

## ORIGINS OF MEXICAN MALPIGHIACEAE

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### ABSTRACT

The approximately 42 lineages of Malpighiaceae currently known in Mexico are identified and briefly described and discussed. All the Mexican lineages have their *ultimate* roots in South America, although in some cases the connections are inferred only through phylogeny and several Mexican genera probably originated in Mexico. All the lineages have effective adaptations for dispersal except the genus *Galphimia*, but distributions outside Mexico and a phylogenetic tree suggest that while many Malpighiaceae reached Mexico through “stepping-stone” dispersal, some lineages probably arrived as the result of episodes of long-distance dispersal from South America.

Key words: biogeography, Malpighiaceae, Mexico, phylogeny.

### RESUMEN

Se identifican y se describen y discuten brevemente los aproximadamente 42 linajes de Malpighiaceae que se conocen hasta ahora para México. Todos los linajes mexicanos tienen sus *últimas* raíces en Sudamérica, aunque en algunos casos las conexiones se infieren únicamente mediante filogenia y algunos géneros mexicanos probablemente se originaron en México. Todos los linajes tienen adaptaciones efectivas para su dispersión excepto el género *Galphimia*, pero las distribuciones fuera de México y un árbol filogenético sugieren que aunque muchas Malpighiaceae llegaron a México mediante el modelo de dispersión de “piedras de paso”, algunos linajes probablemente arribaron desde Sudamérica mediante dispersión a larga distancia.

Palabras clave: biogeografía, filogenia, Malpighiaceae, México.

## INTRODUCTION

In a recent review of the literature on the Mexican seasonally dry tropical flora, Pérez-García et al. (2012, p. 177) stated, “[W]e conclude that treating TDF [tropical dry forest] as a plant community that has a prominent South American component is not warranted, and thus this plant formation cannot be considered as being part of the Neotropical Realm.” They contrasted their conclusion with that of Rzedowski (1991), who stated (p. 4), “An analysis of the geographical affinities of the phanerogamic flora of Mexico indicates that its links with the south are about four times more important than those with the north.” Pérez-García et al. also stated (p. 171) that “More phylogenies of Mexican species and their sister groups occurring beyond the country’s borders are needed in order to determine the ultimate sources and relative ages of the components of this diverse biota . . .” That is the purpose of this paper—as a specialist in the systematics of the family Malpighiaceae, I propose to describe what is known about the relationships of the present Mexican representatives of that family, with special emphasis on the number of lineages of Malpighiaceae in Mexico and the probable ultimate origins of those lineages. In doing that I hope not only to contribute to the ongoing controversy concerning the origins of the Mexican flora, but also to demonstrate what a powerful tool phylogenetic systematics can be in interpreting biogeographical history.

The Malpighiaceae is a family of tropical and subtropical flowering plants, comprising approximately 1300 species in 75 genera; about 80% of the genera and 90% of the species occur mostly or entirely in the New World, with the rest native to the Old World (Anderson et al., 2012). In 1990 I suggested on the basis of morphology that the family originated and diversified in South America, spreading eventually from there to Central America, North America, the West Indies, and the Old World (principally Africa and Asia). Phylogenetic research published in the last 12 years has broadly supported my 1990 suggestion (Cameron et al., 2001; Davis et al., 2001; Davis & Anderson, 2010). Today there are more genera and species of Malpighiaceae in South America than anywhere else (Anderson et al., 2012).

Some of the generic names used in this paper will be unfamiliar to people acquainted with the Mexican flora. The new names and generic interpretations result from an ongoing reassessment of relationships in the family. Anyone puzzled by such unfamiliar names can go to our website (Anderson et al., 2012), where a nomenclatural database will answer questions about what happened to old familiar names. The same website contains references to literature on Malpighiaceae (mostly with pdfs or links to online sources of the original publications) and drawings and photos of most of the genera mentioned in this paper.

## MEXICAN LINEAGES OF MALPIGHIACEAE

Here I list and describe briefly the lineages of Malpighiaceae that I can identify in the Mexican flora. When no source is cited, the reader should assume that these statements represent my own unpublished observations and opinions.

***Adelphia***: four species in South America (W. Anderson, 2006), one of which is also found to the north. *Adelphia* is embedded in the poorly resolved *Hiraea* clade, which is mostly South American (but see also *Hiraea* and *Psychopterys* below). The wholly South American genus *Lophopterys* is sister to the rest of the *Hiraea* clade (Davis & Anderson, 2010), which suggests that the clade originated in South America.

***A. hiraea* (Gaertn.) W. R. Anderson (Fig. 1)**: a vine, wind-dispersed by winged samaras, extending from northwestern South America throughout Central America into Mexico, where it is collected occasionally in wet forests of Chiapas and Tabasco; it also occurs in Jamaica.

***Aspicarpa/Gaudichaudia* (Figs. 2, 3)**: a large, diverse lineage, mostly Mexican except for two species that extend into the United States and two species in Central America, one of which extends into northwestern South America. *Aspicarpa* and *Gaudichaudia* are embedded in the very large, strongly supported, mostly South American *Stigmaphyllon* clade, which is represented in Mexico by six genera [*Aspicarpa* (including *Gaudichaudia*), *Banisteriopsis*, *Bronwenia*, *Cottisia*, *Diplopterys*, and *Stigmaphyllon*] (Davis & Anderson, 2010).

In the traditional sense, *Aspicarpa* comprises several species in southern South America and several species in North America, but the two groups do not constitute a monophyletic group (Davis & Anderson, 2010), so this discussion will ignore the South American species; the type is from Mexico so the name *Aspicarpa* will remain with the North American species. There are approximately 3–6 species of *Aspicarpa* s. str., growing throughout Mexico from Oaxaca to Sonora, Chihuahua, and Coahuila, with two of them occurring also in adjacent areas of the United States (Arizona, New Mexico, and Texas). They grow in diverse habitats, from oak and pine-oak forests to shrubby woodlands to desert scrub. They are erect shrublets or more or less prostrate herbaceous stems from a perennial base that are not or only very weakly twining. The fruit of *Aspicarpa* breaks apart into dry nutlets that are

unwinged but bear a dorsal crest and usually a lateral crest or rudimentary winglet. Such mericarps have no obvious adaptation for dispersal (Fig. 2).

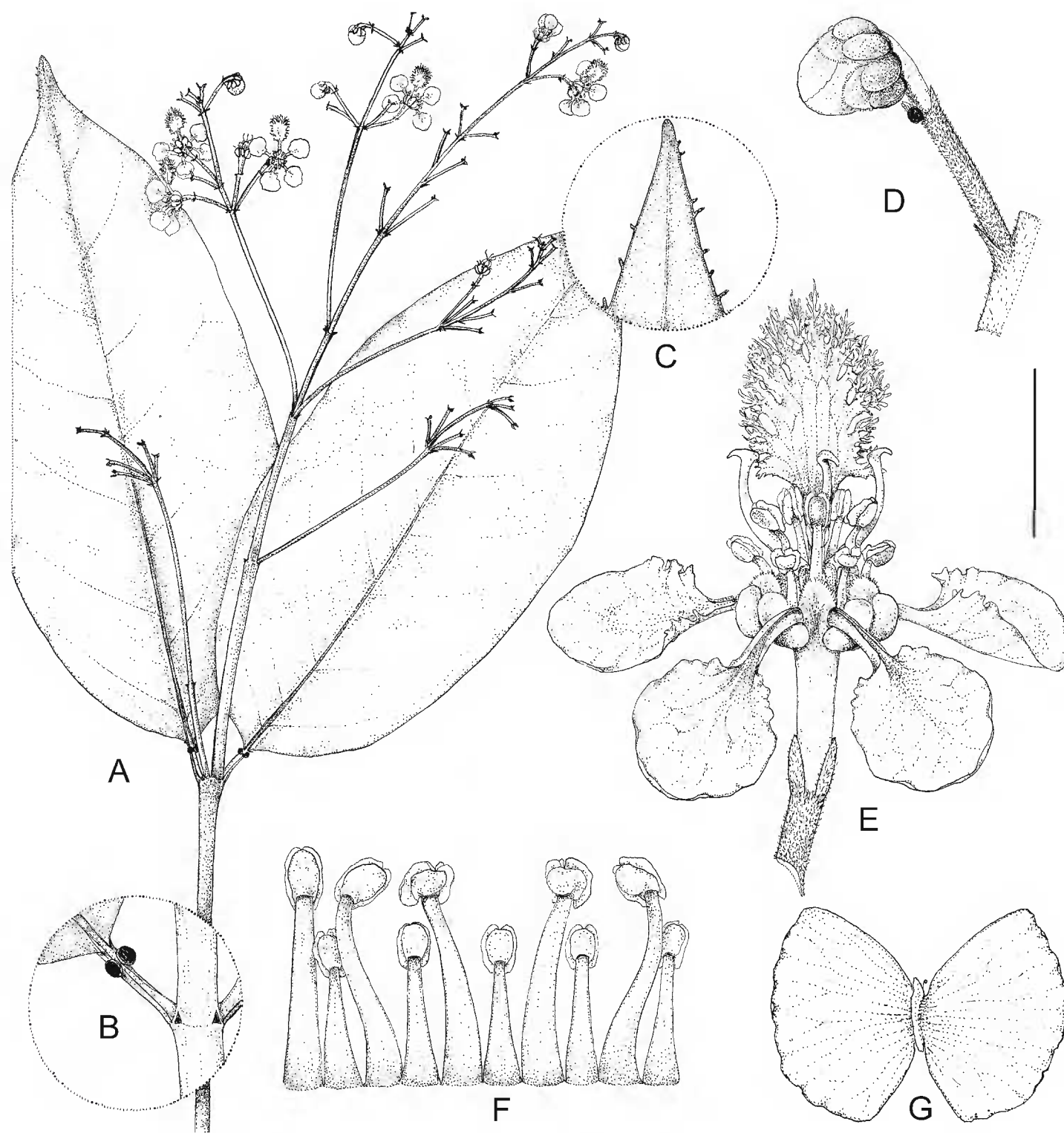


Fig. 1. *Adelfia hiraeta*. A. flowering branch; B. node to show interpetiolar stipules and large glands on petiole; C. apex of lamina to show marginal processes; D. circinate flower bud with one large eccentric gland on one bracteole; E. flower, posterior petal uppermost (eccentric bracteole gland is behind pedicel, below posterior petal); F. androecium laid out, abaxial view, the stamen just above the letter "F" opposite posterior petal; G. samara, abaxial view. Scale bar equivalents: A, 4 cm; B, C, 1.3 cm; D, 8 mm; E, 6 mm; F, 2.7 mm; G, 3 cm. Based on: A–F, *Foster 2313*, MICH; G, *Davidse et al. 20520*, MICH.

