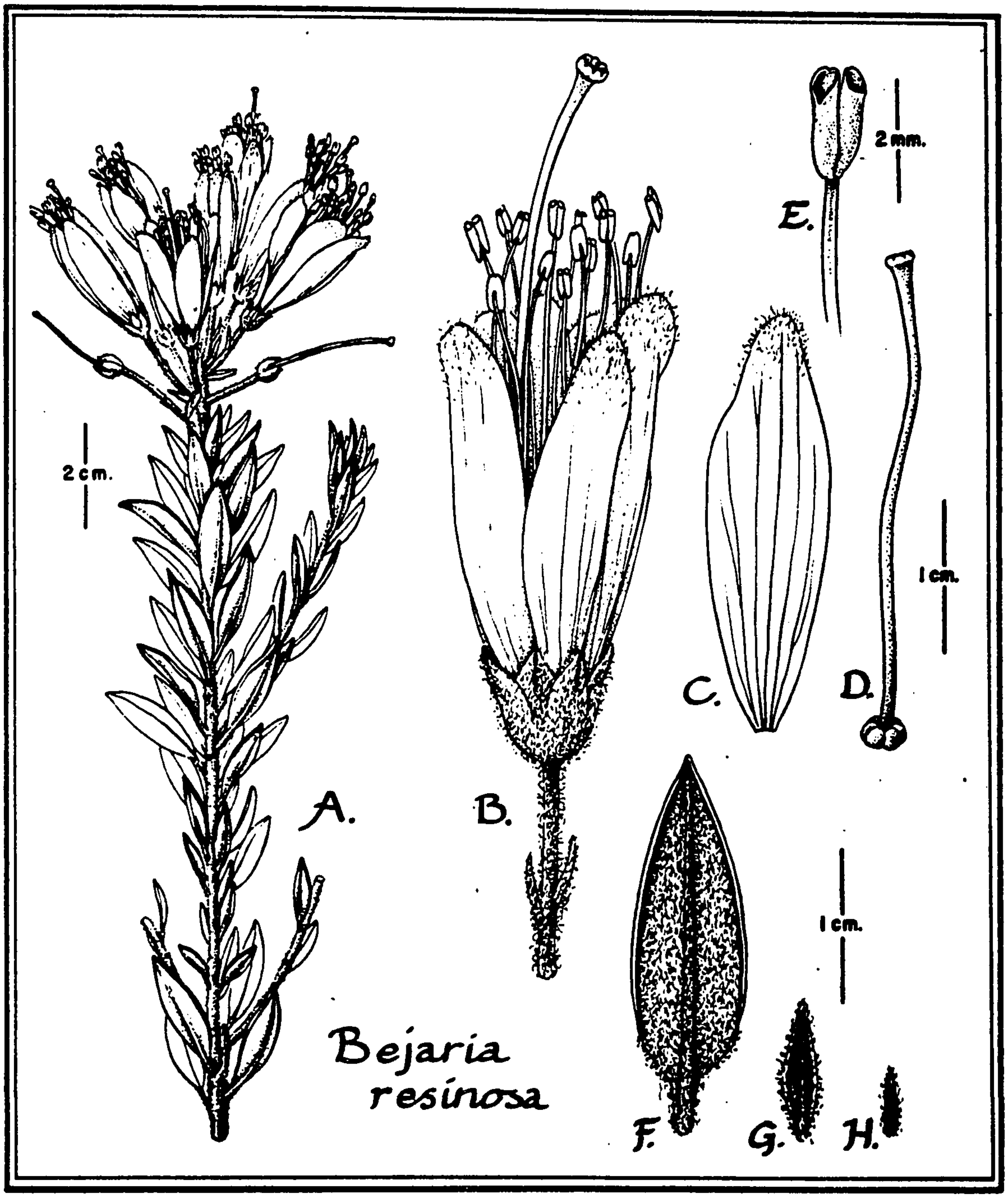

B
C
D

Fig. 37. *Bejaria resinosa*. (*Clemants et al. 2221*) A. Habit. B. Flower C. Petal. D. Style. E. Anther. F. Leaf. G. Floral Bract. H. Bracteole.


A.
B.
C.
D.
E.
F.
G.
H.
2 cm.
2 mm.
1 cm.
1 cm.
Bejaria
resinosa

regarded as the type). The the specimen and copy of the plate at Berlin have been destroyed. I have seen the specimen at MA (duplicate at US) as well as slides of the Mutis plate. However, as with *B. aestuans*, there is no way to tie these elements to the protologue in *Supplementum plantarum*. Although Linné fil. cites a plate by number (at LINN) there is a better choise for the type. Specimens of *B. resinosa* in the Linnaean herbarium (LINN) and in the Montin herbarium (S) are here considered the type. While the Linnaean specimen has only the number "55" written on it, the Montin specimen has written on it that it was donated to him (Montin) by Linnaeus in 1787, indicating that Linnaeus had these specimens in hand before he published the species name. I am therefore lectotypifying *B. resinosa* with the specimen at LINN.

Bejaria resinosa is characterized by large red tube-shaped corollas, long calyx lobes, short thick pedicels and by ovate leaves with acute to acuminate apices, obtuse or rounded bases, and short petioles. The large, red, tube-shaped flowers often indicate hummingbird pollinated plants (Faegri & van der Pijl, 1979), and this species is no exception. Hummingbirds have been seen visiting *B. resinosa* in S Ecuador (Dr. Fernando Ortiz pers. com., and pers. obs.). On the other hand, *Callejas P. et al. 961* reported that rove beetles (Coleoptera, Staphylinidae) visit the flowers. In addition to being visited by hummingbirds, *B. resinosa* flowers are often attacked by flower piercers, demonstrated by the small holes frequently present at the corolla base.

Bejaria resinosa shares large red tube-shaped flowers and presumably hummingbird pollination with two other species, *B. ledifolia* and *B. mathewsii*. *Bejaria ledifolia*, a very closely related species, differs from *B. resinosa* in shorter petals (13-23 mm long vs. (16.5-)20-40 mm long in *B. resinosa*), tightly curled leaves (occasionally found in *B. resinosa*), shorter pedicels and shorter capsules. The two species are also geographically separated, *B. ledifolia* grows on the Coastal Cordillera near Caracas, Venezuela and *B. resinosa*, in the high Andes of Colombia, Ecuador, N Peru, and extreme W Ven. (Fig. 28C)

Another closely related species, *B. mathewsii*, is sympatric with *B. resinosa* throughout much of their range and may intergrade with *B. resinosa*. The two species can usually be separated by leaf shape (elliptic in *B. mathewsii* vs. usually ovate in *B. resinosa*), leaf length (usually more than 3 cm long in *B. mathewsii* vs. less than 3 cm long in *B. resinosa*), and petiole length (usually more than 3.5 mm long in *B. mathewsii* vs. usually less than 3.5 mm long in *B. resinosa*). A combination of characters may be needed in some instances because of apparent intergradation. This intergradation is illustrated in Fig. 34, which shows the relationship of leaf length and petiole length in these two species. *Bejaria mathewsii* is apparently a phylogentic intermediate between *B. aestuans* and *B. resinosa*, it combines large red tube-shaped flowers of *B. resinosa* and long leaves whith long petioles of *B. aestuans*.

Bejaria aestuans is easily separated from *B. resinosa* by corolla shape (spreading or bell-shaped in *B. aestuans* vs. tube-shaped in *B. resinosa*), leaf size (1.5-8 cm long in *B. aestuans* vs. less than 3 cm long in *B. resinosa*), petiole length (3-12 mm long in *B. aestuans* vs. 0.5-4 mm in *B. resinosa*), pedicel length (9-45 mm long in *B. aestuans* vs. 10-18 mm long in *B. resinosa*), leaf shape (usually elliptic in *B. aestuans* vs. usually ovate in *B. resinosa*), and altitude (usually less than 3,000 m in *B. aestuans* vs. usually more than 3,000 m in *B. resinosa*). Although these two species are easily separated, they seemingly hybridize giving rise to a putative hybrid swarm and a species (*B. subsessilis*) in southern Ecuador.

Mansfeld and Sleumer (1935) separated *B. resinosa* into seven species: *B. resinosa*, *B. congesta*, *B. grisea*, *B. dryanderae*, *B. grandiflora*, *B. cinnamomea*, and *B. peruviana*. The differences between these seven species generally are found in the hair types and distribution, and to a lesser extent leaf shape and apex shape. According to their classification (Mansfeld & Sleumer, 1935) *B. resinosa* has glabrous abaxial leaf surfaces and hispid pedicels; *B. congesta* has hispid abaxial leaf surfaces and hispid pedicels; *B. grisea* has glabrous leaves and pedicels and obtuse leaf apices; *B. dryanderae*

Table 53.

Comparison of morphological characters in <u>Bejaria</u> <u>resinosa</u> segregates.

Species	Leaf shape	Leaf size (cm)	Leaf apex
B. resinosa	elliptic - ovate	1.0-2.1(-2.6) x 0.5-1.2(-1.3)	acuminate - acute
B. congesta	lanceolate - ovate, elliptic	1.0-1.8 x 0.4-1.0	acuminate - acute (obt
B. tricolor	elliptic - ovate (obovate - lanceolate)	1.1-2.2 x 0.5-1.1	acuminate - acute, obt
B. dryanderae	lanceolate - elliptic	1.6-3.2 x 0.5-1.1	acuminate - acute (obt
B. cinnamomea	ovate - elliptic, lanceolate	1.6-3.4(-4.9) x 0.7-1.6(-2.4)	acute - obtuse
B. weberbaueriana	elliptic - ovate	1.4-2.2 x 0.6-0.7	acute
B. grandiflora	ovate - elliptic	1.4-2.9(-3.2) x 0.6-1.4	acuminate - acute (obt
B. peruviana	ovate - elliptic	1.5-3.3 x 0.7-1.7	obtuse - acu

Table 53.

in Bejaria resinosa segregates.

	Leaf size (cm)	Leaf apex	Leaf base	Petiole l. (mm)
	1.0-2.1(-2.6) x 0.5-1.2(-1.3)	acuminate - acute	obtuse - round	0.5-3.0
	1.0-1.8 x 0.4-1.0	acuminate - acute (obtuse)	obtuse - cuneate truncate	0.5-2.5
late)	1.1-2.2 x 0.5-1.1	acuminate - acute, obtuse	cuneate	1.0-3.0
ic	1.6-3.2 x 0.5-1.1	acuminate - acute (obtuse)	cuneate (obtuse)	2.0-5.0(-8.5)
	1.6-3.4(-4.9) x 0.7-1.6(-2.4)	acute - obtuse	round - obtuse	1.0-2.5
	1.4-2.2 x 0.6-0.7	acute	cuneate	2.0-3.0
	1.4-2.9(-3.2) x 0.6-1.4	acuminate - acute (obtuse)	obtuse - truncate cuneate	1.0-4.5
	1.5-3.3 x 0.7-1.7	obtuse - acute	cuneate	1.0-2.0

Table 53 cont.

Species	Leaf pubescence[1]					
	abaxial	adaxial	margin	midvein	petiole	length
B. resinosa	G (T)	G (T)	G (T)	G (T)	G (H)	2.6-4.0
B. congesta	G (H)	H	G (H)	G (H)	H	1.6-2.8
B. tricolor	G - T	G - T	G - T	G - T	G - T	1.2-1.6
B. dryanderae	G(T, GL)	G(T & GL)	G or GL	T & GL	various	0.5-3.5
B. cinnamomea	G or T	T	T or GL	T (GL)	T - GL	1.7-6.3
B. weberbaueriana	G	G	G	G	T or G	2.0-3.0
B. grandiflora	G - T	T	H	H	T or H	1.0-7.0
B. peruviana	G or GL	T	G	G	GL	6.0-8.0

[1] G=glabrous, T=tomentose, H=hispid, GL=glandular-hispid,

			Rachis		Pedicel	
margin	midvein	petiole	length (cm)	pubescence[1]	length (cm)	pubescence[1]
G (T)	G (T)	G (H)	2.6-4.0	T & H (T)	0.5-3.0	T & H (T)
G (H)	G (H)	H	1.6-2.8	H	0.5-1.9	H (GL)
G - T	G - T	G - T	1.2-1.6	T	0.5-1.7	T (H or GL)
G or GL	T & GL	various	0.5-3.5	GL & T	0.5-1.6	T & GL
T or GL	T (GL)	T - GL	1.7-6.3	GL & T	1.4-2.4	GL & T
G	G	T or G	2.0-3.0	T	0.9-1.2	T
H	H	T or H	1.0-7.0	T & H	0.4-2.4	T & H
G	G	GL	6.0-8.0	GL	0.7-1.5	GL

glandular-hispid,

Table 53 cont.

Species	Calyx			Petal
	size (mm)	pubescence	margin	length (c
B. resinosa	2.8-7.5 x (2.0-)2.4-4.7	G, T & H	CIO or CI	2.0-3.7
B. congesta	(3.1-)3.4-5.1 x (2.3-)2.7-3.7	S (G)	CI or SER	(1.6-)2.0
B. tricolor	(3.1-)3.8-5.2(-7.6) x 2.4-5.1	G, T (H, GL)	various	2.2-3.6
B. dryanderae	3.7-5.6 x (1.9-)2.3-4.1	G, T, GL	CIO or CI	(2.4-)2.7
B. cinnamomea	3.2-4.3	GL	G-CI	(20.5-)24
B. weberbaueriana	4.3-5	T	CIO	30-32.5
B. grandiflora	(3.1-)3.6-5.4(-6.0) x 2.6-4.5	T (H)	various	1.5-3.7
B. peruviana	3.9-6.0 x (2.0-) 3.0-3.4(-4.0)	GL	G-CI	(2.4-)3.0

[1] G=glabrous, T=tomentose, H=hispid, GL=glandular-hispid,

pubescence	margin	Petal length (cm)	Stamen length (cm)	Distribution
G, T & H	CIO or CI	2.0-3.7	(1.6-)2.0-3.6	Colombia
S (G)	CI or SER	(1.6-)2.0-3.6	2.2-3.8	Venezuela & N. Colombia
G, T (H, GL)	various	2.2-3.6	2.1-4.0	Venezuela N. Colombia
G, T, GL	CIO or CI	(2.4-)2.7-3.6	(2.6-)2.8-4.8	Colombia
GL	G-CI	(20.5-)24-39.5	3.4-4.7	N. Peru
T	CIO	30-32.5	3.8-4.4	N. Peru
T (H)	various	1.5-3.7	1.7-4.1	Ecuador
GL	G-CI	(2.4-)3.0-3.6	(2.3-)3.0-3.5	N. Peru

=glandular-hispid,

has glandular-hispid pedicels and leaves, and elliptic leaves; B. grandiflora has hispid pedicels and densely tomentose abaxial leaf surfaces; B. cinnamomea has glandular-hispid pedicels and densely tomentose and glandular-hispid abaxial leaf surfaces; and B. peruviana has glandular-hispid pedicels and abaxial leaf surfaces and elliptic leaves. This is summarized in Table 54. Although these entities are recognizable and have some geographic similarities, there are many intermediates and some groups grow side-by-side. In Páramo de Saraguro, for instance, both B. cinnamomea and B. grandiflora grow within feet of each other with no obvious morphological differences except for hair type and viscous petals (in B. cinnamomea). In addition some of the hair topographic data is suspect because the lower leaf surfaces are often hispid when young but become glabrous with age.

9. **Bejaria ledifolia** Bonpland in Humboldt & Bonpland, Pl. aequinoct. 2: 124, t. 120. 1813, "Befaria". Type. Venezuela. Distrito Federal: Silla de Caracas, 1936 m, Humboldt 645 (lectotype B-WILLD, n.v., photo, B neg. 4361, F neg. 18287, IDC microfiche of Willdenow herbarium #9127; isotypes, H, P-HBK, n.v., photo IDC microfiche of H.B.K. herbarium sheets 79, row 3, column 2)

Shrub to 2 m tall; older branches smooth or striate, glandular-hispid, bark gray; twigs subterete, dark gray, hispid. Leaves coriaceous, longitudinally curled, ovate to lanceolate when flattened, 1.15-1.9(-3) x 0.45-1.2 cm, apex obtuse to acute, bluntly mucronulate, base obtuse or rarely cuneate, margin glandular-ciliate, revolute, both surfaces glandular-hispid or usually abaxially glabrous; petiole slightly flattened in cross-section, 0.5-2.5 mm long and 1-1.5 mm diam., glandular-hispid. Inflorescence terminal, racemose, 5-11-flowered; rachis 2-5.4 cm long and 1.3-2 mm in diam., brown or black, glandular-hispid; floral bracts lanceolate to ovate or elliptic to narrowly elliptic, longitudinally curled, 3.8-8.5 x 0.8-2 mm, apex acute to acuminate, base cuneate or rarely obtuse, margin glandular-hispid, both surfaces glandular-hispid or adaxial surface glabrous; pedicels ascending, 5.8-14.5 mm long and 0.4-1.1 mm diam., glandular-hispid; bracteoles inserted in lower ½ of pedicel, lanceolate, elliptic, or oblong, flat, (1.4-)2.2-4 x 0.4-1 mm, apex acute to acuminate, base cuneate or truncate, margin glandular-ciliate, abaxial surface glandular-hispid. Flowers (5-)7-merous; calyx 5.1-6.5 mm long and 4.9-7.2 mm diam.; tube 1-2 mm long and 2.8-4 mm in diam., dark brown or dark maroon, glandular-hispid; lobes ovate to lanceolate (2.4-)3.7-5(-5.7) x 1.6-2.7 mm, longest lobe (3.2-)3.9-5.7 mm long, apex acuminate to acute, margin erose, rarely entire, glandular-ciliate, abaxial surface glandular-hispid; corolla tube-shaped; petals imbricate, oblanceolate, pink to red, 13-23 x 3-7 mm, apex obtuse or rounded, base cuneate, margin undulate, glabrous or distally ciliolate, lamina distally slightly tomentose; stamens subequal to corolla or usually long exserted (1-1.6x petal length), 15-29 mm long; filaments 0.3-0.8 mm diam., tomentose; anthers 1.5-2.6 mm long and 0.7-1.2 mm diam., glabrous; ovary glabrous; style exserted, 15-35.5 mm long x 0.3-0.7 mm diam.; stigma capitate and sometimes slightly lobed, 0.6-1.2 mm long and 0.8-2 mm diam. Capsules depressed obloid, 4.7-6 mm long and 6.2-11 mm diam., brown, valves not separating from pericarp; seeds oblong, 0.8-1.7 mm long and 0.26-0.5 mm diam.

Distribution. (Fig. 28C). Bejaria ledifolia is endemic to the shrub paramos of the Coastal Cordillera N of Caracas, Venezuela at 1990-2765 m altitude. It flowers sporadically throughout the year and bears fruit January to June and October.

Representative specimens examined. VENEZUELA. Distrito Federal: Pico Avila-Lagunazo trail, 1990-2225 m, 7 Oct 1982 (fr), Clemants 2483 (NY, VEN); Silla de Caracas, 2120-2420 m, 8 Oct 1842 (fl), Funck 313 (BM, G-BOIS, OXF, W), 2420 m, 21 May 1874 (fl, fr), Kuntze 1623 (K, NY-2 sheets, US), 2400-2500 m, Jan 1842 (fl, fr), Linden 128 (BM, BR-2 sheets, CGE-2 sheets, F, FI, G-BOIS, G-DC-2 sheets, GH, K, LG-2 sheets, MPU, OXF, US, W-2 sheets); Costal Cordillera, El Avila, rd. to Laguniza, 2500 m, 25 Mar 1969 (st), B. Oberwinkler & F. Oberwinkler 15177 (M, VEN); Cordillera del Avila, betw. Los Venados and Pico Oriental, 1675-2640 m, 27-28 Feb 1944 (fl), Steyermark 55623 (F, US). Miranda: Naiguatá, 2420-2730 m, 15 Jul 1929 (fl), Holt 539 (CM, VEN); upper belt of Pico de Naiguatá, south slope, 2400-2765 m, 24-25 May 1913, Pittier 6228 (NY, US-2 sheets); ascent of Pico de Naiguatá, above Los Chorros, 2200-2765 m, 16-17 Jun 1945 (fl, fr), Steyermark 62992 (F, NY, US).

Befaria ledifolia is characterized by small curled leaves, long calyx lobes, rather short red tube-shaped corollas, and glandular-hispid pubescence. It is closely related to B. resinosa with which it shares the red, tube-shaped corollas, and small leaves, but differs by its curled leaves (occasional in B. resinosa), shorter petals (13-22.5 mm long vs. (16.5-)20-40 mm long in B. resinosa), shorter pedicels (5.8-14.5 mm long vs. 10-18 mm long in B. resinosa), and shorter capsules (4-7 mm long vs. 7-9 mm long in B. resinosa). A few collections of B. resinosa from Cundinamarca, near Bogotá, and Boyacá, Colombia, approach B. ledifolia by having curled leaves, but they differ in having much larger flowers and shorter leaves. In addition, these collections are few in number and generally the flowers are poorly preserved.

Mansfeld and Sleumer (1935) and Camp (1941) believed that B. ledifolia was closely related to B. cubensis. I do not believe this. The only resemblance is in the curled leaves and glandular pubescence, whereas the flowers are totally different (see *B. cubensis*). I believe that *B. ledifolia* represents a peripheral population of *B. resinosa* which has differentiated enough to be considered a species.

10. **Bejaria imthurnii** N. E. Brown, Trans. Linn. Soc. London, Bot. ser. 2, 6: 46. 1901, "Befaria". Type. Venezuela. Bolívar: Mt. Roraima, summit, 2610 m, *Im thurn 310* (lectotype, K, n.v.). Lectotypified by Mansfeld and Sleumer (1935). Fig. 36D.

Bejaria tatei Gleason, Bull. Torrey Bot. Club 56: 401. 1929. Type. Venezuela. Bolívar: Mt. Roraima, 2620 m, 24 Nov 1927 (fl), *Tate 408* (holotype, NY, photo NY neg. 10572, microfiche of NY herbarium #760/C10).

Shrub 0.2-3 m tall; older branches fissured, glabrous, bark black or black and white striped; twigs subterete, rusty-red to maroon, glandular-hispid or hispid. *Leaves* coriaceous, flat, elliptic or obovate, occasionally ovate, 1.2-2.8 x 0.5-1.4 cm, apex acute to obtuse, sometimes acuminate, mucronate, base cuneate, margin ciliate, glandular-ciliate, or glandular-pustulate, usually revolute, both surfaces glabrous, abaxial midvein usually hispid or glandular-hispid, sometimes glabrous; petiole subterete or slightly flattened in cross-section, 1-3.5 mm long and 0.7-1.5 mm diam., hispid, glandular-hispid, or glabrous. Inflorescence terminal, racemose, 4-19-flowered; rachis 0.9-4.3 cm and 1.2-2.8 mm diam., rusty-red to maroon, hispid or glandular-hispid; floral bracts elliptic to oblanceolate, flat, 2.7-26 x 0.9-10 mm, apex acute, rarely obtuse, mucronate, base cuneate, margin ciliate, glandular-ciliate, or glabrous, lamina and midvein glabrous; pedicel ascending or divergent, 4-17 mm long and 0.6-1.3 mm diam., densely to sparcely hispid or glandular-hispid, sometimes also tomentose; bracteoles inserted in basal ½ of pedicel, elliptic to oblong, rarely lanceolate, flat, 0.8-4.1 x 0.4-1 mm, apex acute to acuminate, rarely obtuse, usually mucronate, base slightly narrowed, margin glabrous, ciliate, glandular-ciliate, or ciliolate, involute, both surfaces glabrous. Flowers (6-)7(-8)-merous; calyx 3.7-5.4 mm long and 6.1-7.3 mm diam.; tube 0.8-2.3 mm long and 3.3-4 mm diam., light green, tan, or maroon, hispid, glandular-hispid, or glabrous; lobes ovate to depressed ovate or elliptic, 2.3-4.1 x (1.2-)1.7-3.6(-4) mm, longest lobe 2.7-4.1 mm, apex obtuse to acute, margin erose, erose-fimbriate, rarely dentate or entire, glabrous or sometimes ciliolate, abaxial surface usually glabrous, rarely glandular-hispid; corolla bell-shaped; petals spreading or slightly imbricate, oblanceolate, pink or rarely purple, 15-27 x 4-8 mm, apex obtuse, base cuneate, margin undulate or sometimes distally erose, glabrous, lamina glabrous;

stamens subequal to corolla or included, 14-25 mm long; filaments 0.4-1 mm diam., tomentose; anthers 1.6-2.6 mm long and 0.9-1.4 mm diam., glabrous; ovary glabrous; style subequal to corolla or slightly exserted, 16-33 mm long and 0.6-1 mm diam.; stigma 7-lobed, 0.8-1.4 mm long and 1.3-2.3 mm diam. Capsules depressed transversely ellipsoid, 3-5.9 mm long and 5.2-9.3 mm diam., brown, valves not separating from pericarp; seeds ellipsoid, 1.3-1.9 mm long and 0.5-0.7 mm diam.

Distribution. (Fig. 28C). Bejaria imthurnii is common on the exposed rocks and in rock crevices of Mt. Roraima and Cerro Kukenan on the border of Venezuela, Brazil, and Guyana at 2560-2850 m alt. It flowers throughout the year and bears fruit from August to January.

Specimens examined. VENEZUELA. Bolívar: Mt. Roraima, 7 Jan 1939 (fl), Forest Dept. 2876 (K); 1800 m, 17 Apr 1973 (fl), Bechine 40 (MY); 2400-2600 m, Bechine 86 (MY), 90 (MY); summit, 2800 m, 29-30 Sep 1982 (fl), Clemants & Delascio 2453 (NY, VEN), 2454 (NY, VEN), 2467 (NY, VEN), Jan 1977 (fl), Delascio & Brewer-Carias 4809 (VEN), 2300 m, 16 Aug 1976 (bud), Hernández 46 (MY), 1885, Imthurn s.n. (K), 2730 m, 24 Apr 1955 (fl), Irwin 422 (US), 687 (LL), 2850 m, Sept 1927 (fl), Luetzelburg 21566 (M), Oct 1927 (fl), Luetzelburg 21570 (M); 1800 m, 20 Aug 1978 (fl), Moreno 6 (MY), 2640 m, 7 Jan 1939 (fl, fr), Pinkus 108 (NA, NY, US); Autumn 1898 (fl), Quelch &

McConnell 646 (BM), Jul 1899 (fl), *Quelch & McConnell 648* (BM); 2255-2620 m, 27 Sep 1944 (fl), *Steyermark 58779* (A, F); 2560-2620 m, 27 Sep 1944, *Steyermark 58785* (F, US), *59886* (F), NW portion, N and NW of Summit camp, 2620-2740 m, 27 Sep 1944, *Steyermark 58816* (A, F, VEN), S half between summit camp, great central rift, central swamp, and portion at S end, 2700-2740 m, 28 Sep 1944, *Steyermark 58894* (A, F, VEN), *58900* (A, F); summit, 2620-2740 m, without date, *Steyermark 68816* (frag. US), 2750-2800 m, 26 Aug-2 Sep 1976 (fl, fr), *Steyermark et al. 112504* (NY), *112504a* (VEN), *Steyermark 112517* (VEN), head of "El Valle", headwaters or Río Arabapó, *Steyermark et al. 112562* (NY); E of heliport, nr. Brazilian border, *Steyermark et al. 112612* (VEN); summit, 24 Nov 1927 (fr), *Tate 407* (NY), 408 (NY), 2500 m, Dec 1909-Jan 1910 (fl), *Ule 8710* (B, G-DEL-2 sheets, K, U, US, frag. F); summit of Kukenan tepuy, Jan 1977 (fl), *Delascio & Brewer-Carias 4923* (VEN).