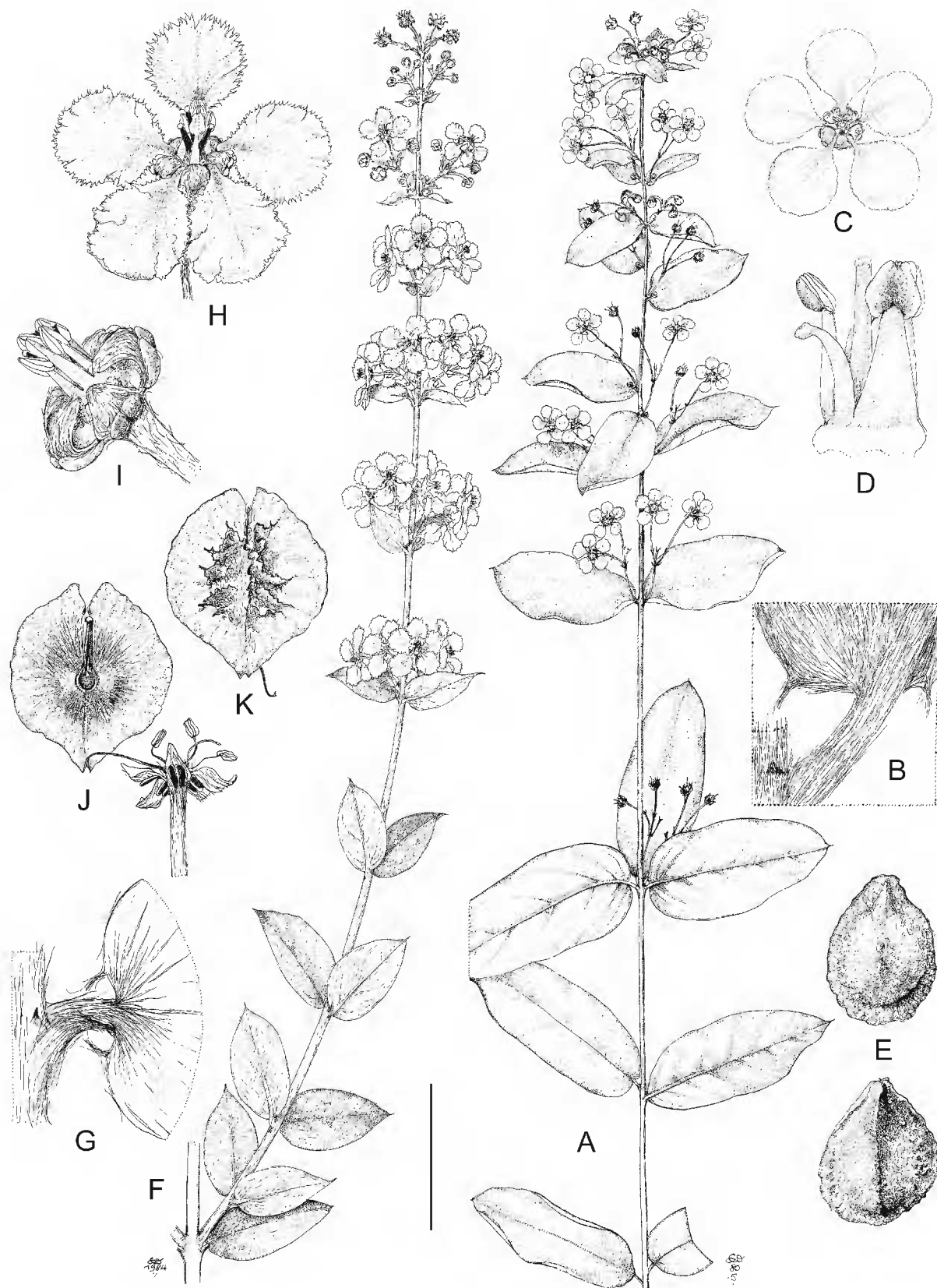


Fig. 2. *Aspiscarpa* and *Gaudichaudia*. A–E, *A. brevipes* (DC.) W. R. Anderson. A. flowering branch; B. base of leaf, abaxial view, and adjacent node with stipule; C. flower, posterior petal uppermost; D. androecium and gynoecium, stamen at left opposite anterior sepal; E. mericarps, adaxial view (above) and abaxial view (below). F–K, *G. krusei* W. R. Anderson. F. flowering branch; G. base of leaf, adaxial view, and adjacent node with stipule; H. flower, posterior petal uppermost; I. flower with petals removed, lateral view; J. samara, adaxial view, still attached to receptacle by carpophore; K. samara, abaxial view. Scale bar equivalents: A, 4 cm; B, 4 mm; C, 8 mm; D, 2 mm; E, 8 mm; F, 4 cm; G, 4 mm; H, 8 mm; I, 5 mm; J, K, 8 mm. Based on: A–E, Pringle 4422, US; F–I, Anderson 12868, MICH; J, K, Koch & Fryxell 8264, MICH.

*Gaudichaudia* comprises 15–40? species; the definition of species in this group is made difficult by the widespread occurrence of hybridization and polyploidy (W. Anderson, 1993). Most species are found in southern Mexico, but two

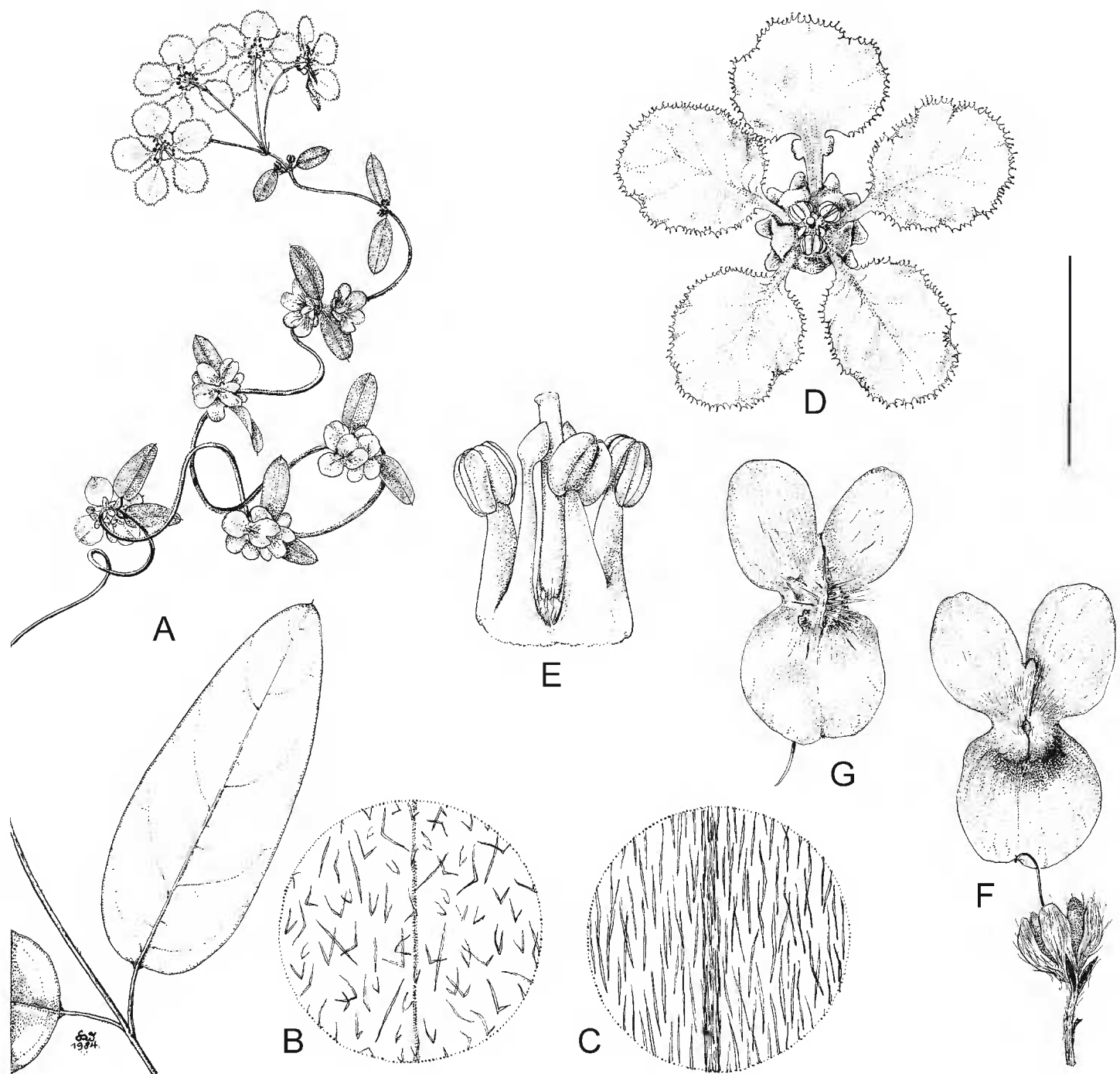


Fig. 3. *Gaudichaudia galeottiana* (Nied.) Chodat. A. branch with chasmogamous flowers and fruits from cleistogamous flowers; B, C. enlargement of surfaces of small young leaves, adaxial side (B) and abaxial side (C); D. chasmogamous flower, posterior petal uppermost; E. androecium and gynoecium of chasmogamous flower, the stamen at left opposite anterior sepal; F. samara, adaxial view, still attached to cleistogamous flower by carpophore; G. samara from cleistogamous flower, abaxial view. Scale bar equivalents: A, 4 cm; B, C, 4 mm; D, 1 cm; E, 4 mm; F, G, 8 mm. Based on *Anderson & Laskowski 4087, MICH.*

closely related species extend into Central America and one extends into Colombia and Venezuela. They occur in the same assortment of habitats as *Aspicarpa*. A few are erect shrublets, but most are twining herbaceous vines from a perennial base. The fruit breaks apart into dry winged samaras, well adapted for wind-dispersal (Figs. 2, 3).

The latest phylogeny of Malpighiaceae (Davis & Anderson, 2010) indicates that *Aspicarpa* and *Gaudichaudia* together form a monophyletic group, but that neither is monophyletic without the other—the three sequenced species of *Aspicarpa* are distributed among the six sequenced species of *Gaudichaudia*. Therefore, for the purposes of this paper we should treat *Aspicarpa/Gaudichaudia* as a single large and diverse Mexican lineage. On morphological grounds it seems safe to say that the ancestor of the lineage was probably a plant with a lateral-winged samara that reached western Mexico via long-distance dispersal from southern South America, where *Camarea*, the sister genus, occurs. That ancestor (unlike anything that now occurs in South America) presumably found open, seasonally dry habitats that it was able to exploit and into which its descendants were able to expand.

***Banisteriopsis*:** approximately 70 species, all South American (Gates, 1982; Anderson & Davis, 2006, 2007). Two species that are not closely related within the genus (Gates, 1982) have reached Mexico; both are vines and wind-dispersed by winged samaras. *Banisteriopsis* is a member of the *Stigmaphyllon* clade; see note above under *Aspicarpa*.

***B. elegans* (Triana & Planch.) Sandwith:** growing in mesic forests from northwestern South America throughout Central America to Guatemala, known in Mexico from a single collection from a wet forest in Chiapas.

***B. muricata* (Cav.) Cuatrec. (Fig. 4):** very widely distributed in South and Central America, growing in diverse habitats (wet forests, dry forests, roadside thickets); known in Mexico from numerous collections in Chiapas and several in Oaxaca, mostly from tropical deciduous forests.

***Bronwenia*:** ten species, all South American (Anderson & Davis, 2007); two of those species, both woody vines that are sometimes shrubby and both wind-dispersed by winged samaras, have reached Mexico. The genus is in the *Stigmaphyllon* clade (Davis & Anderson, 2010), where it is sister to the rest of the clade; see also note above under *Aspicarpa*.