Befaria imthurnii is characterized by short rachises, long petals, and oblanceolate or sometimes elliptic leaves with short petioles. It differs from *B. aestuans* by leaf shape (usually oblanceolate vs. usually elliptic in *B. aestuans*) and petiole length (1-3.5 mm long vs. (1-)3-12 mm long in *B. aestuans*).

Bejaria imthurnii differs from the other small-leaved, short-petioled species (*B. steyermarkii* and *B. neblinensis*) in petal length, pedicel length, and leaf shape.

11. **Bejaria steyermarkii** A. C. Smith, Fieldiana, Bot. 28(3): 449. 1953, "Befaria". Type. Venezuela. Sucre: In valley betw. base of Cerro de Diablo (W extension of S peak of Cerro Turumiquire) and Cerro de Neveri, along headwaters of Río de Amana, 2000 m, 11 May 1945 (fl), Steyermark 62711 (holotype, F, photo, F neg. 52521, NY neg. 9622; isotypes, A, L, US, VEN).

Shrub 0.3-1.2 m tall; older branches fissured, glabrous, bark gray to dark gray; twigs subterete, gray or dark gray, slightly hispid or glabrous. Leaves coriaceous, flat or slightly longitudinally curled, lanceolate to elliptic, 1-1.8 x 0.2-0.45 cm, apex acuminate, mucronate, base cuneate, margin glabrous, revolute, both surfaces and midveins glabrous; petiole subterete, 0.8-1.7 mm long and 0.3-0.8 mm diam., glabrous. Inflorescence terminal, racemose, 5-12-flowered; rachis 0.6-1.8 cm long and 0.8-1.3 mm diam., maroon to dark maroon, hispid; floral bracts linear-lanceolate, flat, 2.2-5 x 0.5-0.8 mm, apex acuminate, rarely acute, base cuneate or rarely truncate, margin cililate or glabrous, revolute, both surfaces glabrous; pedicel ascending or divergent, 3.5-7.5 mm long and 0.6-0.8 mm diam., hispid; bracteoles inserted near middle of pedicel, narrowly elliptic, flat, 1.4-3 x 0.4-0.5 mm, apex acuminate to acute, base cuneate, margin ciliate, flat or involute, both surfaces glabrous. Flowers 7-merous; calyx 3.6-3.8 mm long and 5-5.2 mm diam.; tube 1.4-1.6 mm long and 3.8-4 mm diam., dull purple-red to orange, glabrous; lobes ovate to depressed-ovate, 1.8-2.6 x 1.5-2.7 mm, longest lobe 2.3-2.6 mm, apex, obtuse, or caudate, margin erose, ciliolate, abaxial surface glabrous; corolla bell-shaped; petals imbricate or slightly spreading, oblanceolate, pink, sometimes white basally, 14-17 x 3.7-6.8 mm, apex obtuse, base cuneate or attenuate, margin undulate, distally ciliolate, lamina glabrous; stamens included, 11.5-15 mm long; filaments 0.3-0.7 mm diam., tomentose; anthers 1.3-1.7 mm long and 1-1.4 mm diam., glabrous; ovary glabrous; style subequal to corolla, 16-18 mm long and 0.8-1.2 mm diam.; stigma capitate or 7-lobed, 1.1-1.4 mm long and 1.1-1.2 mm diam. Capsules depressed obloid, 4-4.8 mm long and 5.1-6.5 mm diam., dark gray, valves not separating from pericarp; seeds oblong, 1.2-1.3 mm long and 0.4-0.5 mm diam.

Distribution. (Fig. 28D). Bejaria steyermarkii is endemic to subparamo sandstone areas of Cerro Turumiquire, Sucre, Venezuela at 2000-2950 m alt. Flowering and fruiting specimens have been collected in May.

Specimens examined. VENEZUELA. Sucre: Cerro Turumiquire, summit of E peak, 2500 m, 6 May 1945 (fl, fr), Steyermark 62614 (F, MO, US, VEN); Cerro Turumiquire, 2950 m, 1925, Tate 199 (US), 200 (US), 201 (US), 218 (US).

Table 54.

Morphological comparison of *Bejaria nana*, *B. tachirensis*, and *B. steyermarkii*.

	B. nana	*B. tachirensis*	*B. steyermarkii*
Height (m)	0.4-2.0	0.3-1.0	0.3-1.2
Leaf size (mm)	8.5-18 x 1.5-2.5	8-23 x 2.5-7	10.5-18 x 2.2-4.4
Leaf shape	linear	lanceolate to ovate	lanceolate to elliptic
Leaf curling	curled	flat or revolute	revolute
Pedicel length (mm)	1-4.5	6.5-14	3.5-7.5
Calyx lobe length (mm)	2.3-2.9	2.5-3.3	2.3-2.6
Corolla shape	cup-shaped	cup-shaped	bell-shaped
Petal color	red-scarlet	rose-red	pink
Petal length (mm)	5-11 x 2.7-4.3	11-12 x 5.1-8.2	14-17 x 3.7-6.8
Elevation	2700-3350	2400-3560	2000-2950

Bejaria steyermarkii is characterized by small, elliptic leaves with acuminate apices, bell-shaped corollas, and short pedicels. It seems to be an intermediate between *B. aestuans* on the one hand and *B. tachirensis* and *B. nana* on the other. Although it lacks the cup-shaped flowers of *B. tachirensis* and *B. nana*, the petals are short and the leaves are small as in those species. It differs from *B. nana* and *B. tachirensis* particularly by corolla shape and petal length (more than 12 mm long vs. 10-11 mm long in *B. tachirensis* and less than 10 mm long in *B. nana*). Table 54 summarizes these differences. It differs from *B. aestuans* in petiole length (0.8-1.7 mm long vs. (1-)3-12 mm long in *B. aestuans*), pedicel length (3.5-7.5 mm long vs. (3-)9-45 mm long in *B. aestuans*), leaf size (10.8-18 mm long vs. (8-)15-80(-125) mm long in *B. aestuans*), and by lacking of axillary racemes (often present in *B. aestuans*).

12. **Bejaria neblinensis** Maguire, Steyermark, & Luteyn, Mem. New York Bot. Gard. 29: 141. 1978, "Befaria". Type. Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, base of Pico Phelps, 2500-2800 m, 2 Dec 1965 (fl, fr), *Maguire & Pires 60477* (holotype, NY, photo, NY neg. 10570, microfiche of NY herbarium #760/C5; isotypes, F, K, NY, VEN, photo, NY neg. 105469, 9671, microfiche of NY herbarium #760/C6).

Shrub to 1 m tall; older branches striate, glandular-hispid, bark gray and tan striped; twigs subterete, dark brown or black, glandular-hispid. Leaves coriaceous, flat, elliptic, 1.3-1.6 x 0.5-0.6 cm, apex acute to acuminate or cuspidate, mucronate, base cuneate, margin glandular-ciliate, flat or usually revolute, both surfaces and midveins glandular-hispid; petiole slightly flattened in cross-section, 1-2.5 mm long, and 0.7-1 mm diam., glandular-hispid. Inflorescence terminal, racemose, 7-13-flowered; rachis ca. 3.8 cm long and 1.5 mm diam., brown or dark maroon, glandular-hispid; floral bracts elliptic, flat, 8.3-10.2 x 2.9-3.6 mm, apex acute, base cuneate, margin glabrous, adaxial surface glandular-hispid, abaxial surface glabrous; pedicels ascending, 13-20 mm long and 0.6-0.8 mm diam., glandular-hispid; bracteoles inserted in basal ½ of pedicel, oblong, flat, 3.2-3.6 x 0.7-0.8 mm, apex acuminate, base cuneate, margin glabrous, both surfaces glandular-hispid. Flowers 7-merous; calyx ca. 5.3 mm long and 8 mm diam.; tube ca. 1.8 mm long and 3.5 mm diam., brown or orangish-brown, glandular-hispid; lobes ovate, 2.9-3.6 x 2.9-3.4 mm, longest lobe 3.4 mm, apex acute or truncate, margin entire, ciliolate and glandular-ciliate, abaxial surface glandular-hispid; corolla bell-shaped; petals imbricate, oblanceolate, pink, 16.5-17.5 x 3.8-6.1 mm, apex obtuse, base cuneate, margin undulate, lamina glabrous; stamens included, 12.5-15.5 mm long; filaments

0.6-1 mm diam., tomentose; anthers 1.2-1.6 mm long and 1-1.2 mm diam., glabrous; ovary glabrous; style slightly exserted, 20 mm long and 0.8 mm diam.; stigma capitate, 1.1 mm long, and 1.7 mm diam. Capsules depressed transversely ellipsoid, 4.4 mm long and 8.3 mm diam., brown, valves not separating from pericarp; seeds unknown.

Distribution. (Fig. 27D). *Bejaria neblinensis* is rare on open slopes of Cerro de la Neblina (Pico Phelps) at 2500-2800 m alt. It was collected in flower and fruit in December.

Specimens examined. This species is known only from the type collection.

Bejaria neblenensis is poorly known. Since the shape of the flower is not known for certain, relationships are also not know. Generally *B. neblinensis* can be characterized by the short petals, small leaves and short petioles. It is similiar to *B. tachirensis* but is geographically isolated from it and has copius glandular-hispid pubescence.

13. **Bejaria tachirensis** A. C. Smith, Fieldiana, Bot. 28(3): 450. 1953, "Befaria". Type. Venezuela. Táchira: Páramo de Tamá, 3045-3475 m, 15 Jul 1944 (fl, fr), *Steyermark 57412* (holotype, F; photos, F neg. 52522, NY neg. 9672; isotypes, A, frag. US, photos F neg. 52522, US neg. 3227). Fig. 37A-B. Fig. 38.

Shrub 0.3-1.0 m tall; older branches fissured, glabrous, bark gray, with persistent and projecting leaf bases; twigs bluntly angled, maroon, hispid or sometimes glandular-hispid. Leaves coriaceous, flat or slightly longitudinally curled, lanceolate to ovate, 0.8-2.3 x 0.25-0.7 cm, apex acute, bluntly mucronulate, base cuneate, margins glabrous, slightly revolute, lamina and midvein glabrous; petiole slightly flattened in cross-section, 0.7-2.2(-3) mm long and 0.5-1.2 mm diam., glabrous. Inflorescence terminal, racemose, 2-14-flowered; rachis 0.9-2.1 cm long and 0.5-0.7 mm diam., reddish-purple, hispid or sometimes glandular-hispid; floral bracts lanceolate to ovate, flat, 4.2-15 x 0.5-3.8 mm, apex acuminate, mucronate, base cuneate, margin glabrous, revolute, both surfaces glabrous; pedicels ascending or divergent, 6.5-14 mm long and 0.5-0.7 mm diam., hispid or sometimes glandular-hispid; bracteoles inserted near middle of pedicel, linear to lanceolate, flat, 1.8-3 x 0.3-0.5 mm, apex acuminate, base cuneate, margin glabrous, often involute, both surfaces glabrous or slightly tomentose. Flowers 7-merous; calyx 3-4.3 mm long and (3.9-)5.1-7.7 mm in diam.; tube 0.7-2 mm long and 2.2-3.5 mm diam., orange, brown, red, or maroon, glabrous; lobes ovate to widely ovate, 2.5-3.3 x 2-3 mm, longest lobe 2.8-3.3 mm, apex acute to acuminate, margin entire, ciliolate, abaxial surface glabrous; corolla cup-shaped; petals imbricate, obovate to widely obovate, pink or red, 11-12 x 5.1-8.2 mm, apex obtuse, base attenuate or cuneate, margin entire, distally ciliolate, lamina glabrous; stamens included, alternately 5.4-6.8 mm and 7.1-9.2 mm long; filaments 0.4-0.8 mm diam., tomentose; anthers alternately 1.5-1.9 mm long and 1-1.4 mm diam, glabrous; ovary glabrous; style included, 9.5-10 mm long and 0.5 mm diam.; stigma 7-lobed, 0.7-0.9 mm long and 1.6-1.7 mm diam. Capsules depressed transversely ellipsoid, 3.5-5 mm long and 6.3-11 mm diam., orange-brown, valves not separating from pericarp; seeds ellipsoid, 0.9-1.4 mm long and 0.3-0.5 mm diam.

Distribution. (Fig. 28D). Bejaria tachirensis is native to Páramo de Tamá and the Sierra de Cocuy, where it occurs primarily on limestone outcrops and grass paramos, at 2400-3560 m alt. Flowering specimens have been collected from october to June, while fruiting specimens have been collected sporatically throughout the year.

Specimens examined: COLOMBIA. Arauca: Sierra Nevada de Cocuy, Quebrada El Playón, 3150 m, 10 Jun 1973 (fl), Cleef 10138 (COL). Boyacá: Vado Hondo, Siberia, páramo betw. Peña de Arnical and Alto de Mogotes, 3290 m, 3 Apr 1973 (fl), Cleef 9333 (COL); Peña de Arnical, N of Vado Honda, 3600 m, 6 Apr 1973 (fl), Cleef 9438 (COL), 3560 m, 7 Apr 1973 (fl), Cleef 9479 (COL, L, NY, U). Norte de Santander: Páramo de Tamá, 3000-3200 m, 28 Oct 1941 (fl, fr), Cuatrecasas et al. 12682 (GH, US).

VENEZUELA. Apure: Dto. Páez, nr. base of E cliffs of

Fig. 38. _Bejaria tachirensis_ (_Luteyn et al. 5903_). A. Habit. B. Flower. C. Stamen. D. Ovary and Style. E. Petal. F. Leaf. G. Floral Bract. H. Bracteole. I. Fruit. J. Overall Habit.

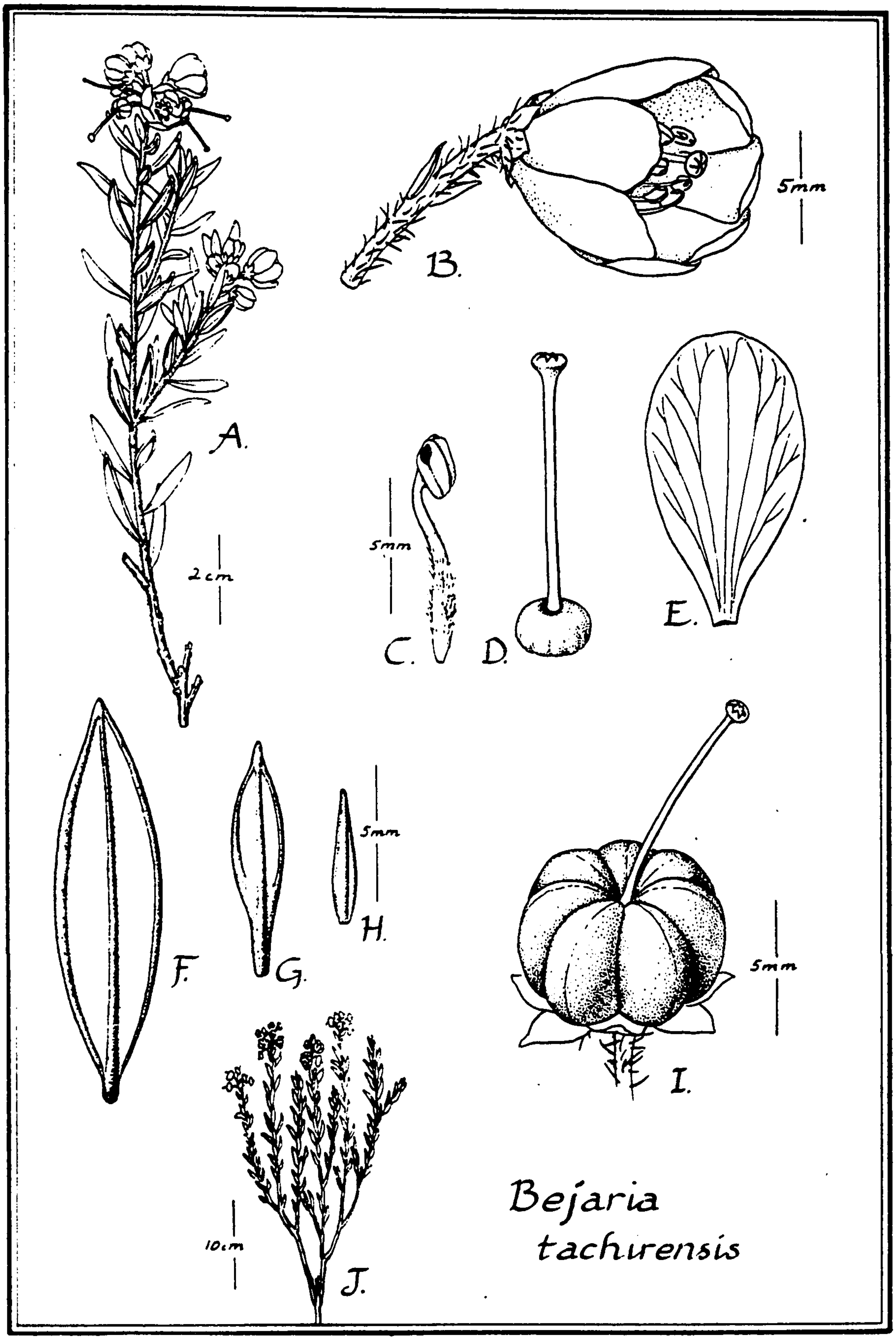
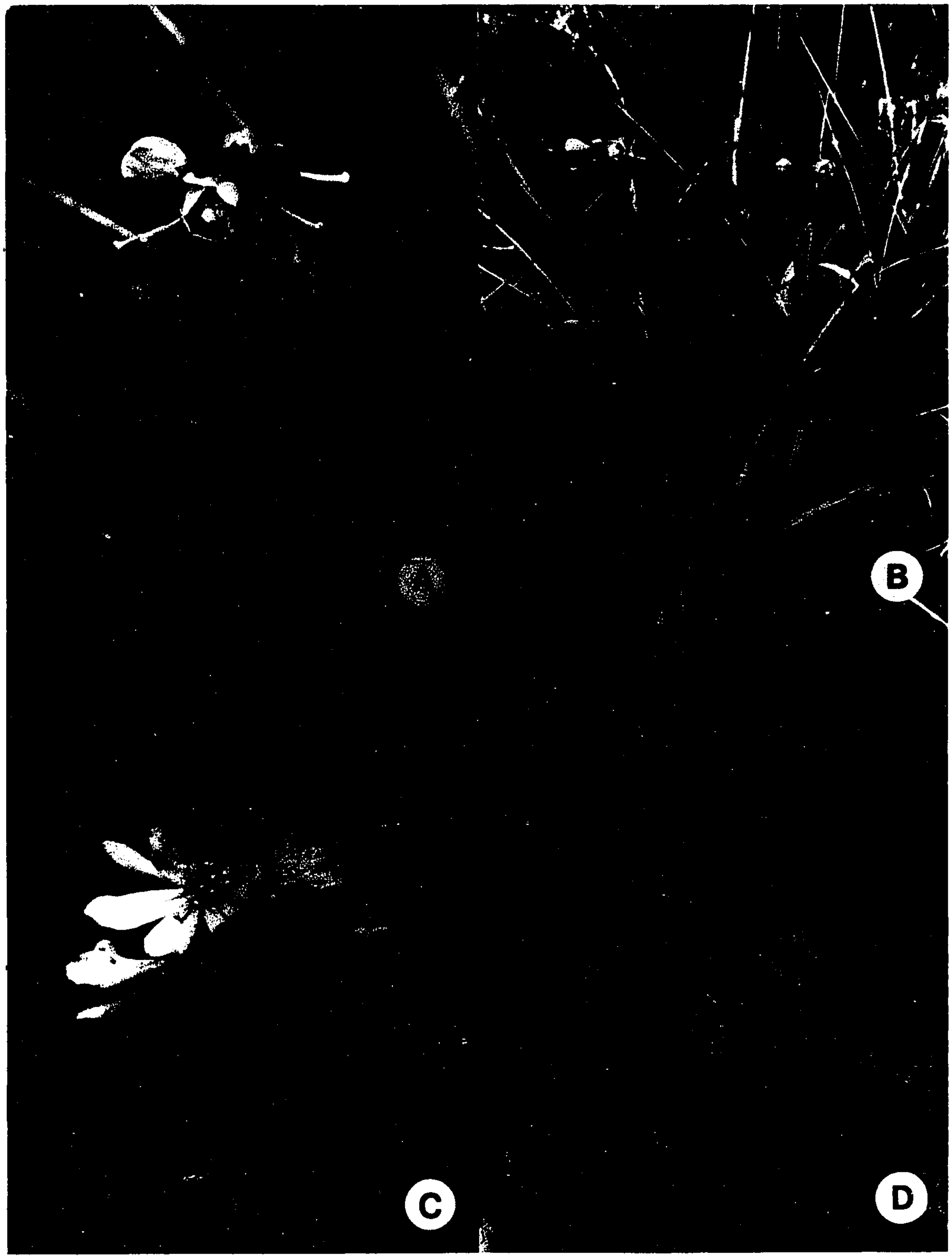

A.
B.
5mm
C.
5mm
D.
E.
2cm
F.
G.
H.
5mm
I.
5mm
J.
10cm
Bejaria
tachirensis

Fig. 39. A-B. _Bejaria tachirensis_. _Luteyn et al. 5903_. A. Inflorescence, B. Habit. C. _Bejaria subsessilis_, Inflorescence, _Clemants 2278_. D. _Bejaria_ hybrid. Flowers, _Clemants & Luteyn 1678_. (Fig. A-B by Luteyn, Fig. C-D by Clemants).


B
C
D

Pata de Judío, 1 km W of La Línea, E cliff of the Grand Páramo de Tamá, 3200 m, 27 Jun 1973 (fl, fr), *Ruíz-Terán & López-Figueiras 8888* (MERF, NY); Páramo de Pata de Judío, SE Páramo de Tamá, 3000-3200 m, 19 Jan 1968 (fl, fr), *Steyermark et al. 101117* (F, K, L, MO, NY, U, US, VEN). Tachirá: Páramo de Tamá, 3100-3300 m, 1938, *Cardona 142* (VEN), *148* (VEN), Jul 1939 (fr), *Cardona 317* (US, VEN), 3000-3250 m, 12 Nov 1976 (fl, fr), *Charpin et al. 13199* (G, NY), 3000-3200 m, 18 Mar 1973 (fl), *Fernández P. 2087* (MY); trail leading to summit, 29 Jan 1978 (fl), *Luteyn et al. 5303* (NY); NE side, 18 Oct 1978 (fl), *Luteyn et al. 5903* (NY, VEN); summit of El Cobre, Páramo de Tamá, 13 Dec 1970 (fl), *Ruíz-Terán & López-Figueiras 1225* (L, MERF, NY); W slope of Banderas, 2500-3200 m, 16 Dec 1970 (fl, fr), *Ruíz-Terán & López-Figueiras 1339* (L, MERF, NY); lower slope of Banderas, 3300-2400 m, 28 Nov 1972 (fl, fr), *Ruíz-Terán et al. 8166* (MERF, NY); Páramo de Tamá, 3045-3475 m, 15 Jul 1944 (fr), *Steyermark 57412* (VEN), 3000-3200 m, 20-23 May 1967 (fl), *Steyermark et al. 98632* (L, MER, MO, VEN).

Bejaria tachirensis is characterized by small, cup-shaped corollas, small flat leaves, and terminal racemes. For a discussion of the differences between this species, *B. nana*, *B. steyermarkii*, and *B. neblinensis* see the discussion following *B. steyermarkii*.

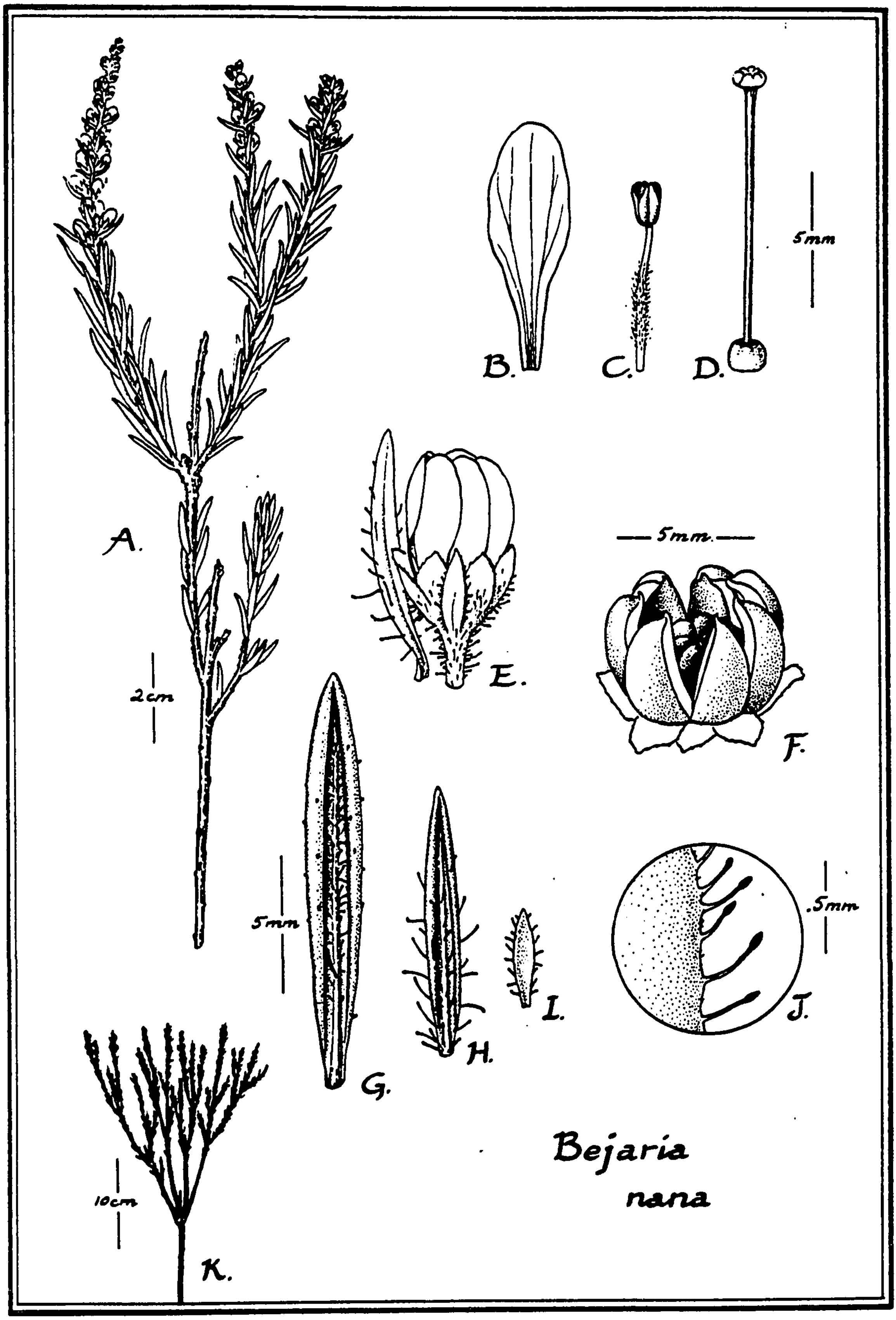
14. **Bejaria nana** A. C. Smith & Ewan, Contr. U.S. Natl.