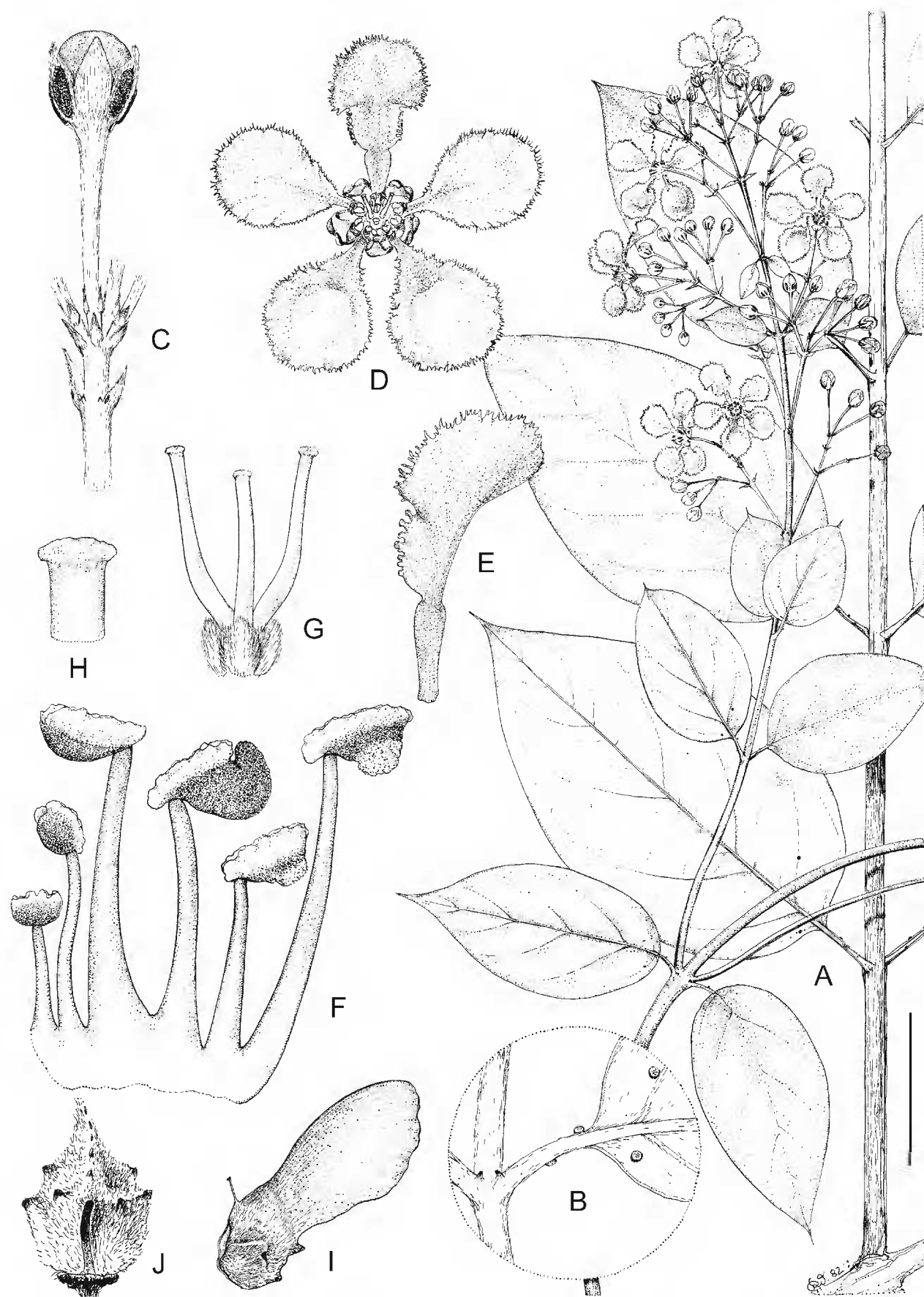


Fig. 4. *Banisteriopsis muricata*. A. leafy and flowering branches; B. node to show stipules and abaxial base of leaf; C. flower bud and umbel; D. flower, posterior petal uppermost; E. posterior petal, lateral-abaxial view; F. portion of androecium, abaxial view, stamen opposite posterior petal to left; G. gynoecium, anterior style in center; H. apex of style; I. samara; J. nut of samara, abaxial view, to show carpophore. Scale bar equivalents: A, 3 cm; B, C, 6 mm; D, 8.6 mm; E, 4.3 mm; F, 1.5 mm; G, 3 mm; H, 1 mm; I, 1.5 cm; J, 6 mm. Based on: A–I, *Schinini 14735*, MICH; J, *Maguire & Maguire 40235*, MICH.



***B. acapulcensis* (Rose) W. R. Anderson & C. Davis (Fig. 5):** northwestern South America, common in Central America, occasional in Oaxaca and Guerrero in tropical deciduous forest.

***B. cornifolia* (Kunth) W. R. Anderson & C. Davis:** northwestern South America, common in Central America, occasional in Chiapas, Veracruz, and Oaxaca in tropical deciduous forest and more mesic forest.

These two species are closely related, but unless one wants to suggest that they diverged in Mexico (and given their rarity in Mexico that seems unlikely) they must have reached Mexico independently and thus should be considered two Mexican lineages.

***Bunchosia* (Fig. 6):** approximately 75 species of trees and shrubs, bird-dispersed by fleshy berries; South America, Central America, Mexico, and the West Indies (Anderson et al., 2012). The latest phylogenetic tree for Malpighiaceae (Davis & Anderson, 2010) does not establish where the genus originated, but it is noteworthy that the sister genus, *Thryallis*, is limited to southeastern Brazil and adjacent Paraguay and Bolivia (C. Anderson, 1995). There are at least 20 species of *Bunchosia* in southern Mexico, over half of them endemic, the rest also in Central America and two also in the West Indies; they occupy diverse habitats, from open dry shrubby associations and tropical deciduous forests to mesic and wet forests. The uniform morphology of *Bunchosia* does not permit me to recognize obvious groups at this time, as in some other genera (e.g., *Heteropterys*, see below), and so it is impossible to say whether the assemblage of Mexican species descended from a single immigrant or from several immigrants. Consequently, I am forced for the present to consider the Mexican species of *Bunchosia* a single lineage, but it will not be surprising if future studies establish that *Bunchosia* in Mexico comprises more than one lineage.

***Byrsonima*:** approximately 130 species of trees, shrubs, and subshrubs, bird-dispersed by fleshy drupe-like fruits. Most species are South American, but there are a few species in Central America, Mexico, and the Caribbean (including southernmost Florida). *Byrsonima* is in the *Byrsonima* clade; its two sister genera, *Blepharandra* and *Diacidia*, are wholly South American, as is the *Acmanthera* clade, sister to the *Byrsonima* clade (Davis & Anderson, 2010). There are two species of *Byrsonima* in Mexico; they are not closely related.

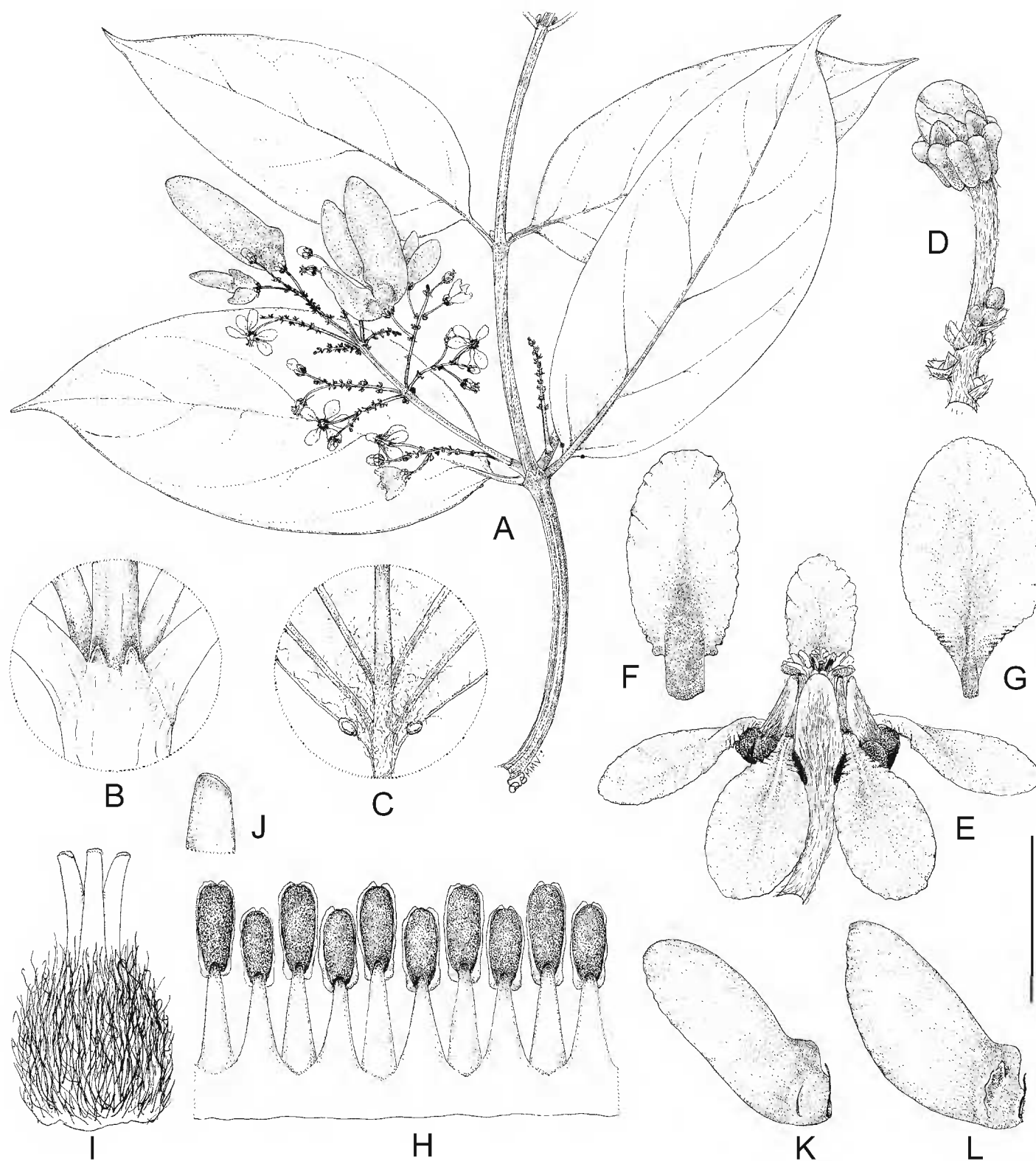


Fig. 5. *Bronwenia acapulcensis*. A. branch with flowers and fruits; B. node with interpetiolar stipules; C. base of lamina, abaxial view; D. flower bud and portion of inflorescence axis; E. flower, posterior petal uppermost; F. posterior petal, abaxial view; G. lateral petal, abaxial view; H. androecium laid out, abaxial view, stamen above letter "H" opposite posterior petal; I. gynoecium; J. apex of style; K. samara with crest on side of nut; L. samara with winglet on side of nut. Scale bar equivalents: A, 4 cm; B, 4 mm; C, D, 8 mm; E, 5.7 mm; F, G, 4 mm; H, I, 2 mm; J, 1 mm; K, L, 2 cm. Based on: A, E–K, *Burnham 977*, MICH; B–D, *Burnham 976*, MICH; L, *Almeda 3983*, MICH.

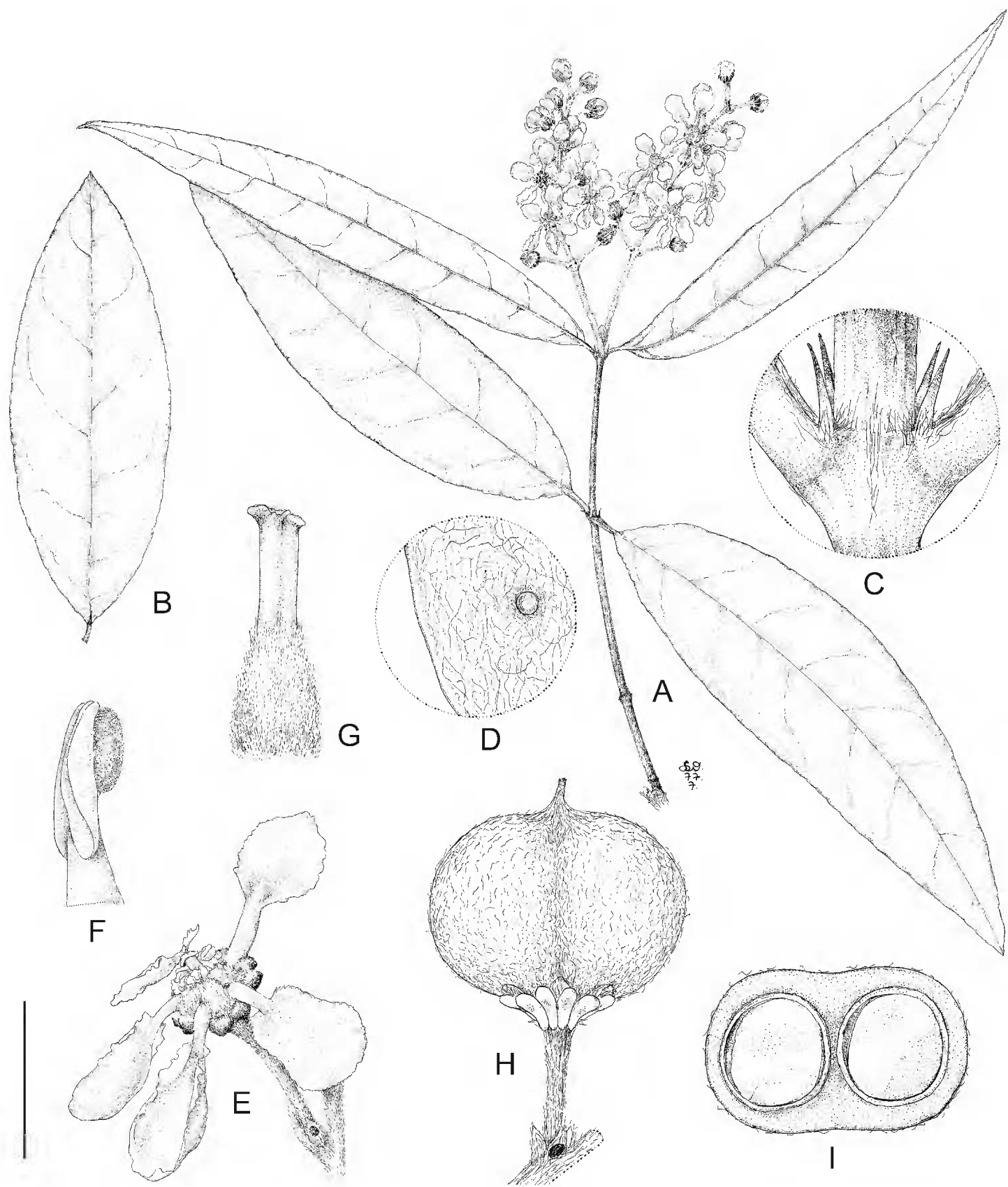


Fig. 6. *Bunchosia mcvaughii* W. R. Anderson. A. flowering branch; B. detached smaller leaf from same plant; C. node with epipetiolar stipules; D. abaxial leaf surface to show gland; E. flower, posterior petal uppermost; F. anther; G. gynoecium; H. fruit; I. cross-section of fruit. Scale bar equivalents: A, B, 4 cm; C, 4 mm; D, 2 mm; E, 1 cm; F, 2 mm; G, 3.3 mm; H, I, 1 cm. Based on: A–G, *McVaugh 25107*, MICH; H, I, *Pérez J. 1704*, MICH.