Herb. 29: 333. 1950, "Befaria". Type. Colombia. Magdalena: Sierra Perijá, Tres Tetas (S peak), 3000 m, 28 Apr-4 May 1942 (fl), Carriker 16 (holotype, US; isotype, COL). Fig. 40.

Shrub or small tree 0.4-2 m tall; older branches fissured, glabrous, bark gray to black, often with persistent and projecting leaf bases; twigs subterete, covered with persistant and projecting leaf bases, dark brown to black, glandular-hispid. Leaves coriaceous, longitudinally curled, linear, 0.85-1.8 x 0.15-0.25 cm, apex acute to acuminate, sometimes glandular-mucronate, base attenuate or cuneate, margin glandular-ciliate, revolute, both surfaces and midveins glandular-hispid or sometimes adaxial surface glabrous; petiole slightly flattened adaxially, 0.5-2.5 mm long and 0.4-0.6 mm diam., glandular-hispid. Inflorescence terminal, spike-like racemes, 8-20-flowered; rachis 1.5-4.4 cm long and 1-1.5 mm diam., orange, brown, or gray, densely glandular-hispid; floral bracts elliptic to linear, rarely ovate, flat or longitudinally curled, 3.1-14.5 x 0.9-1.8 mm, apex acute to acuminate, base cuneate, margin glandular-ciliate, revolute, abaxial surface glandular-hispid; pedicels ascending or usually divergent, 1-4.5 mm long and 0.6-0.9 mm diam., densely glandular-hispid; bracteoles inserted in apical ½ of pedicel or often immediately below the calyx, elliptic or oblong, flat, 2-4 x 0.4-1 mm, apex acute to acuminate, rarely obtuse, base cuneate, margin glandular-ciliate, both surfaces glandular-ciliate. Flowers 7-merous; calyx 2.7-4.4 mm long and 4-5.9 mm diam.; tube 1-2.7 mm long and 3.2-4 mm diam., orange, brown, or purple, glandular-hispid; lobes ovate to deltate or sometimes elliptic, (1.5-)2-2.8 x (1.1-)1.4-2.9 mm, longest lobes 2.3-2.9 mm, apex caudate or acute, margin dentate or entire, glabrous or sometimes glandular-ciliate, abaxial surface glandular-hispid, rarely only tomentose; corolla cup-shape; petals imbricate, oblanceolate, red to scarlet, 5-11 x 2.7-4.3 mm, apex obtuse, base cuneate, margin undulate, glabrous or sometimes distally slightly ciliolate, lamina glabrous; stamens included, 8-11 mm long; filaments 0.3-0.7 mm diam., tomentose; anthers 1.2-1.8 mm long and 0.8-1.1 mm diam., glabrous; ovary glabrous; style subequal to corolla, 8.5-11 mm long and 0.5-0.7 mm diam.; stigma 7-lobed, 0.7-0.9 mm long and 1.3-1.7 mm diam. Capsules depressed obloid, 3.4-4.5 mm long and 4.9-6.4 mm diam., brown to black, valves separating from pericarp; seeds oblong or ellipsoid, 0.8-1.1 mm long and 0.3-0.4 mm diam.

Distribution. (Fig. 28D). *Bejaria nana* is endemic to the Sierra de Perijá along the border of Colombia and Venezuela where it is found usually in paramos, rarely in montane forests, at 2700-3350 m alt. Flowering specimens were collected from February to May and November, fruiting

Fig. 40. _Bejaria nana._ (_Cuatrecasas & Romero-Castañeda 21521_) A. Habit. B. Petal. C. Stamen. D. Ovary and Style. E. Bud. F. Fruit. G. Leaf. H. Floral Bract. I. Bracteole. J. Close-up of Bracteole margin. K. Overall habit.


A.
2cm
B.
C.
D.
5mm
E.
5mm
F.
5mm
G.
H.
I.
.5mm
J.
10cm
K.
Bejaria
nana

specimens were collected from November to March.

Specimens examined. COLOMBIA. Cesar: Mpio. Valledupar, Corregimiento de Manaure, Serrania de Los Motilones, 2800 m, 1979, *J. V. Rodríguez s.n.* (COL). Magdalena: Sierra de Perijá, E of Manaure, Sabana Rubia, 3000-3100 m, 6 Nov 1959 (fr), *Cuatrecasas & Romero-Castañeda 25039* (COL, US); plain betw. Cerro Venado and Cerro Avión, 3270-3350 m, 8 Nov 1959 (fl, fr), *Cuatrecasas & Romero-Castañeda 25121* (COL, US); E of Manaure, Quebrada de Floridablanca, 2700-2800 m, 10 Nov 1959 (fl), *Cuatrecasas & Romero-Castañeda 25167* (COL, US); 12 kms ENE of Manaure, 48 kms E of Valldeupar, 1 km from Venezuelan border, 3000 m, 5 Feb 1945 (fl, fr), *Grant 10844* (NA, US); Mpio. Robles, Manaure, 2800 m, 3 Mar 1959 (fr), *Romero-Castañeda 7326* (AAU); Corregimiento de Manaure, Sabana Rubia, 2800 m, 3 Mar 1959 (fl), *Romero-Castañeda 7333* (COL).

VENEZUELA. Zulia: Perijá, 2800-2900 m, 29 Dec 1950 (bud), *Gines 1985* (US); Cerro Getarí, Perijá, Apr 1952 (fl), *Urbano 9* (VEN).

Bejaria nana is characterized by small cup-shaped corollas, small curled leaves, and terminal spike-like racemes. It differs from *B. tachirensis* by its curled leaves (usually flat in *B. tachirensis*), spike-like raceme (not spike-like in *B. tachirensis*), and glandular-hispid pubescence (rare in B. tachirensis). Bejaria tachiresis and B. nana differ from B. steyermarkii in shorter (less than 12 mm) cup-shaped corollas (bell-shaped and more than 12 mm long in B. steyermarkii).

15. **Bejaria subsessilis** Bentham, Pl. hartw. 143. 1845, "Befaria". Type. Ecuador. Loja: Loja, 1842 (fl), Hartweg 797 (holotype, K, photo NY neg. 11703; isotypes, CGE-2 sheets, G, LD, LE, OXF, P, W, photo, F neg. 28916.). Fig. 39C.

Shrub to 1 m tall; older branches striate, glabrous or sometimes hispid, bark dark gray or gray and brown; twigs subterete, ferruginous, hispid. Leaves coriaceous, flat, ovate, 1.65-3.9 x 0.9-2 cm, apex acute or obtuse, bluntly mucronate, base obtuse or truncate, margin glabrous, rarely sparcely ciliate near base of lamina, slightly revolute, both surfaces glabrous or sparcely hispid along midvein especially proximally; petiole slightly flattened in cross-section, 1-3.5 mm long and 1-1.5 mm diam., hispid. Inflorescence terminal, racemose, 8-19-flowered; rachis 3.5-7.6 cm long and 1.3-1.9 mm diam., rusty-red, hispid; floral bracts elliptic to lanceolate or oblanceolate, flat, 2.5-15.5 x 0.5-5.3 mm, apex acute to acuminate, base cuneate, margin glabrous, sometimes ciliate, slightly revolute, both surfaces glabrous, midvein sometimes hispid; pedicels ascending, 16.5-26 mm long and 0.5-1.1 mm diam., usually sparcely hispid, sometimes glabrous, or tomentose; bracteoles inserted in basal ½ of pedicel, linear to lanceolate, sometimes elliptic, flat, 2.2-3.6 x 0.8-1 mm, apex acuminate, base truncate, margin glabrous, often slightly involute, both surfaces glabrous or slightly tomentose. Flowers (6-)7(-8)-merous; calyx 4.7-5.3 mm long and 4.9-6.2 mm diam.; tube 1.3-2.2 mm long and 4.2-4.7 mm diam., dark red to maroon, glabrous; lobes ovate to very widely ovate, 2.6-4.3 x 2.4-3.8 mm, longest lobes 3-4.3 mm, apex obtuse to acute, margin entire, glabrous or sometimes ciliolate, abaxial surface glabrous; corolla bell-shaped or spreading; petals spreading, oblanceolate to spatulate, pink to light red, sometimes red striped, 24-37 x 5-10 mm, apex obtuse, base cuneate, margin entire, glabrous or distally ciliolate, lamina slightly tomentose distally; stamens subequal to corolla, 21.5-35.5 mm long; filaments 0.4-0.9 mm diam., tomentose; anther 2.1-3 mm long and 0.9-1.4 mm diam., glabrous; ovary glabrous; style exserted, 30.5-42 mm long and 0.7-1 mm diam.; stigma capitate, 1.3-1.8 mm long and 1.7-2.9 mm diam. Capsules depressed obloid, 5.5-6 mm long and ±9 mm diam., brown, valves not separating from pericarp; seeds not seen.

Distribution. (Fig. 28C). Bejaria subsessilis is endemic to the dry hills south of the town of Loja at 2200-2800 m alt. It flowers from March to April and July to November, and bears fruit in April, July, and October.

Specimens examined. ECUADOR. Loja: S of Loja, ca. 2350 m, 4 Oct 1955 (fl, fr), *Asplund* *17923* (L, S); Nudo de Cajanuma, 8000 ft, 4 Oct 1944 (fl, fr), *Camp* *565* (NY); S of Loja, Aug 1982, *Clemants* *2278* (NY, QCA); without locality, Jul 1884 (fl), *Cross* *s*.*n*. (BM); Namanda, 2400-2500 m, 18 Apr 1946 (fl), *Espinosa* *171* (NY); Loja, 2200 m, 13 Jul 1977 (fl), *Harling* *1643* (L, S); rd. Loja-Zamora, 2550 m, 1319, 20 Mar 1972 (fl), *Harling* *11319* (GB, NY); Loja, 1842, *Hartweg* *797* (CGE, G, LD, OXF, W, photo F neg. 28916); betw. La Toma and Loja, 1800-2600 m, 4 Sep 1923 (fl), *Hitchcock* *21422* (NY, US); hills nr. Loja, Sep 1864 (fl), *Jameson* *s*.*n*. (E, W), nr. Loja, Oct 1864 (fl), *Jameson* *s*.*n*. (BM), without locality or date, *Jameson* *s*.*n*. (NY-3 sheets, US-3 sheets), Loja, 8 Sep 1865, *Jameson* *79* (K); ca. 6 km SW of Loja, 2700 m, 3 Apr 1965 (fl), *Knight* *76* (WIS); 4 km S of Loja, 2700 m, 17 Apr 1966 (fr), *Knight* *471* (WIS); 2400 m, 10 Jul 1965, *Knight* *823*; E of Loja, 2500-2800 m, Oct-Nov (fl), *Lehmann* *4964* (F); Loja-Zamora rd., 207 km W of pass, 2400-2700 m, 17 Jun 1979 (fl), *Lojtnant* *&* *Molau* *15010* (AAU, GB); nr. Loja, 2300 m, 27 Jul 1939 (fl), *Penland* *&* *Summers* *1117* (F, GH); without locality, Aug 1847 (fl), *Seeman* *862* (GH, K); mts. of Samora, S of Loja, Jul 1864, *Veitch* *s*.*n*. (K); Loja, *Warszewitz* *s*.*n*. (B, n.v., photo F neg. 18293).

Bejaria *subsessilis* is characterized by the ovate, subsessile leaves, large flowers and long setae. It

Fig. 41. Graph showing the relationship of calyx lobe length and petal length in *B. aestuans*, *B. resinosa*, and *B. subsessilis*. This graph also shows the intermediate nature of *B. subsessilis*.

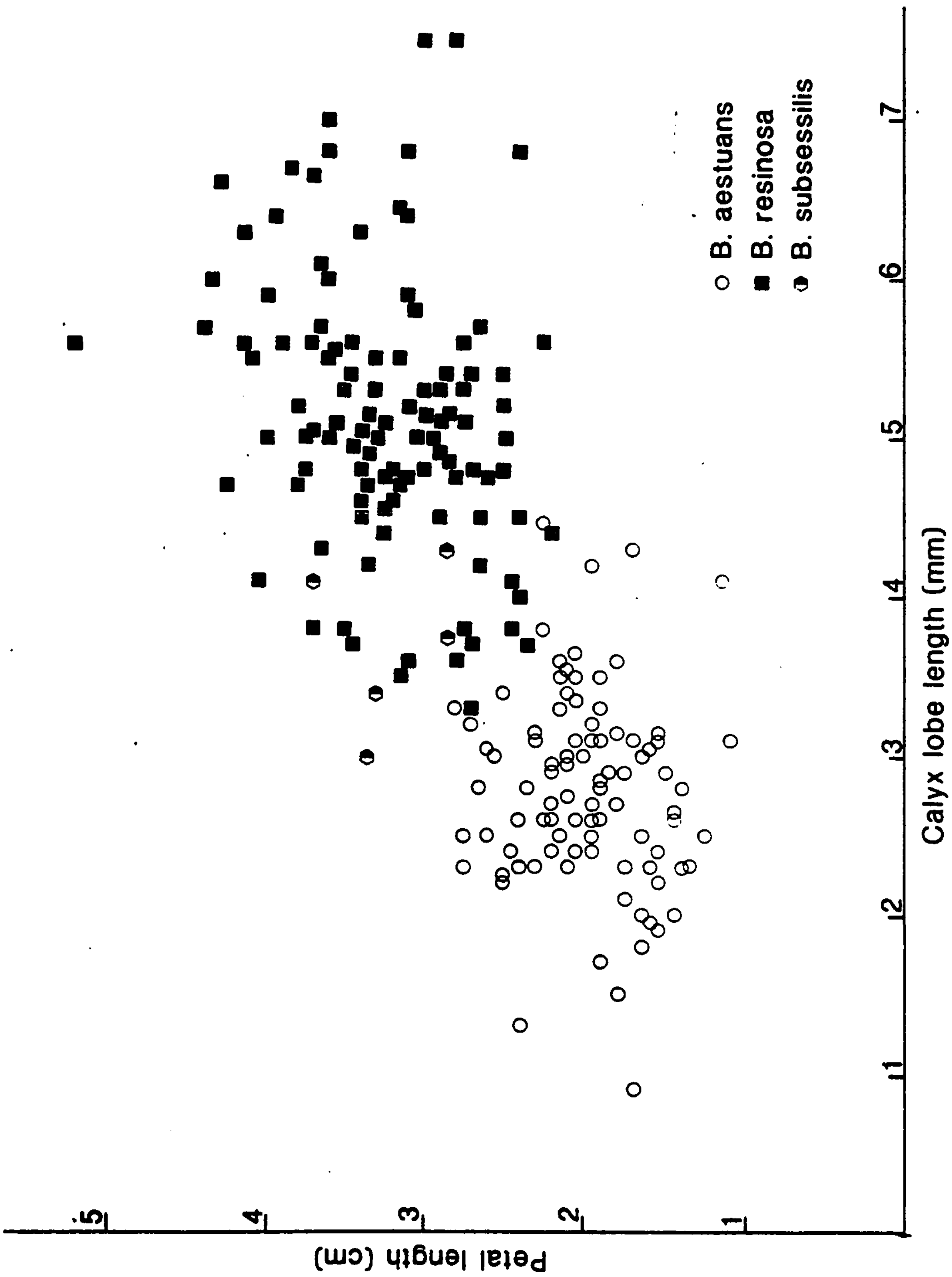

Petal length (cm)
.5
4
3
2
1
Calyx lobe length (mm)
11
12
13
14
15
16
17
○ B. aestuans
■ B. resinosa
◆ B. subsessilis

Table 55. Morphological comparison of *Bejaria subsessilis* and its putative parents.

	B. aestuans	*B. subsessilis*	*B. resinosa*
Leaf shape	elliptic (lanceolate)	ovate	ovate to elliptic
Leaf length (cm)	(0.8-)1.5-8(-12.5)	1.6-3.9	(0.7-)1-2.5
Leaf apex	obtuse to acute	acute to obtuse	acute to acuminate
Leaf base	cuneate	obtuse to rounded	obtuse to rounded
Petiole length (mm)	(1-)3-12	1-3.5	0.5-4
Rachis length (cm)	(0.5-)1.8-18	3.5-7.6	1-3.6
Pedicel length (mm)	(3-)9-45	16.5-26	10-18
Calyx lobe lengths (mm)	(0.9-)2.3-3.7(-4.6)	3-4.3	3.8-7.5
Flower color	pink to white (red)	pink to light red	red to purple
Petal length (mm)	(8.5-)12-27.5(-45)	24-37	(16.5-)20-40
Capsule length (mm)	4-8	5.5-6	7-9

probably represents a species of hybrid origin. The putative parents would be *B. aestuans* and *B. resinosa*. *Bejaria subsessilis* has the spreading pink corolla, long pedicels, and long rachises of *B. aestuans*, the ovate leaf, short petiole, and obtuse leaf base of *B. resinosa*, and is intermediate in leaf length, calyx lobe length, and petal length. These differences are also shown in Table 55, and the intermediacy with respect to calyx lobe length and petal length is shown in Fig. 41.

Bejaria subsessilis is easily distinguished from *B. resinosa* and the hybrid swarm by its spreading flowers (tube-shaped in *B. resinosa* and only slightly tube-shaped in the hybrid, Fig. 39D). It differs from *B. aestuans* by leaf shape (usually elliptic in *B. aestuans*), shorter petioles (1-3.5 mm long vs. (1-)3-12 in *B. aestuans*), and the longer petals (24-37 mm long vs. 12-27.5(-45) mm in *B. aestuans*).

Doubtful Names

Bejaria microphylla Planchon ex Hérincq, Rev. Hort. sér. 3, 4: 185. 1850, nomen nudum. No specimens annotated *B. microphylla* have been found.

Bejaria densa Planchon ex Hérincq, Rev. Hort. sér. 3, 4: 185. 1850, nomen nudum. Type: probably *Linden 65*

(W, photo NY neg. 11695) which has *B. densa* written on the label. This is a specimen of *B. aestuans*.

Bejaria sandiensis Mansfeld & Sleumer, Notizbl. Bot. Gart. Berlin-Dahlem, 12: 273. 1935, "Befaria". Type. Peru. Puno: Prov. Sandia, Sandia, 2200 m, 3 Apr 1902 (fl), *Weberbauer 659* (holotype, B+, n.v.). I have seen no type specimen, nor are any other specimens cited. Mansfeld and Sleumer (1935) place *B. sandiensis* in an informal association with *B. sprucei*, *B. schomburgkii*, *B. hispida*, and *B. variabilis*, but based on the protologue this species would seem to be a synonym of *B. aestuans* because it does not have the long exserted stamens of *B. sprucei*. I have not placed it in formal synonomy because I do not know the shape of the corolla.

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4. *B. aestuans*
5. *B. zamorae*
6. *B. sprucei*
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8. *B. resinosa*
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Cleef, A. M. & T. Duncan, 3191 (8).

Cleef, A. M. et al., 3531 (4).

Clemants, S. E., 2045 (8); 2046 (7); 2274 (8); 2275 (4); 2276 (hybrid betw. 4 & 8); 2277 (8); 2278 (15); 2295, 2345 (4); 2396, 2397 (8); 2482 (4); 2483 (9).

Clemants, S. E. & F. Delascio, 2453, 2454, 2467 (10); 2479, 2480, 2481 (6).

Clemants, S. E. & D. Díaz, 2420, 2447 (4).

Clemants, S. E. & J. A. Dugarte, 2415, 2421, 2427, 2428, 2429, 2434, 2441, 2443, 2445 (4).

Clemants, S. E. & R. Fernândez, 2000 (6); 2007 (3); 2019 (4).

Clemants, S. E. & J. L. Luteyn, 1668 (4); 1669 (8); 1670, 1671, 1672, 1673, 1674 (4); 1675, 1676 (8); 1677 (4); 1678 (hybrid betw. 4 & 8); 1679 (4); 1680 (8); 1681, 1682 (4); 1683 (8); 1684 (4); 1685, 1686 (8); 1687 (4); 1688 (8).

Clemants, S. E. & A. Miller, 1583 to 1614, 1616 to 1667 (1).

Clemants, S. E. & D. Wm. Stevenson, 2500, 2501, 2502 (4).

Clemants, S. E. et al., 2220, 2221 (8).

Clements, R., 37 (4).

Clifton, M. S., s.n. (3 Jul 1976) (1).

Clinton, G. W., s.n. (coll. 1870) (1).

Coile, N. C., 924 (1).

Coker, W. C., s.n. (28 Jan 1933), s.n. (3 Feb 1933), s.n. (23 Dec 1935), s.n. (8 Jan 1948), s.n. (22 Jan 1948), s.n. (24 Jan 1948) (1).

Cole, D., s.n. (12 Jan 1975) (1).

Conard, H. S., s.n. (6 Sep 1963), s.n. (15 Jun 1968) (1).

Conzatti, C., 2529, 2530, 4355, 6000 (4).

Cook, O. F. & G. B. Gilbert, 1024, 1396 (4).

Cooley, G. R., et al., 7554, 7555 (1).

Cooper, Dr., s.n. (coll. 1859) (1).

Corcoran, C. M. & G. M. Diggs, 1679 (4).

Core, E. L., 33 (8); 49, 241 (7); 546 (8); 694, 765 (4); 895 (8).

Correa V., J. & F. A. Barkley 18A047 (4).

Correll, D. S., E393 (4); 5505, 5741, 47179 (1).

Cosentino, K., 219 (4).

Cowan, R. S. & T. R. Soderstrom, 2168a, 2187 (6).

Cozzens, F., s.n. (Alabama), s.n. (Florida) (1).

Craighead, F. C., s.n. (7 Sep 1971) (1).

Creager, D. B., 611 (1).

Creager, F. C. & D. B. Creager, 145 (1).

Croizat, L., s.n. (Pico Bolivar), 190 (4).

Crosby, G. T., 277 (1).

Cross, R. M., s.n. (8 and 15).

Cruger, O., 28 (4).

Cuadros V., H., 1477 (4).

Cuatrecasas, J., 18, 345, 1185, 1769, 1818, 2686, 5011, 5051, 5625, 5626 (8); 7152 (6); 9508, 9534, 10327, 10351, 10400 (8); 11956A (7); 13384, 13426 (4); 13817 (7); 17915 (8); 18167 (7); 18846, 19254 (8); 20032 (7); 20063, 20570, 20838 (8); 21591 (7); 21831 (8).

Cuarecasas, J. & H. García-Barriga, 9743, 9915, 10195 (8).

Cuatrecasas, J. & H. Cuadros, 28889 (8).

Cuatrecasas, J. & R. Jaramillo M., 25951, 26759 (8).

Cuatrecasas J. & L. Rodriguez 27746, 27747 (8); 27962 (4).

Cuatrecasas, J. & R. Romero-Castañeda, 24747 (4); 25039, 25121 (14); 25166 (4); 25167 (14).

Cuatrecasas, J. & L. Willard, 26468 (7).

Cuatrecasas, J. et al., 12272 (4); 12274 (8); 12500 (4); 12682 (13); 25670, 25681 (7); 27550, 28316, 28317 (8); 28445, 28472 (4); 28989 (8); 29001 (4).

Cuming, H., s.n. (Bolivia), s.n. (Mexico) (4).

Curran, H. M., 1 or 583, 2150 (4).

Curran, H. M. & M. Haman, 1115 (4).

Curtis, M. A., s.n. (Florida) (1).

Curtiss, A. H., s.n. (coll. 1875), s.n. (coll. 1876), 1728, 4360, 4922 (1).

Cuthbert, A., 1329 (1).

Daniel, Bro., 21 (4); 1446, 1832 (8); 4240 (4).

D'Arcy, Wm. G., 1645 (1).

Davé, W. T., 5 (8).

Davidse, G., 4676 (6).

Davidse, G. & A. González, 19498, 19800 (6).

Davidse, G. & O. Huber, 22687, 22699 (6).

Davidse, G. & R. W. Pohl, 2252 (4).

Davis, E. W. & E. Turner, 703 (8).

Davis, J. H., s.n. (7 Oct 1941) (1).

Dawe, M. T., 701 (4).

Delascio, F. & C. Brewer-Carias, 4809, 4923 (10).

Delgado, E., 231 (9); 598 (4).

Delgado, M., 6, 7, 8, 19, 20, 21 (4).

Delgado S., A. et al., 505 (4).

Demaree, D., 50216 (1).

Dennis, R. W. G., 2001 (4); 2235 (9).

Denslow, J., 2116 (4).

DeVall, W., s.n. (16 Jun 1939) (1).

Díaz, B., 2 (4).

Eaton, A. A., 1020 (1).

Eggers, H., 13569 (4).

Ekman, E. L., 13812, 16714 (2).

Ellenberg, H., 818 (?) (4); 3008 (8).

Erazo P., M., 123 (4).

Ern, H., 608 (4).

Espinal T., S., 908 (7); 1233 (4); 1729 (8); 3108 (7).

Espinal T., S. & J. E. Ramos, 2447 (8); 2850, 2892, 2995, 3392 (7).