***B. bucidifolia* Standl. (Fig. 7):** endemic to the Yucatán Peninsula of Mexico (Campeche, Quintana Roo, Yucatán) and adjacent Belize and Guatemala, often in tropical deciduous forest but also in more mesic habitats. The petals are white and pink or red (probably white turning pink and then red in age), and the connectives of the anthers do not exceed the locules at the apex; those characters suggest a relationship with the Caribbean species *B. lucida* (Mill.) DC., and it is possible that *B. bucidifolia* descended from a Caribbean ancestor, but similar characters are not rare among the many South American species of this genus, so caution is in order until we can obtain molecular sequences for *B. bucidifolia*. See also the discussion of *Eoglandulosa* below, preceding the Conclusions.

***B. crassifolia* (L.) Kunth:** a species or species-complex that is very widespread in South America, Central America, southern Mexico, and the West Indies. Related species are all South American; the taxonomy of the yellow-flowered species of *Byrsonima* is exceedingly difficult and needs a great deal of work. In Mexico *B. crassifolia* inhabits diverse habitats, from dry to mesic, and is often prominent in shrubby savannas.

***Callicola* (Fig. 8):** two species of shrubs, wind-dispersed by winged samaras, endemic to central, seasonally dry Mexico from Coahuila to Oaxaca, growing in open deciduous woods, thorn-scrub, or desert scrub on rocky or sandy limestone slopes (Anderson & Davis, 2007). This genus is sister to *Malpighia* and a large group of Old World genera, with *Mascagnia* sister to the whole clade (Davis & Anderson, 2010), and its morphology reflects that position (Anderson et al., 2012). It is probably descended from a mascagniid ancestor that came originally from South America; see discussion below under *Malpighia* and *Mascagnia*.

***Callaeum* (Fig. 9):** 11 species of South America, Central America, and Mexico, woody vines, all but one South American species wind-dispersed by winged samaras (Johnson, 1986; Anderson et al., 2012). There are three South American species, one species found only in northern Central America except for a single collection from Chiapas [*C. nicaraguense* (Griseb.) Small], one species in southern and southeastern Mexico and northern Central America [*C. malpighioides* (Turcz.) D. M. Johnson], and six species endemic to Mexico and adjacent Texas. The sister to *Callaeum* is the South American genus *Alicia* (Davis & Anderson, 2010), which suggests that the genus may have originated in South America, but the resolution within *Callaeum* in our phylogenetic tree is weak, so it is not possible to say much more about the origins

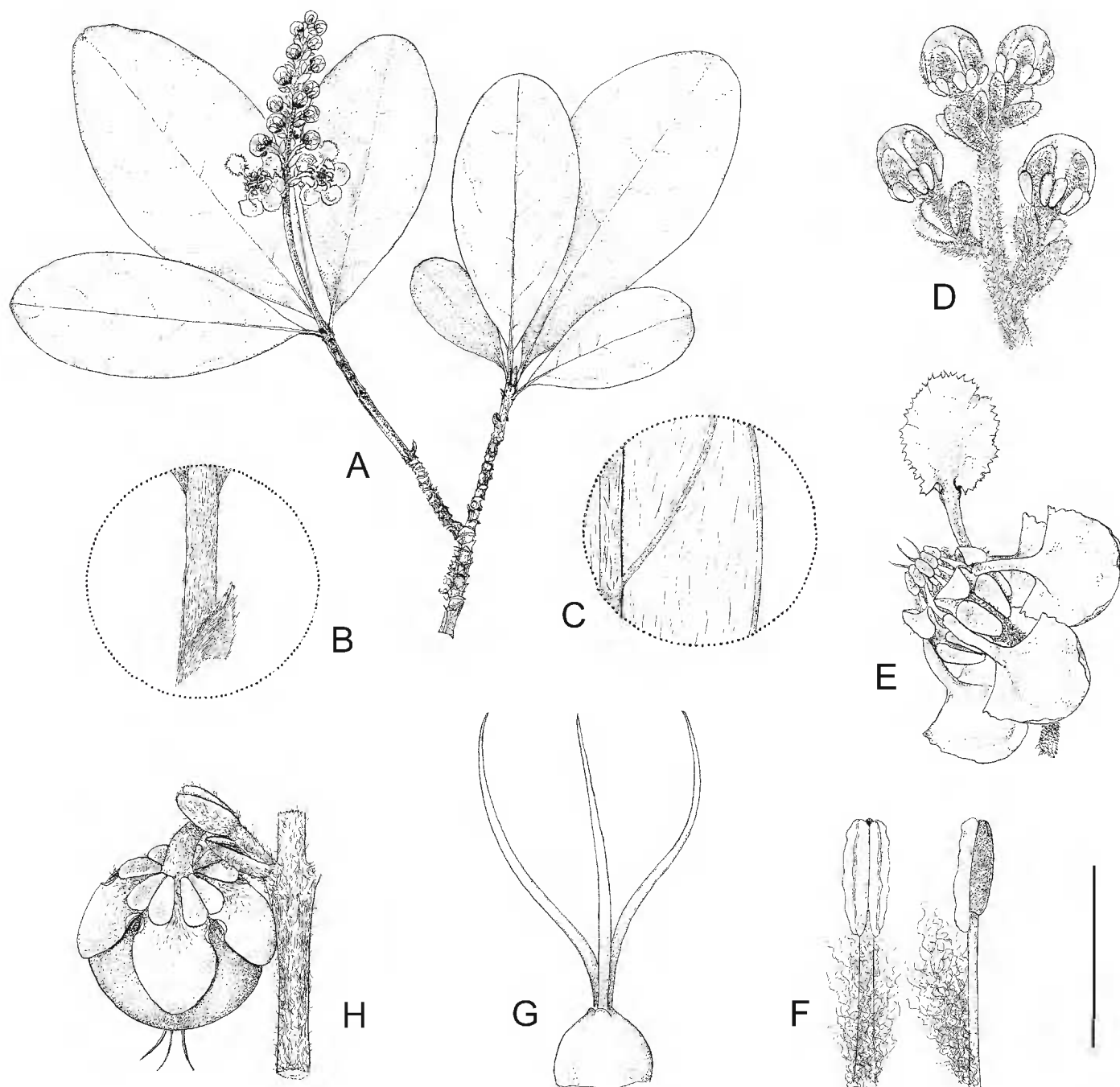


Fig. 7. *Byrsonima bucidifolia*. A. flowering branch; B. stipules on inner base of petiole; C. abaxial leaf surface to show persistent hairs; D. flower buds; E. flower, lateral view, posterior petal uppermost; F. stamens, adaxial view (left) and lateral view (right); G. gynoecium; H. fruit. Scale bar equivalents: A, 4 cm; B, C, 4 mm; D, E, 8 mm; F, G, 2.7 mm; H, 1 cm. Based on: A–C, *Lundell & Lundell 7772*, MICH; D–G, *Lundell & Lundell 7448*, MICH; H, *Davidse et al. 20622*, MICH.

of the Mexican species at this time. They are best treated as a single lineage for now, but the present structure of our phylogenetic tree suggests that *Callaeum* may have reached Mexico twice. The widespread and common Mexican species occur most often in tropical deciduous forests and other open, seasonally dry habitats, but also in more mesic and even wet forests, especially in southeastern Mexico.

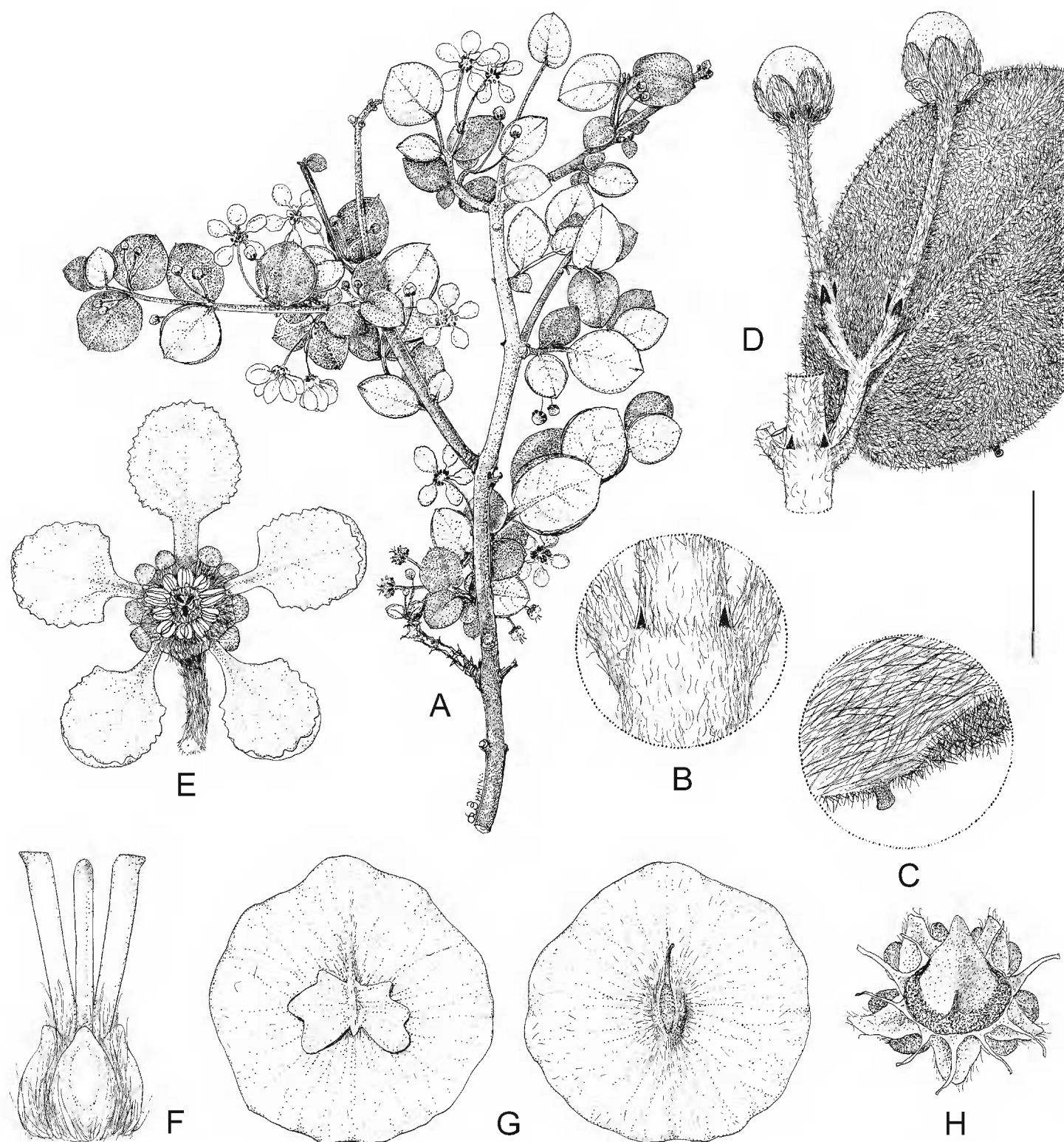


Fig. 8. *Calcicola parvifolia* (A. Juss.) W. R. Anderson & C. Davis. A. flowering branch; B. node with interpetiolar stipules; C. edge of lamina with marginal gland, abaxial view except where turned to show adaxial vestiture; D. node and leaf (adaxial view) with axillary inflorescence; E. flower, posterior petal uppermost; F. gynoecium, anterior style in center; G. samaras, abaxial view (left) and adaxial view (right); H. old flower after fall of samaras, pyramidal torus in center, surrounded by lobed disc. Scale bar equivalents: A, 4 cm; B, C, 4 mm; D, E, 8 mm; F, 2 mm; G, 1 cm; H, 4 mm. Based on: A, D–F, *Breckon et al.* 2343, MICH; B, C, *Schoenwetter JSOX-91*, MICH; G, *García M.* 3297, MICH; H, *McVaugh* 24000, MICH.

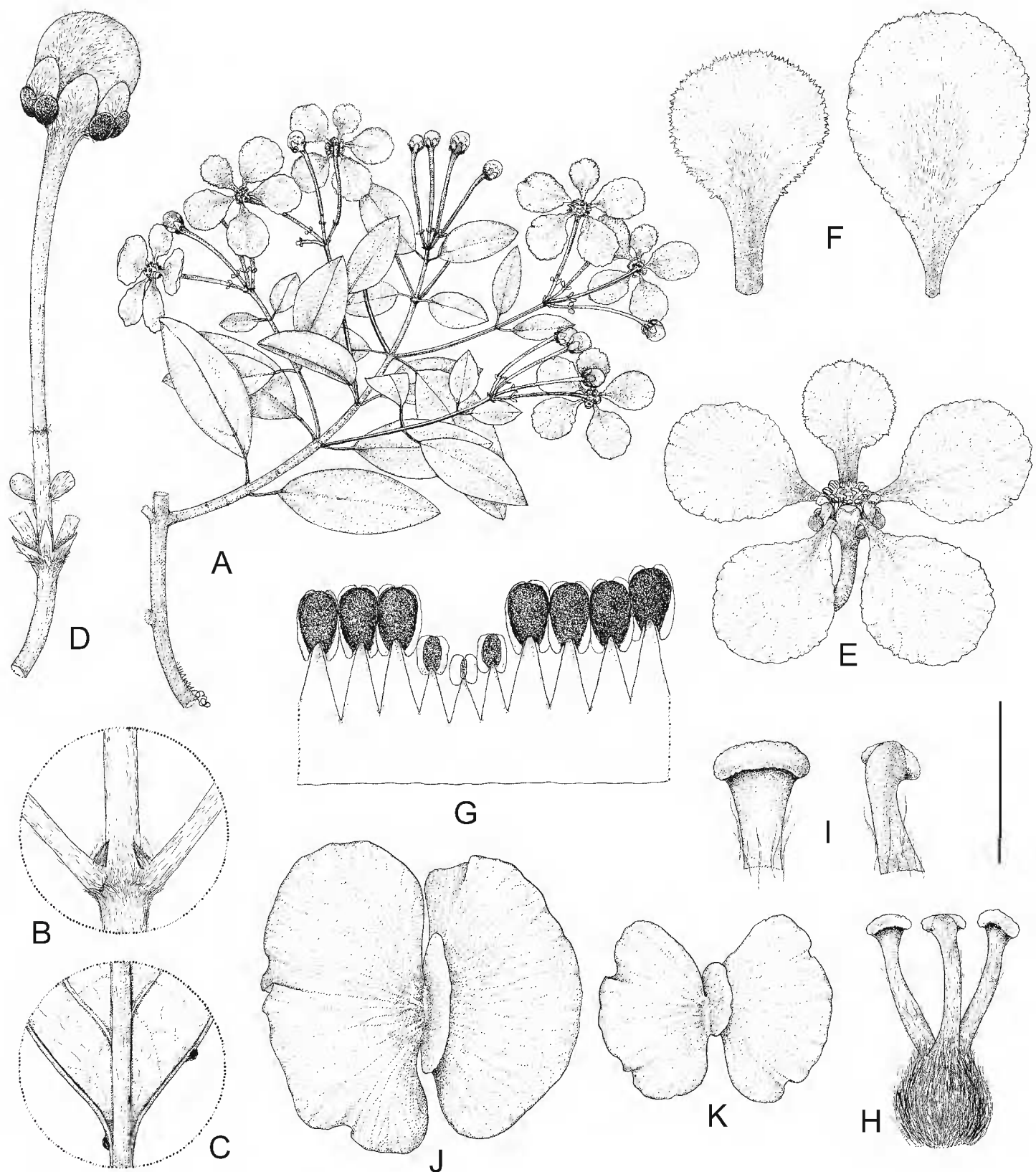


Fig. 9. *Callaeum septentrionale* (A. Juss.) D. M. Johnson. A. flowering branch; B. node with epipetiolar stipules; C. base of lamina, abaxial view, showing marginal glands; D. flower bud in umbel; E. flower, posterior petal uppermost; F. petals, abaxial view, posterior petal (left) and lateral petal (right); G. androecium laid out, abaxial view, the smallest stamen opposite posterior petal; H. gynoecium; I. distal portion of styles, adaxial view (left) and abaxial view (right); J. samara, abaxial view; K. samara, abaxial view. Scale bar equivalents: A, 4 cm; B, C, 4 mm; D, 8 mm; E, 1.3 cm; F, 8 mm; G, H, 2.7 mm; I, 1.3 mm; J, K, 2.7 cm. Based on: A–I, *Daniel 287*, MICH; J, *Anderson 13314*, MICH; K, *Anderson & Laskowski 4078*, MICH.

***Carolus***: six species, four endemic to South America, one endemic to Panama, and one distributed from South America to Mexico. *Carolus* is embedded in a clade comprising two Old World genera (*Flabellariopsis* and *Hiptage*) and two South American genera (*Dicella* and *Tricomaria*); it is not morphologically similar to either group (Davis & Anderson, 2010; Anderson et al., 2012). The evidence, such as it is, suggests an origin in South America.

***C. sinemariensis* (Aubl.) W. R. Anderson (Fig. 10)**: a woody vine, in most populations dispersed by winged samaras, in northern South America, Central America, and at scattered localities across southern Mexico, mostly in mesic forests or secondary associations, but sometimes also in tropical deciduous forest.

***Christianella***: five species, all vines and wind-dispersed by winged samaras (W. Anderson, 2006); four are found only in South America, the fifth is found only in Central America and Mexico. *Christianella* is sister to the other six genera of the *Christianella* clade, all limited to South America and southern Central America except for the African genus *Flabellaria* and the genus *Callaeum*, which is discussed above.

***C. mesoamericana* (W. R. Anderson) W. R. Anderson (Fig. 11)**: known from five collections from Panama, Costa Rica, and Guatemala and one from Chiapas; the habitat, so far as it is known, is “mixed forest.”

***Cottsia* (Fig. 12)**: three species endemic to the deserts of northern Mexico and adjacent United States, all vines wind-dispersed by winged samaras (Anderson & Davis, 2007; Anderson et al., 2012). *Cottsia* is sister to the rest of the *Aspicarpa* clade [*Camarea*, South American; *Janusia*, South American; *Aspicarpa* s. l., South American; and *Aspicarpa* s. str./*Gaudichaudia*, Mexican], but no lineage is known that could have been directly ancestral to *Cottsia*. Sister to the *Aspicarpa* clade is the *Cordobia* clade (*Mionandra*, *Cordobia*, *Gallardoa*, and *Peixotoa*), all South American (Anderson & Davis, 2007; Davis & Anderson, 2010; Anderson et al., 2012). It is difficult to escape the conclusion that the ancestor of *Cottsia* must have travelled via long-distance dispersal from southern South America to northern Mexico, quite independently of the ancestor of *Aspicarpa*/*Gaudichaudia* (Anderson & Davis, 2007).

***Diplopterys***: 31 species, all but one mostly South American with two of those reaching Panama or Costa Rica (Gates, 1982; Anderson & Davis, 2006). *Diplopterys* is in



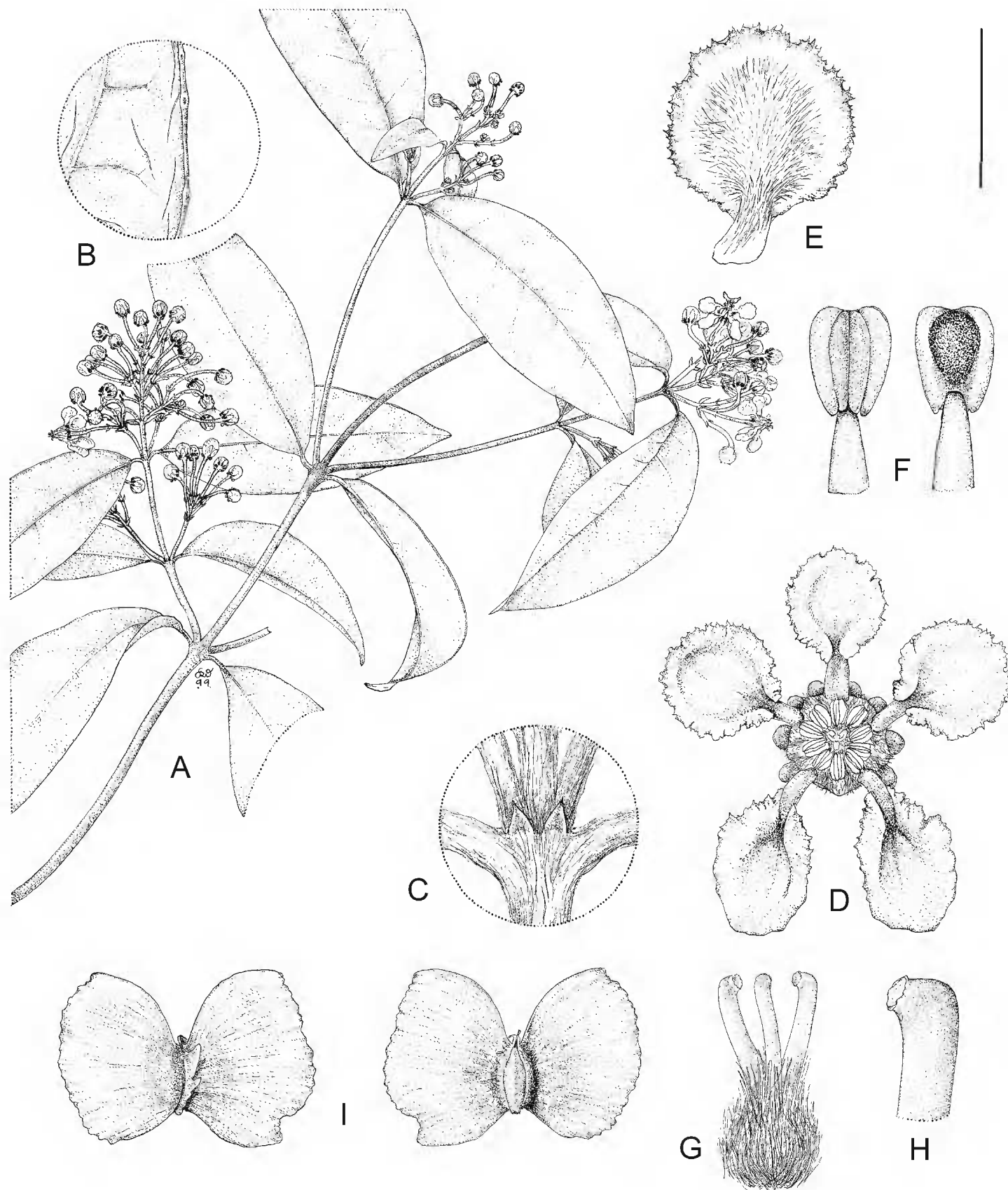


Fig. 10. *Carolus sinemariensis*. A. flowering branch; B. abaxial margin of lamina; C. node with stipules; D. flower, posterior petal uppermost; E. lateral petal, abaxial view; F. anthers, adaxial view (left) and abaxial view (right); G. gynoecium; H. apex of style; I. samaras, abaxial view (left) and adaxial view (right). Scale bar equivalents: A, 4 cm; B, C, 4 mm; D, 7 mm; E, 4 mm; F, 2 mm; G, 2.7 mm; H, 1.3 mm; I, 2 cm. Based on: A–H, *Wilbur & Wilbur 2394*, MICH; I, *Cochrane et al. 12331*, MICH.