Espinal T., S. et al., 1521 (4).

Espinosa, R., 171 (15); 307, 781, 913, 914, 2211 (8); 3063 (7).

Ewan, J. A., 15638 (8); 15951, 16142, 16580 (7); 16942 (4).

Ewel, J., 20 (4); 169 (6).

Faircloth, W. R. et al., 1826 (1).

Farenholtz, H., 1836 (4).

Fasset, N. C., 25696 (4).

Feddema, C., 2886 (4).

Fendler, A., 743 (4).

Ferguson, A. M., s.n. (Jun-Jul 1898) (1).

Fernândez, Ant., 888 (4).

Fernândez P., Alv., 218 (9); 888 (4); 2087 (13); 2726, 2727, 2826 (7).

Fernândez P., Alv. & R. Jaramillo M., 5749 (8).

Fernândez P., Alv. & S. Yepes-Agredo, 83 (7).

Ferrari, G., 879, 884 (4); 1048 (6); 1180 (4).

Ferreyra, R., 284, 1852, 3593, 3660, 3671, 6670, 6863, 8187, 9445, 11402 (4); 18479 (6).

Foldats, E., 26 (4); 2607, 7106, 7199, 7202 (6).

Forero, E., 3695 (8).

Forero, E. & R. Jaramillo M., 3719 (8).

Fosberg, F. R., 19073 (8); 19093 (4); 19706, 20200, 20211 (8); 20313 (7); 21348 (8); 21622, 27727, 27830 (4).

Fosberg, F. R., & M. A. Giler, 22834, 22839, 22840 (8); 22871, 23120 (4).

Foster, M. B. & E. Smith, 1506 (4).

Foster, R. B., 9007 (4).

Fox, W. B., 525 (1).

Franco, s.n. (coll. 1842) (4).

Fredholm, A., 5288, 5857 (1).

Friedberg, C., s.n. (coll. 1961) (4); 314 (8).

Fulton, A., 238 (1).

Funck, N., 83, 85 (4); 313, 384 (9).

Funck, N. & L. Schlim, s.n. (Pomplona) (8); 104, 159, 874 (4); 1329, 1330 (8); 1331, 1332, 1456 (4); 1475 (8); 1600, 1604, 1639, 1664 (4).

Galeotti, H. G., 1811, 1812, 1821 (4).

Garber, A. P., s.n. (Feb 1876), s.n. (May 1876), s.n. (Jul 1877) (1).

García, M. M., 88 (4).

García-Barriga, H., 6227 (8); 11035 (7); 11084 (4); 11625, 11948 (8); 12455 (4); 12638 (8); 13303 (4); 13380, 13386, 13394, 15304 (8); 17234, 17458, 17480, 18082 (4); 19414 (8); 19843 (4).

García-Barriga, H. & J. G. Hawkes, 12693, 12744 (7).

García-Barriga, H. & R. Jaramillo M., 19654, 19663 (4); 19743 (8); 19843, 19922, 19929 (4); 20250 (8); 20255 (4); 20698 (8); 20739 (4).

García-Barriga, H. & R. E. Schultes, 13517, 13520, 13544 (8).

García-Barriga, H. et al., 13582 (8).

Garganta F., M. de., 653 (4); 710 (8); 756, 1176 (4); 1286, 2187 (8).

Gärtner A., N., s.n. (22 Sep. 1959) (4).

Gehriger, W., 363 (4).

Genelle, P. & G. Fleming, 251, 933, 2086, 2105, 2171, 2854 (1).

Gentry, A. & C. Bonifaz, 34735 (8).

Gentry, A. & H. León, 20304 (4).

Gentry, A. et al., 8914 (8); 11064, 19402 (4).

Ghiesbreght, A., s.n. (coll. 1842-1843), 31 (4).

Giacometto, J., 104 (4).

Gillett, J. M. & R. Jaramillo M., 16562 (8).

Gillis, Wm. T., 11404, 12496 (1).

Gines, H., 419, 1172, 1229, 1978 (4); 1985 (14); 1999, 2019, 4243 (4).

Glassman, S. F., 1953 (4).

Glasnevin, R. B. G., 4 (4).

Godfrey, R. K., 60089, 68578, 68606, 74315 (1).

Godfrey, R. K. & R. Kral, 53808 (1).

Gómez, M. & V. Conzatti, 6000 (4).

Gómez-Pompa, A., 690 (4).

González M., R. & Bro. Daniel, 1832 (8).

González Ortega, J. G., 319, 4073 (4).

Goudot, J., s.n. (Bogotá), 1, 2 (8).

Grant, M. L., 9428 (8); 9643, 9750 (4); 10679, (7); 10844 (14); 10849, 10941 (4).

Grubb, P. J. et al., 611 (4).

Guevara Amórtegui, B., A-23, 247 (8).

Guízar, E. & A. Niembro, 1850 (4).

Gutiérrez V., G., 266 (8).

Gutiérrez V., G. & A. L. Delisle, 1123 (4).

Gutiérrez V., G. & R. E. Schultes, 605 (6).

Gutiérrez V., G. et al., 2, 5, 6, 7 (4); 18C267 (7).

Haenke, T., s.n. (4 and 8).

Halberg, B., s.n. (9 Jun 1961) (4).

Hall, J. M., s.n. (20 May 1934) (1).

Hamilton, A. C. & P. M. Holligan, 2008 (7).

Hammen, T. vander, 67 (8); 1137 (4).

Hanbury-Tracy, J., 69, 377 (4).

Handover, W. P., 37 (4).

Hansen, B. & W. DeVall, s.n. (21 Jun 1942) (1).

Hansen, B. & J. Hansen, 4809 (1).

Hansen, B. & D. Richardson, 5639 (1).

Hansen, B. et al., 5087, 5101, 5427 (1).

Harbrison, T. G., s.n. (17 Sep 1914), 14, 23, 4638 or 45, 13418 (1).

Hardin, J. W. & W. H. Duncan, 13791 (1).

Harling, G., 1643 (15); 5819 (4); 5820 (8); 5991 (8); 6064, 6167 (4); 6225 (8); 6230 (4); 6256 (8); 11319 (15).

Harling, G. & L. Andersson, 13407 (4); 13483, 14486, 14510 (8).

Harling, G. et al., 15106 (4).

Harmer, W. J., 1480 (1).

Harmon, W. E. & J. A. Fuentes, 6374 (4).

Harper, R. M., 1539 (1).

Harris, J. A., C1980, N194, N2339 (1).

Harshberger, J. W., s.n. (4 Jun 1912) (1).

Hart, J. A., 977, 1337 (8); 1495 (4); 1527 (8).

Hartweg, K. T., s.n. (Nov 1842), 10, 92, 478, 479, 795 (4); 796 (8); 797 (15); 1231 (7).

Harvey, H. W., s.n. (22 May 1939) (1).

Hatheway, Wm. H., 1112 (8); 1552, 1568, 1571 (4).

Haught, O., 4109 (4); 5055, 5633 (8).

Hawkes, J. G., 572 (4).

Hebbard, R., s.n. (27-29 Jul 1920) (4).

Héguert, J. S. d', 38 (9).

Hermann, F. J., 10891 (4); 11270, 11343 (8).

Hernândez, F., s.n. (Oct 1945) (4).

Hernândez, J. M., 46 (10).

Hernândez M., R., 314, 1471, 1591 (4).

Hernândez M., R. et al., 5174 (4).

Hernândez M., M. & J. Hernândez R., 5263 (4).

Herzog, T., 1611 (4).

Hildegard Türpe, A. M. et al., 5141 (4).

Hilsenbeck, R. & P. Hilsenbeck, 672 (1).

Hinton, G. B., 9760, 9763, 9935, 11221, 14106, 14200, 14237 (4).

Hirsch, R., P2250 (8).

Hitchcock, A. S., s.n. (30 Jan 1891), s.n. (Jun-Jul 1894), s.n. (26 Dec 1895-11 Jan 1896), s.n. (Jun-Jul 1898), 193 (1); 21416 (4); 21422 (15); 21575 (8).

Hodge, W. H., 6465 (8); 6525, 6698 (4).

Hoffmann, W., 238 (4).

Holm-Nielsen, L., 18774 (8).

Holm-Nielsen, L. et al., 4882, 4952, 5104 (8).

Holmquist, J. de Dios, 14 (6).

Holt, E., 539 (9).

Holton, I. F., 635 (8).

Hood, S. C., s.n. (10 Aug 1910), 3523 (1).

Hooker (herb.), s.n. (recieved 1867), (8).

Howell, A. H., 1095 (1).

Hoyos, J. & G. Morillo, 40 (6).

Hubbel, T. H., s.n. (18 Jul 1948) (4).

Huber, O., 4915, 6133 (6).

Huber, O. & C. Alarcón, 6673 (6).

Huber, O. & J. A. Steyermark, 7031 (6).

Huber, O. et al., 6849, 7297 (6).

Huck, R. B., 1097 (1).

Hueck, K., s.n. (Aug. 1958), s.n. (Sep 1958) (4).

Huertas G. & L. A. Camargo G., 282 (8); 1077 (4); 4448, 5045, 6165, 6404, 6861 (8).

Humbert, H. et al., 26845, 46845 (8).

Humboldt, F. & A. Bonpland, s.n. (Ecuador) (4); s.n. (Páramo de Saraguro), s.n. (Cajamarca, Peru) (8).

Hunnewell, F. W., 9026, 10439 (1).

Hunt, D. R., 228 (4).

Hutchison, P. C. & J. K. Wright, 3951 (3); 5705 (8); 5726 (7); 6919 (8).

Idrobo M., J. M. & R. E. Schultes, 863 (6).

Idrobo, P. & Bischler, 3443 (7); 3797 (8); 3975 (7).

Iglesias, M. C., 258 (8).

Ignacio Oropeza, M., 3 (4).

Ijjasz, E., 172, 223, 249, 382 (4).

Iltis, H. H. et al., 1081 (4).

ImThurn, E. F., s.n. (31 Jul 1879), s.n. (Aug 1885) (6); s.n. (Aug 1885) (10); 112 (6); 310 (10).

Infantes V., J., 1506, 3989 (4).

Inzunza, F. M., 105 (4).

Irwin, H. S., 422, 687 (10).

Jahn, A., s.n. (Río de Nuestra Señora), 89, 90, 109, 202, 539, 715, 716, 717, 763, 951, 959 (4).

Jameson, M., s.n. (4, 8 and 15), 1 (4); 3, 39 (8); 79 (15); 164 (8).

Janish, C. & J. Janish, 368, 385 (1).

Jaramillo M., R., 13 (4).

Jaramillo, J. & F. Coello, 1430 (8).

Jaramillo, J. & W. Jaramillo, 840, 3838 (8).

Jeffrey, C., et al., 2134 (4).

Johnson, W. M. & F. A. Barkley, 18C774 (4).

Jones, S. B. & C. Jones, 15751 (1).

Jones, S. B. & J. Loew, 23358 (1).

Jones, S. B. et al., 23098 (1).

Jorgensen, H. & F. Prieto, JP-56 (8).

Joseph, A., s.n. (Bogota) (8).

Judd, W. S., 305, 307, 312, 316, 1673, 1693, 1734 (1).

Judd, W. S. & B. Judd, 2842 (1).

Jurgensen, C., 391, 562, 857 (4).

Kaisin, F. O., s.n. (Loja) (8).

Kalbreyer, W., s.n., 441 (8); 867, 868 (4).

Karsten, s.n. (Bucaramanga, Colombia), s.n. (Susumuco, Bogotá), s.n. (Tucujo, Mérida), s.n. (Choroní), s.n. (Zumbador, Mérida), s.n. (Páramo Boconó), s.n. (Mérida, Peurtaduecto), s.n. (Páramo San Miguel, Sierra Nevada de Santa Marta), s.n. (coll. 1846) (4); s.n. (Popayán), s.n. (Nariño, Pasto) (7); s.n. (Pomplona), s.n. (Páramo de Cáduri), s.n. (Bogotá) (8); 55 (4 & 7).

Karwinski von Karwin, W. F., s.n. (Mexico) (4).

Keeler, H. D., s.n. (coll. 1870-1876), 39 (1).

Keerl, F. W., s.n. (coll. 1833) (4).

Kelly, I., 542 (4).

Kernan, H. S. (coll. by M. A. Carrilus), 114 (4).

Killip, E. P., 34200 (8).

Killip E. P. & H. García-Barriga, 33730 (6).

Killip, E. P. & F. C. Lehmann, 38486, 38490 (7).

Killip E. P. & A. C. Smith, 15001, 16770, 17217 (4); 17274, 17719, 18213, 18390 (8); 18877, 18880, 19083 (4); 19531 (8); 19815 (4); 20687 (8); 24213, 24243, 24779, 24978, 25684 (4).

King, A.-L., 96 (1).

King, R. M. & F. Almeda, 7811 (8).

Klug, G., 3251 (6); 3610 (4); 3628 (6).

Knight, D. H., 35, 68 (8); 76 (15); 117, 152 (4); 471 (15); 475 (8); 823 (15); 1162 (8).

Køie, M., 5096, 5193 (8); 5262, 5268 (4).

Koyama, T. & G. Agostini, 7348 (6).

Kral, R., 2511, 4876, 7634 (1).

Kral, R. & M. Kral, 6715, 7002 (1).

Kuck, M. J., 21 (1).

Kuntz, W. A., s.n. (25 May 1925) (1).

Kuntze, O., s.n. (coll. 1892), 1502 (4); 1623 (9).

Labbiente, R., 131 (4).

Lakela, O., 24187, 24368, 25028, 25040, 25116, 25198, 27183, 27428, 28332, 28702, 28731, 29005, 30829A (1).

Lakela, O. & F. Almeda, 30014 (1).

Lakela, O. & G. M. Riegler, 24242 (1).

Lakela, O. et al., 27002, 29771 (1).

Lamas R., R. et al., 191 (4).

Landrum, L. R., 4587 (4).

van Landsberge, M., 196, 287 (4); 465, 466 (9); 929 (4); 979 (9).

Langenheim, J. H., 3040, 3258, 3350 (4); 3437 (8).

Langlassé, E., 54, 55 (7); 789 (4).

Lasser, T., 17, 329 (4); 1346, 1503, 1921 (6).

Leavenworth, M. C., s.n. (coll. 1838) (1).

Lechowicz, M. J. et al., 29 (1).

LeConte, s.n. (Georgia) (1).

Lee, F. S., s.n. (21 Mar 1914) (1).

Lee, N. E., s.n. (17 Jun 1973) (1).

Lehmann, F. C., 212 (4); 220, 564, B.T.569, 823, B.T.957, 2010, 2838 (7); 3633 (8); 4451 (7); 4962 (8); 4964 (15); 7526, 7892, 7893 (4).

León, Bro., 3396, 14328 (2).

León, Bro. & Bro. M. Victorin, 18736 (2).

Leonard, S. W., 7041 (1).

Leonard, S. W. & A. E. Radford, 2869 (1).

Lewton, F. L., s.n. (20 Jun 1894) (1).

Liebman, F., 8592, 8593, 8594 (4).

Liesner, R. & A. Gonzâlez, 10081 (4).

Liesner, R. et al., 8312, 8406 (4).

Lighthipe, L. H., s.n. (15 Jun 1896), 355, 27382 (1).

Lindeman, J. C., 6224 (8).

Linden, J. J., s.n. (coll. 1842) (4); s.n. (Bogotá), s.n. (Jul 1842) (9); 12 (4); 126 (8); 128 (9); 256, 387, 766 (4); 773, 1351, 1353 (8); 1363, 1618 (4).

Lipp, F. J., 55, 80 (4).

Little, E. L., Jr., 7189, 7190, 7329, 8136, 8141 (7); 15394, 15598 (4).

Little, E. L., Jr. & R. R. Little, 9206 (8).

Lobb, Wm., s.n. (3, 4 and 8); 13 (?) (7); 30, 238 (8); 243 (4); 276 (8); 277 (3); 278 (4); 279 (8); 280, 299 (4).

Lobo A., A., 78 (7).

Løjtnant B. & U. Molau, 14967 (8); 15010 (15).

Lombo, R., s.n. (1 Oct 1965) (4).

Lôpez, A. & A. Sagâstegui A., 2814 (8).

Lôpez O., M. & A. Corso M., 20 (8).

Lôpez-Palacios, S., 1132, 2579, 4121 (4).

Lozano C., G. & J. Díaz, 3280 (4).

Lozano C., G. & P. M. Ruíz, 1545 (7).

Luetzelburg, P. von, 21566, 21570 (10).

Lumer, s.n. (Bogotá) (8).

Luteyn, J. L. & M. Lebrôn-Luteyn, 5516, 5534 (3); 6366, 6401, 6425 (4); 6895 (7); 7726 (8).

Luteyn, J. L. et al., 4803 (8); 5004 (7); 5184, 5192, 5213, 5254, 5270, 5276, 5296 (4); 5303 (13); 5304, 5314 (8); 5372, 5377, 5386, 5400, 5411 (4); 5903 (13); 5911 (8); 6065, 6066 (4); 6275, 6283 (6); 6549 (4); 6677 (8); 7014 (4); 7580, 7586 (8); 7614, 7616, 7618 (4); 7681, 7687 (8).

Maas, P. J. M. et al., 2620, 5706, 5822, (6).

Macbride, J. F., 4992 (4).

MacDougall, T., s.n. (3 Dec 1953), s.n. (23 Mar 1964), s.n. (21 May 1969), s.n. (3 Jan 1971) (4).

Madison, M. et al., 7487 (8).

Magallanes, J. A. S., 1217 (4).

Maguire, B., 32665, 33310, 33598 (orig. 33548), 33630, 33641, 33654, 33722, 37010 (6).

Maguire, B. & D. B. Fanshawe, 23268, 32183, 32473, 32641 (6).

Maguire, B. & B. Maguire Jr., 29110, 29140 (6).

Maguire, B. & C. K. Maguire, 35137, 35145, 35293, 35310, 35364, 35412, 40091, 40158, 40420 (6); 44345 (4).

Maguire, B. & M. Pires, 60477 (12).

Maguire, B. & L. Politi, 27653A, 27653B, 27806, 27918, 28020, 28090, 28190, 28236, 28254, 28335, 28460 (6).

Maguire, B. & J. Wurdack, 33911, 33941 (6).

Maguire, B. et al., 29565, 29672, 30516, 30669, 31763, 40603A, 42232, 45987A, 46156, 53636 (6); 65569 (13).

Manara, B., s.n. (24 Sep 1977) (4); (31 Jul 1976) (9).

Mandon, G., 563 (4).

Mangasl, C., 38 (4).

Marin, F., 1506, 2246 (4).

Marquand, E. C., s.n. (17 Feb 1930) (1).

Martin, D. L. & S. T. Cooper, 610 (1).

Martínez, M., s.n. (Jun 1939), s.n. (12 Apr 1941), s.n. (5 Dec 1942) (4).

Mason, H. L., 13721, 13728 (8).

Mathews, A., s.n. (3, 4, 7 and 8); s.n. (coll. 1836) (8); 114H (3); 116H (8); 712 (4); 713 (7), 1423 (8); 1424 (3); 1425 (3 & 4); 1426 (7); 1427 (3 & 4); 3039 (4); 3040 (3, 7 & 8); 9748, 9957 (4).

Matos, F., Bail-9 (4).

Matuda, E., 430, 859, 1837, 2589, 16261, 17737, 18127 (4).

McAtee, W. L., 3269 (1).

McCarroll, D., 116 (4).

McCart, Wm. L., 10767 (1).

McCarty, S. S., 119 (4).

McDaniel, S., 9132 (1).

McFarlin. J. B., s.n. (coll. 1925), 4051, 5581, 7941 (1).

McKee, H. S., 10750 (4).

McVaugh, R., 13799, 14235, 20346, 21346, 25520, 25951, 26423 (4).

Meebold, A. K., 27947 (1).

Mejía, M. P., 77 (4).

Melampy, M., 1, 20, 315 (8); 938 (4); 1233, 1234 (8).

Mellinger, E. O., s.n. (11 Jun 1960) (1).

Metcalf, R. D., 30510, 30628 (4); 30788 (7).

Metcalf, R. D. & J. Cuatrecasas, 30156 (8).

Mexía, Y., 1840, 4272, 8956, 9276 (4).

Meyer, F. G., 9908 (4).

Michaux, A., s.n. (Florida) (1).

Miller, V. D. & B. D. Miller, 62 (7).

Milligan, J. M., s.n. (May 1890) (1).

Miranda, F., 3056, 6544 (4).

Mocquerys, 1211 (4).

Moldenke, A. L. & H. N. Moldenke, 29550 (1).

Moldenke, H. N., 601 (1).

Molina R., A., 42, 1005, 1117, 1623, 2807, 3300, 6361, 7295, 8667, 10116, 10137, 10748, 11022, 11039, 14391, 14502, 14601, 18759, 22654 (4).

Molina R., A. & A. R. Molina, 26111 (4).

Molina R., A. et al., 17005 (4).

Montaldo, P., 3853 (4).

Moore, H. E., Jr., 2318, 2431 (4).

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Mora O., L. E., 445 (8); 2355, 2461 (7).

Moreno, A., 6 (10).

Mori, S. & R. Dressler, 7830, 7833 (4).

Mori, S. & J. Kallunki, 5811 (4).

Morillo, G. & B. Manara, 1437, 1722 (4).

Moritz, K., s.n. (coll. 1863), s.n. (coll. 1865) (4); 365 (9); 478 (4); 640 (9); 1350 (4); 1351 (4).

Muenscher, W. C. & M. W. Muenscher, 14105 (1).

Murrill, W. A., s.n. (27 May 1939), s.n. (25 Nov 1939), s.n. (19 Jun 1941), 215 (1).

Mutis, J. C., 55 (8), 2268 (4); 2787, 3892, 4169, 4170 (8); 4638, 4639 (7); 4640, 4641 (8).

Nargas, M. J., 254 (4).

Nash, G. V., 803, 1926 (1).

Née, L., s.n. (4).

Nee, M. & B. F. Hansen, 18728 (4).

Nee, M. & G. Diggs, 24887 (4).

Nelson, E. W., 781, 2075, 2184 (4).

Niemeyer, E., 142 (8).

Norris, D. H. & D. J. Taranto, 14245 (4).

Norsworthy, J., 323 (1).

Norsworthy, J. & E. Wetherington, 307 (1).

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Ohlinger, L. B., 569, 1393 (1).

Øllgaard, B. & H. Balslev, 9549 (8); 9738, 9747 (7).

O'Neill, H. T., s.n. (Jun 1925), s.n. (21 May 1927), s.n. (2 Aug 1929) (1).

Orbigny, A. D. d', 404, 480 (4).

Ortíz, F. I., s.n. (27 Dec 1981) (8).

Osla, E., 640 (9).

Otto, E., 696 (4).

Pabón E., M., 5, 28 (8).

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Palacios, P. A. & S. Díaz P., 62 (8).

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Palmer, E., 323 or 4683 (1).

Palmer, Wm. & J. H. Riley, 204, 205, 310 (2).

Patin, C., s.n. (Medellín) (8).

Pearce, R. W., s.n. (Jun 1865) (4); s.n. (8).

Penland, C. W. & R. H. Summers, 1117 (8 & 15).

Pennell, F. W., 2105, 2201, 2201A (8); 3195 (7); 4274 (8); 10965, 14085 (4); 15593 (3); 15845 (7).

Pennell, F. W. & E. P. Killip, 6292, 6342, 6404, 7412, 8150 (7).

Pentland, M., 204 (4).

Pérez-Arbeláez, E., 54, 1094, 1494, 1543 (8).

Pérez-Arbeláez, E. & J. Cuatrecasas, 5808, 6010, 6300 (7).

Pérez-Levis, T. M., 25 (4).

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Perkins, A. E., s.n. (22 Feb 1931), s.n. (16 Apr 1933), s.n. (5 May 1934) (1).

Peyton, B., 1479 (4).

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Phelps, K. D. & C. B. Hitchcock, 41, 130, 447 (6).

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Popenoe, J., 629 (1).

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Schiefer, H., 388, 932, 934, 940 (8).

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Schultez, s.n. (Mexico) (4).

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Thorne, R. F. & E. Lathrop, 40347 (4).

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Tillett, S. S., 673-357 (4).

Tillett, S. S. & C. L. Tillett, 45570, 45676 (6).

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Tomâs, Bro., 1868 (7).

Toro, R., 724 (4).

Torres-Romero, J. H. & G. Lozano-Contreras, 62 (7).

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Torrey, J., s.n. (Florida), s.n. (Georgia) (1).

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Totten, H. R., 1 (1).

Tracey, I. A., s.n.(13 Apr 1922), 377 (4); 378 (7).

Tracy, S. M., 6572A, 6862 (1).

Triana, J. J., s.n. (Susumaco) (4); s.n. (Bogotâ), s.n. (coll. 1866) (8); 126, 256, 308 (4); 310, 319 (8); 348 (4); 349, 350, 351 (8); 2720 (4); 4342 (4 & 8).

Troll, C., 1037, 1798, 2591 (4).

Trujillo, B., 1335 (9); 4172, 5307, 7621 (4).

Trujillo, B. & O. del Castillo, 1121, 8045, 8204 (4).

Trujillo, B. & Alv. Fernândez, 385, 606, 783, 965 (4).

Trujillo, R., 7621 (4).

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Vareschi, V. & E. Foldats, 4680, 4840 (6).

Vargas C., C., 38/7060, 1281, 2723 (4).

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Veitch (herb.), s.n. (Recieved Jul 1964) (15).

Velasco, R., 23 (9); 203 (4).

Velasco, R. & M. Ramia, 379, 504, 515 (4).

Ventenat, E. P., s.n. (1).

Ventura A., F., 1076, 3512, 5012, 12779, 12841 (4).

Vesterlund, P. O., s.n. (May 1889) (1).

Viereck, H. L., s.n. (14 Dec 1922) (4).

Villarreal de Puga, L. M., 5936 (4).

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Vivar C., J. F., s.n. (Loja, 11 May 1982), s.n. (Saraguro) (8); s.n. (rd. to Zamora), s.n. (Selva Alegre) (4); 18 (8).

Vogl, Padre C., 104, 128, 310, 426 (4); 680 (9); 712 (4).

Wagner, s.n. (coll. 1853) (4).

Wall, W. E., 31 (1).

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Warsowitz, s.n. (Magdalene) (4).

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Weed, A. S., s.n. (3 May 1939) (1).

Weir, J. R., s.n. (Pacho, Colombia), s.n. (Jirón, Colombia), s.n. (nr. Bucaramanga, Colombia), 98 (4).

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