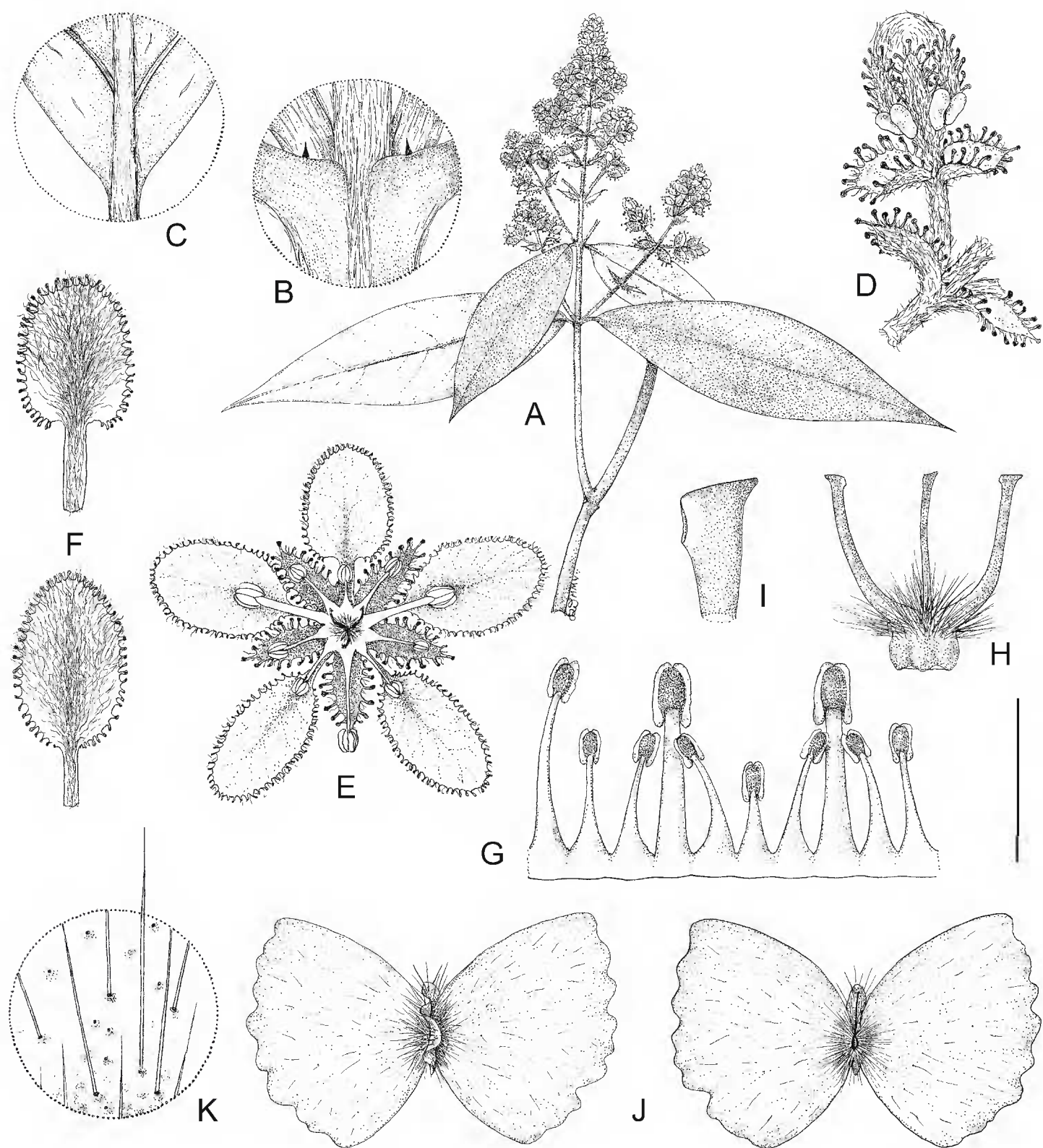


Fig. 11. *Christianella mesoamericana*. A. flowering branch; B. node to show stipules; C. abaxial base of lamina; D. flower bud; E. flower from above, posterior petal uppermost; F. abaxial views of posterior petal (above) and lateral petal (below); G. androecium laid out, abaxial view, the shortest stamen opposite posterior petal; H. gynoecium, anterior style in center; I. apex of style; J. samaras, abaxial view (left) and adaxial view (right); K. hairs on abaxial surface of samara wing. Scale bar equivalents: A, 4 cm; B, 2 mm; C, 4 mm; D, E, 8 mm; F, 5.7 mm; G, H, 4 mm; I, 1 mm; J, 2 cm; K, 2 mm. Based on: A, C–H, *Sytsma & D'Arcy 3278, MICH*; B, *Matuda 18577*, F; I–K, *Standley 87301*, F.

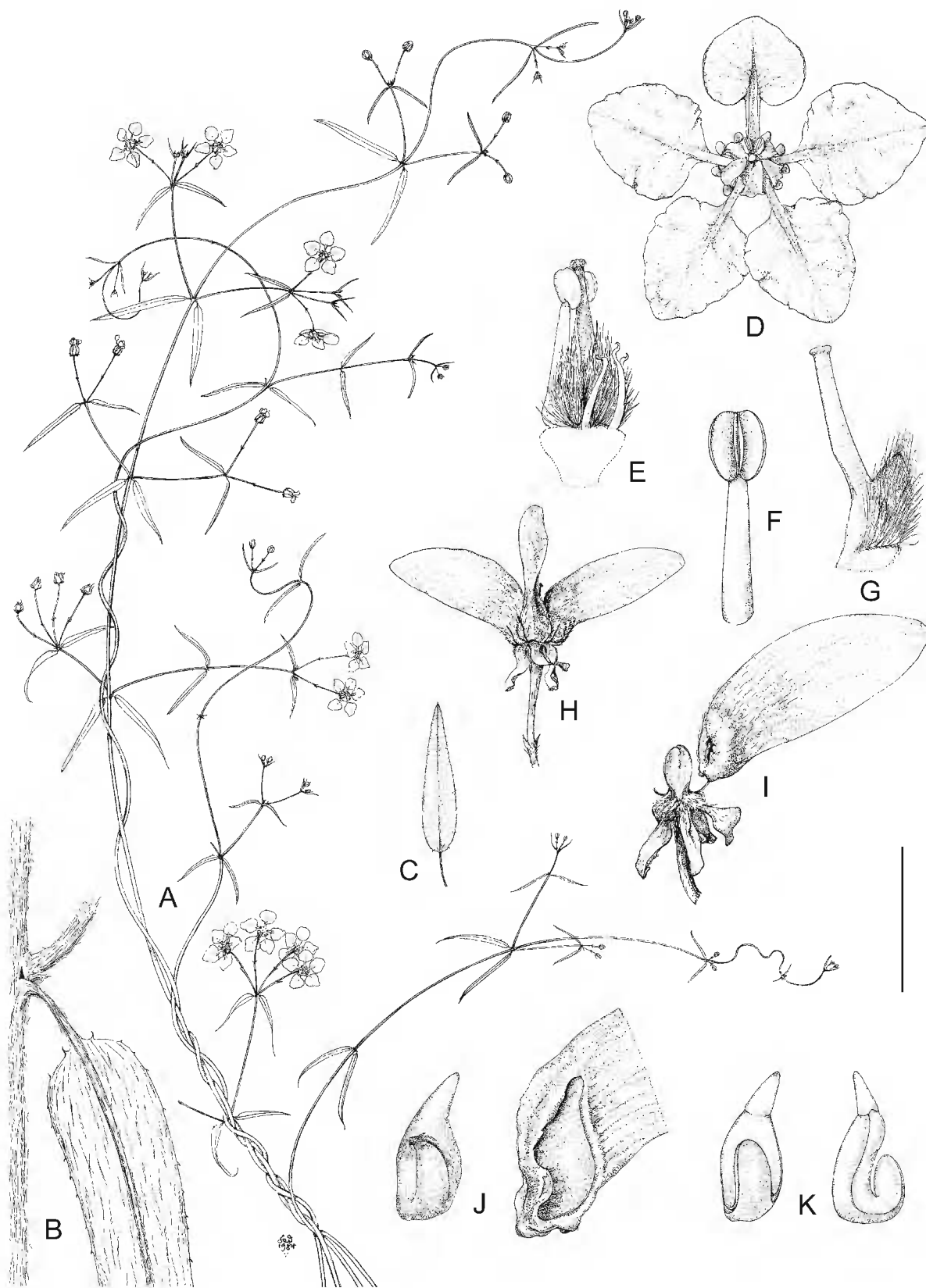


Fig. 12. *Cottisia gracilis* (A. Gray) W. R. Anderson & C. Davis. A. flowering branches; B. base of leaf and adjacent stem to show stipule and marginal processes; C. detached, relatively broad leaf; D. flower, posterior petal uppermost; E. androecium and gynoecium, with two fertile posterior stamens and three anterior staminodes; F. fertile stamen, adaxial view; G. anterior carpel; H. fruit; I. fruit base and torus with one samara attached by carpophore; J. seed (left) and nut of samara in longitudinal section with seed removed (right); K. embryos. Scale bar equivalents: A, 4 cm; B, 4 mm; C, 4 cm; D, 5.7 mm; E, 2.9 mm; F, G, 2 mm; H, 1 cm; I, 5.7 mm; J, K, 4 mm. Based on: A, B, *Monson 8*, CAS; C–G, *Anderson 12552*, MICH; H–K, *Anderson & Laskowski 3520*, MICH.

the *Stigmaphyllon* clade and is sister to *Stigmaphyllon* (Davis & Anderson, 2010). The one species not found in South America is endemic to Mexico.

***D. mexicana* B. Gates:** known only from the type, a woody vine collected in primary wet forest in Veracruz. The fruit is unknown; the peculiar bracts and bracteoles are of a type found otherwise in six species that grow only in South America. Among those species two produce wind-dispersed winged samaras and the other four have the wings greatly reduced and the mericarps probably dispersed by water. The ancestor of *D. mexicana* surely came from South America, and it will be a surprise if the fruit, when found, does not break apart into wind-dispersed samaras.

***Echinopterys* (Fig. 13):** two species endemic to Mexico, growing in tropical deciduous forest, desert scrub, and other seasonally dry habitats; shrubs or woody vines, wind-dispersed by bristly fruits. *Echinopterys* is sister to the rest of the *Bunchosia* subclade of the *Bunchosia* clade, while sister to that subclade is the *Tristellateia* subclade, with *Henleophytum* and *Heladena* basal in this subclade (Davis & Anderson, 2010; Anderson et al., 2012). *Henleophytum* is a Cuban endemic that has bristly fruits similar to those of *Echinopterys*. Both of those subclades are strongly supported, so unless bristly fruits are plesiomorphic in the clade, it is difficult to explain their independent appearance in those two genera. Aside from *Henleophytum*, no likely source for the ancestor of *Echinopterys* is known. However, it is interesting to note that the sister of *Henleophytum* is *Heladena*, a genus of South America, so the *ultimate* source of *Echinopterys* was probably South American. *Echinopterys* is one of the most enigmatic and interesting genera of Malpighiaceae endemic to Mexico.

***Galphimia* (Figs. 14, 15):** 26 species, 4 in southern South America and 22 in Mexico, with one of the Mexican species extending into Texas and another extending into Central America as far south as Nicaragua (C. Anderson, 2007). *Galphimia* is a genus of perennial herbs, subshrubs, shrubs, and small trees, occurring throughout Mexico in diverse habitats, both dry and mesic. The fruit breaks apart into small dry cocci that are without wings or any other adaptation for dispersal. Some of the Mexican species (e.g., *G. glauca* Cav.) have the petals persistent and drying below the enlarging fruit, suggesting a possible aid to dispersal, but C. Anderson (pers. comm.) reports that the cocci fall freely at maturity and there is no obvious tendency for the flower to detach with the fruit intact, so she doubts that the dried corolla is actually active in dispersal. Besides, such a dry, persistent corolla is not basal in

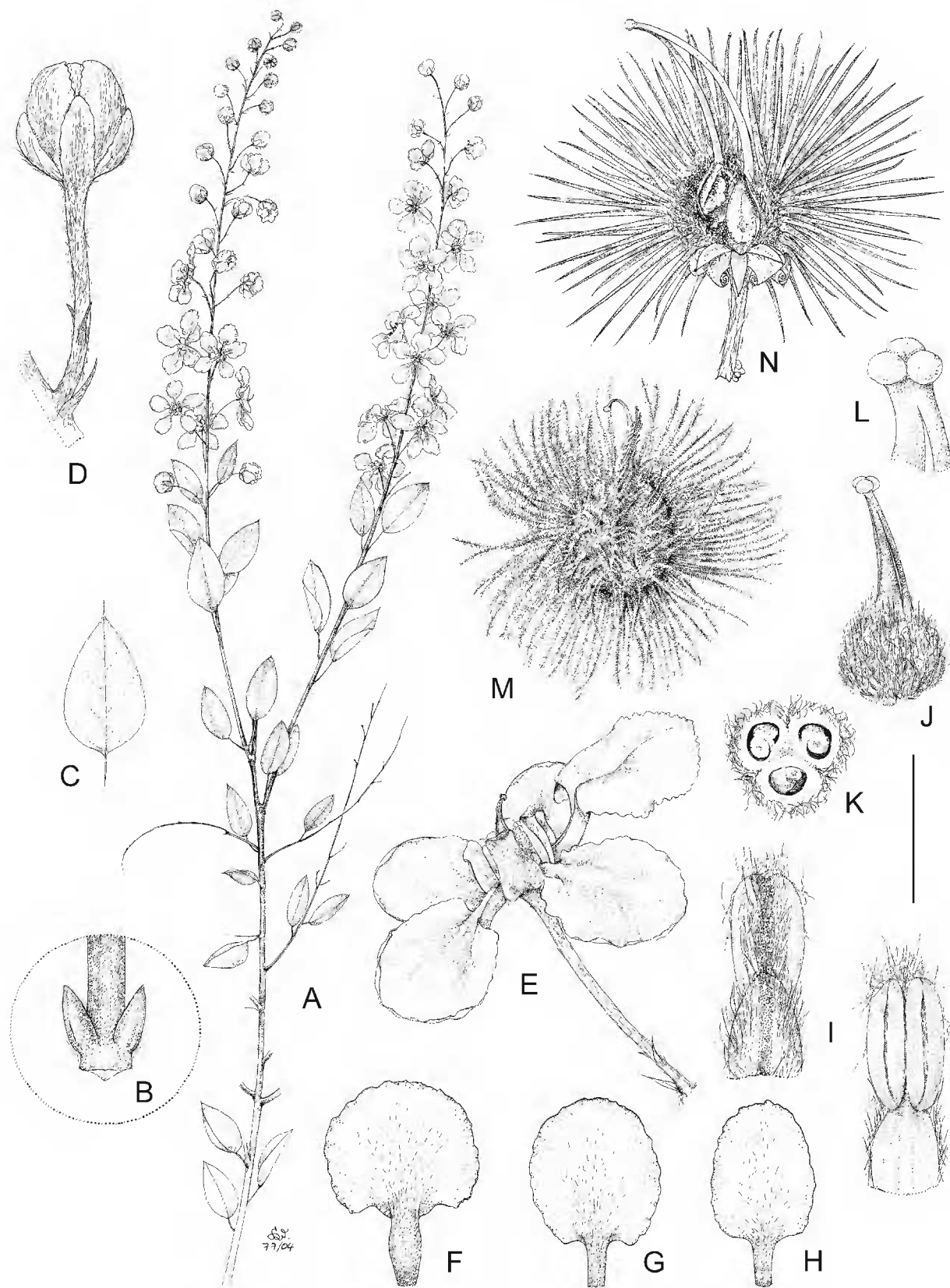


Fig. 13. *Echinopterys*. A–M, *E. eglandulosa* (A. Gray) Small. A. flowering branch; B. base of petiole, adaxial view, to show stipules; C. detached leaf; D. flower bud; E. flower, posterior petal at upper right; F. posterior petal, abaxial view; G. posterior-lateral petal, abaxial view; H. anterior-lateral petal, abaxial view; I. stamens, abaxial view (left) and adaxial view (right); J. gynoecium; K. cross-section of ovary; L. coherent apices of styles; M. mericarp, abaxial view. N, *E. setosa* Brandegee. Mature fruit, one mericarp removed, the other two mericarps separating from torus. Scale bar equivalents: A, 4 cm; B, 2 mm; C, 4 cm; D, 6.7 mm; E–H, 8 mm; I, 2 mm; J, K, 2.7 mm; L, 1 mm; M, N, 4 mm. Based on: A, B, D, *Feddema* 2370, MICH; C, E–M, *McVaugh* 25850, MICH; N, *Muller* 3281, MICH.

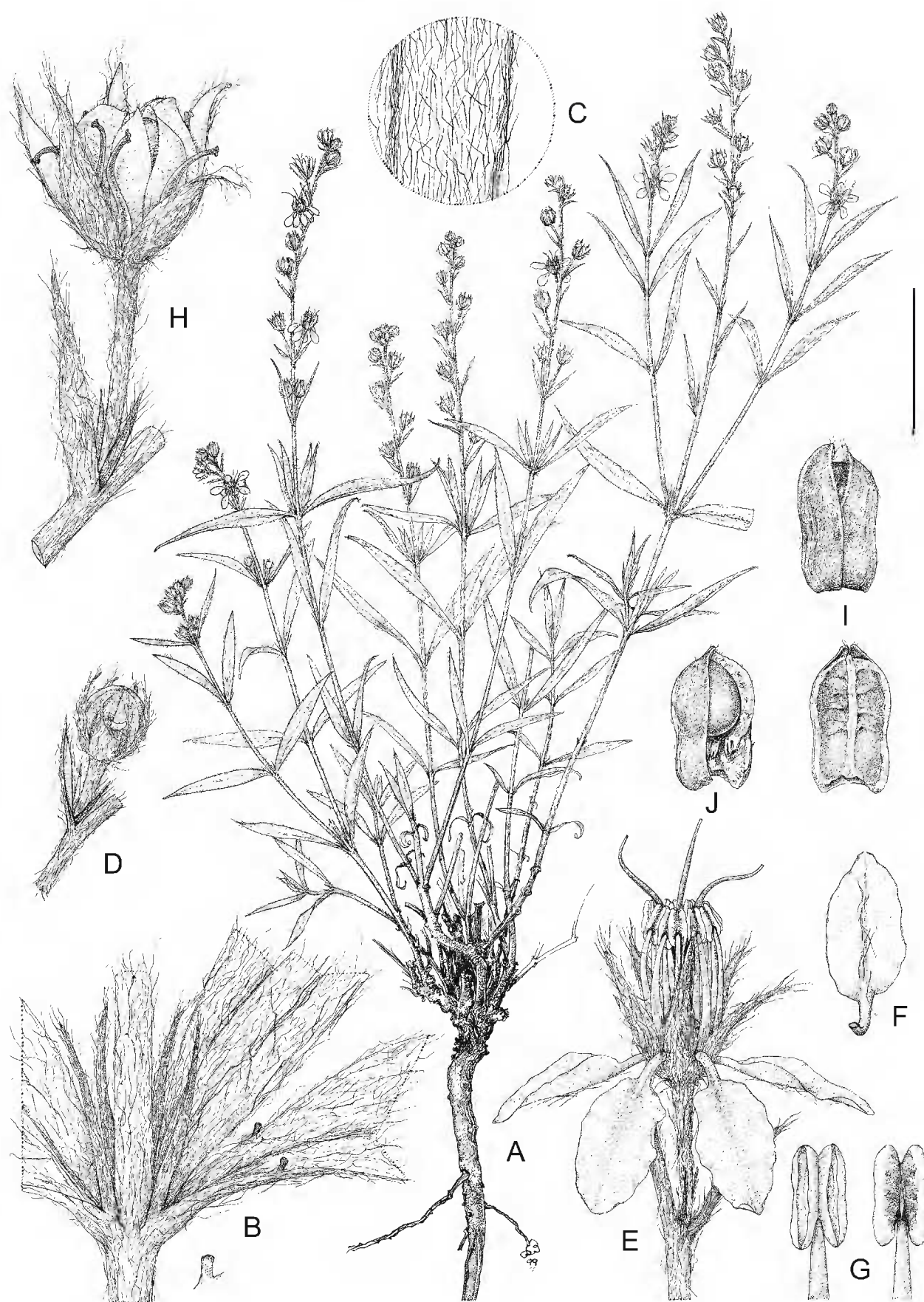


Fig. 14. *Galphimia vestita* S. Watson. A. habit; B. node with stipules (and detached marginal leaf gland); C. abaxial leaf surface; D. flower bud, anterior sepal bent down; E. flower; F. petal, abaxial view; G. anthers, adaxial view (left) and abaxial view (right); H. fruit; I. cocci, abaxial view (above) and adaxial view (below); J. coccus with half of abaxial wall removed. Scale bar equivalents: A, 4 cm; B, 4 mm (2 mm); C, 4 mm; D, 5.7 mm; E, F, 5 mm; G, 2 mm; H–J, 4 mm. Based on: A–D, *White 3574* (Sonora), GH; E–J, *Wiggins 7471* (Sonora), DS.

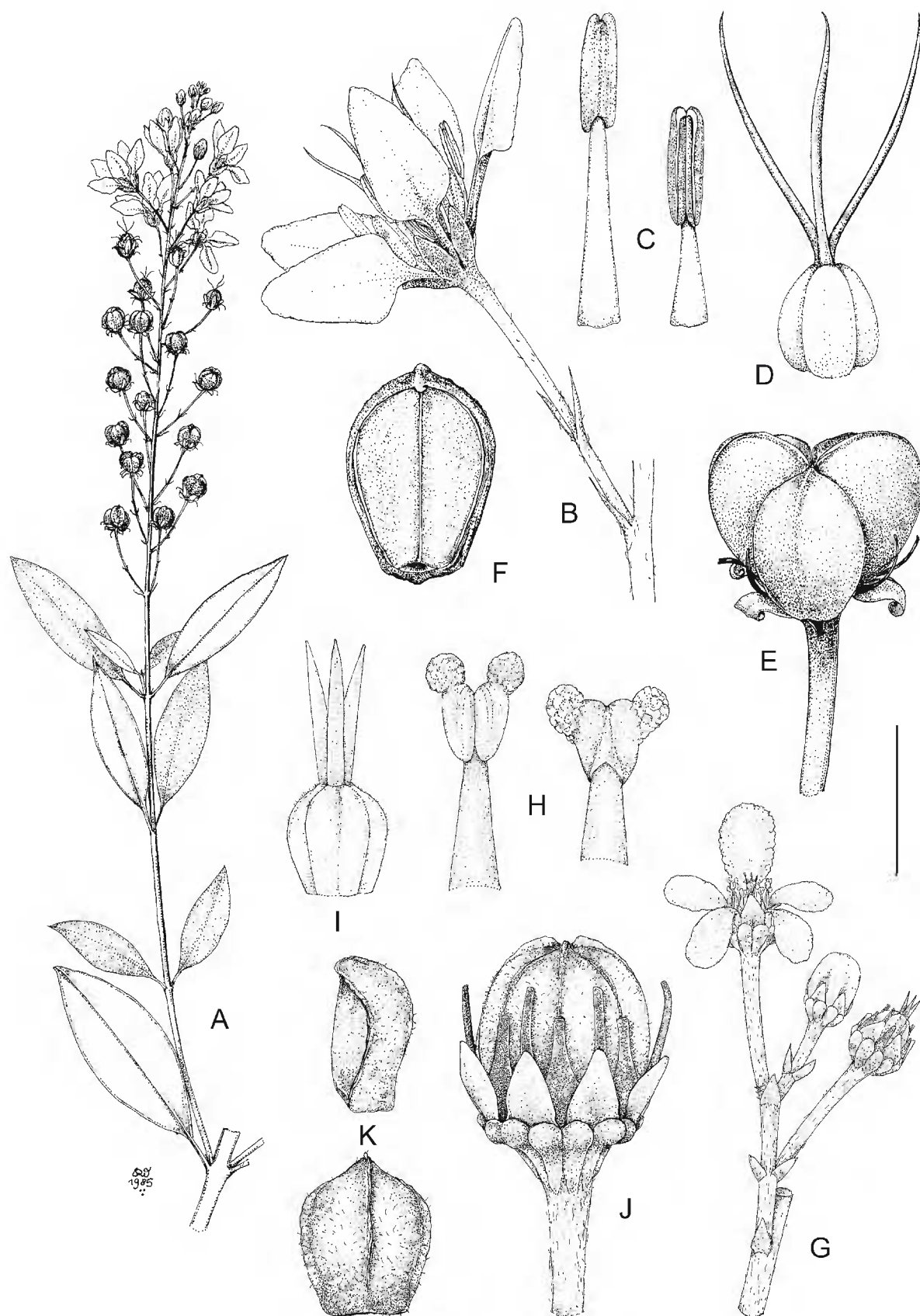


Fig. 15. *Galphimia* and *Verrucularia*. A–F, *G. gracilis* Bartl. A. flowering and fruiting branch; B. flower, lateral view, posterior petal at upper right; C. stamens, abaxial view (left) and adaxial view (right); D. gynoecium; E. intact fruit; F. coccus, adaxial view. G–K, *V. glaucophylla* A. Juss. G. portion of inflorescence; H. stamens, adaxial view (left) and abaxial view (right); I. gynoecium; J. intact fruit; K. cocci, lateral view (above) and abaxial view (below). Scale bar equivalents: A, 3 cm; B, 6 mm; C, D, 3 mm; E, 4.2 mm; F, 3 mm; G, 1 cm; H, I, 1.3 mm; J, K, 4 mm. Based on: A–F, Fryxell & Anderson 3484, MICH; G–I, Harley et al. 25901, MICH; J, K, Carvalho et al. 1036, MICH.

the genus (Davis & Anderson, 2010), so at most the effectiveness of such dispersal would be local within Mexico. The sister of *Galphimia* is *Verrucularia* (W. R. Anderson, 1981; Davis & Anderson, 2010), a genus of two species in southeastern and northern Brazil, which has a similar fruit, so it seems most likely that the ancestor of *Galphimia* migrated to Mexico from South America but it is not at all obvious how that ancestor travelled so far; the Central American species, *G. speciosa* C. E. Anderson, is not basal in the clade (Davis & Anderson, 2010), so its distribution seems most likely to be the result of back-migration from Mexico southward, not a remnant from the northbound ancestor of *Galphimia*. The clade of four species in southern South America, represented in our recent phylogeny (Davis & Anderson, 2010) by *G. brasiliensis* (L.) A. Juss. and *G. platyphylla* Chodat, is sister to a Mexican species, *G. gracilis* Bartl., and that clade is sister to the rest of *Galphimia*, so *Galphimia* in Mexico may represent two lineages, but another way to interpret that tree is that *Galphimia* in Mexico is a single lineage, one representative of which migrated to southern South America and diversified to produce the four species currently there.

***Gaudichaudia***—See *Aspicarpa/Gaudichaudia*.

***Heteropterys***: approximately 150 species, mostly South American but also widespread in Central America, Mexico, and the West Indies; one mostly Caribbean species has reached West Africa (Anderson et al., 2012). *Heteropterys* reached Mexico at least four times, with the Mexican species falling into three distinct groups that were recognized by Niedenzu (1928) and our phylogenetic tree (Davis & Anderson, 2010).

***H. brachiata* (L.) DC., *H. cotinifolia* A. Juss., *H. palmeri* Rose, and *H. panamensis* Cuatrec. & Croat (Fig. 16)**: these species represent a large South American group of pink- or pink and white-flowered species called ser. *Rhodopetalis* by Niedenzu (1928), represented in our phylogenetic tree by *H. brachiata* and *H. rufula* A. Juss. (Davis & Anderson, 2010). All four species are woody vines (occasionally shrubby) wind-dispersed by winged samaras. *Heteropterys brachiata* occurs from westernmost South America throughout Central America and is common across central and southern Mexico, where it grows in diverse dry and mesic habitats; *H. cotinifolia* is endemic to Mexico from Sonora to Chiapas, in tropical deciduous forests; *H. palmeri* is endemic to Mexico except for one collection from El Salvador, growing in tropical deciduous forests from Sonora and Sinaloa across southern Mexico to Oaxaca; *H. panamensis* occurs in more or less



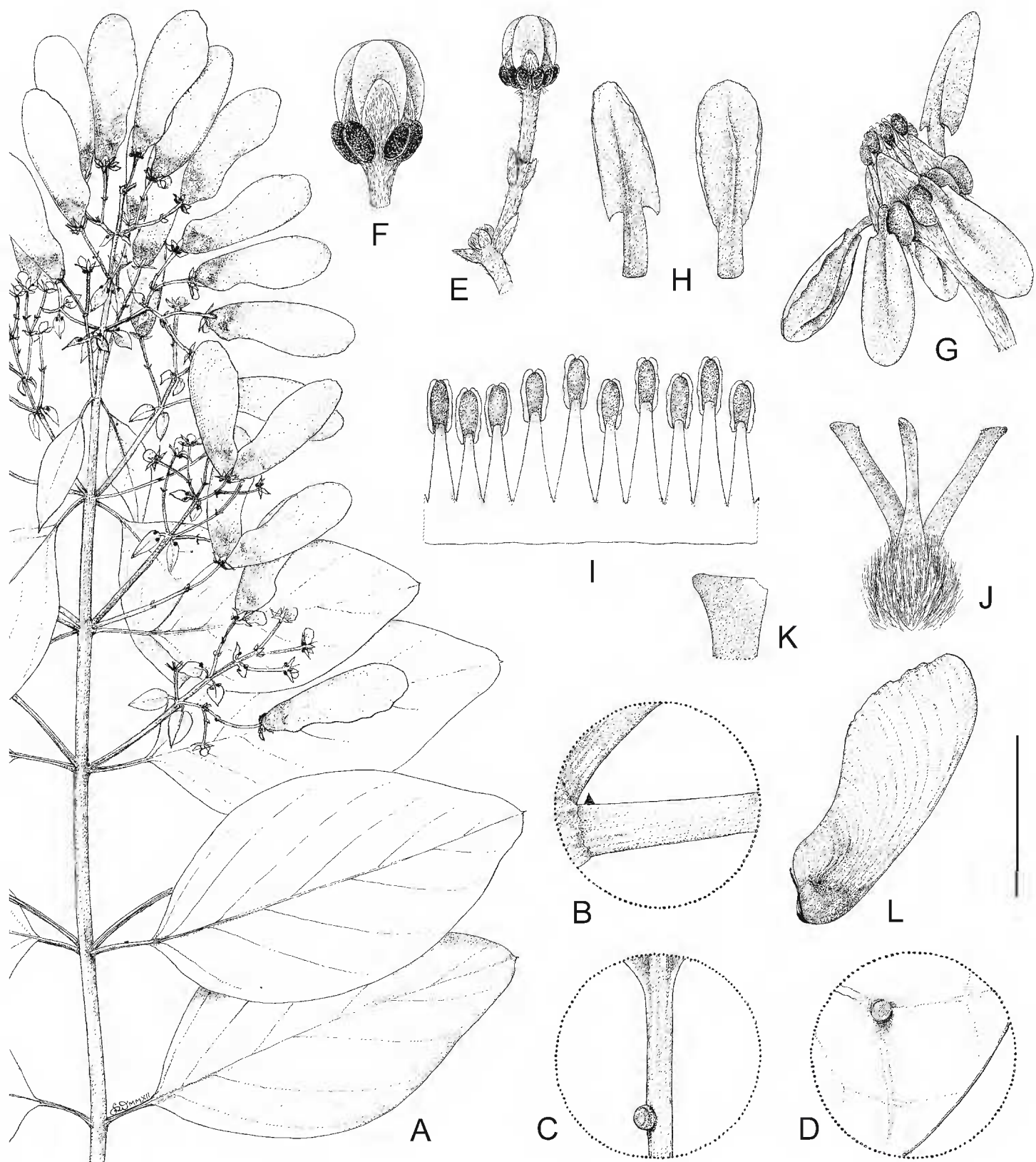


Fig. 16. *Heteropterys cotinifolia*. A. fruiting branch; B. epipetiolar stipule; C. gland on petiole; D. gland on abaxial leaf surface; E. flower bud borne on pedicel and peduncle; F. flower bud enlarged to show keeled petals; G. flower, lateral view, posterior petal uppermost; H. petals, abaxial views, lateral petal (right) and posterior petal (left); I. androecium laid out, abaxial view, stamen second from left opposite posterior petal; J. gynoecium, anterior style in center; K. distal portion of style, lateral view; L. samara. Scale bar equivalents: A, 4 cm; B, 4 mm; C–E, 8 mm; F, G, 5.7 mm; H, 5 mm; I, 4 mm; J, 2.7 mm; K, 1 mm; L, 2 cm. Based on: A–D, L, *Anderson & Laskowski 4330*, MICH; E–K, *Flores-Franco et al. 2692*, MICH.

mesic forests from Panama to Nicaragua with three collections from Chiapas. These four species probably represent two lineages in Mexico. The two species endemic to Mexico were most likely derived from *H. brachiata* after its arrival in Mexico, while *H. panamensis* was probably derived from *H. brachiata* in Central America and subsequently invaded Mexico, penetrating only as far as Chiapas.

***H. laurifolia* (L.) A. Juss. and *H. lindeniana* A. Juss. (Fig. 17):** these belong to subg. *Parabanisteria*, a mostly South American group of yellow-flowered species with long, eventually revolute sepals; the subgenus is represented in our phylogenetic tree by *H. byrsonimifolia* A. Juss. and *H. leona* (Cav.) Exell (Davis & Anderson, 2010). *H. laurifolia* is common and widely distributed in western South America, Central America, the West Indies, and across southern Mexico from the Yucatán Peninsula to Sinaloa; it is a woody vine or large shrub sometimes described as a small tree, wind-dispersed by winged samaras, growing in both seasonally dry and more mesic vegetation. *Heteropterys lindeniana* is a shrub or small tree growing usually along streams or in mangrove swamps in the Yucatán Peninsula of Mexico and Belize and in coastal areas of northern Central America; it resembles *H. laurifolia* in most characters but its mericarp has been modified from the wind-dispersed samara of *H. laurifolia* by the nearly complete loss of the dorsal wing, almost certainly as an adaptation to dispersal by water. It seems likely that the two species represent a single lineage, with *H. lindeniana* derived from *H. laurifolia* in Mexico or adjacent Central America.

***H. macrostachya* A. Juss.:** widely distributed in South America and in Central America to Nicaragua; not reported from Honduras or Guatemala but rare in Belize and Chiapas, in diverse habitats but most commonly in mesic or seasonally dry forest, a woody vine (sometimes shrubby) wind-dispersed by winged samaras. This species belongs to a group of yellow-flowered species with the leaves abaxially densely sericeous, mostly limited to eastern and southern Brazil (ser. *Metallophyllis* of Niedenzu, 1928); the group is represented in our phylogenetic tree by six species, including *H. macrostachya* (Davis & Anderson, 2010).

***Hiraea*:** at least 75 species (C. Anderson, pers. comm.), mostly South American but with approximately ten species in Central America, four in Mexico, and one in the Lesser Antilles, the Mesoamerican species all woody vines wind-dispersed by winged samaras. The Mexican species fall into three groups, which could represent either three or four Mexican lineages:

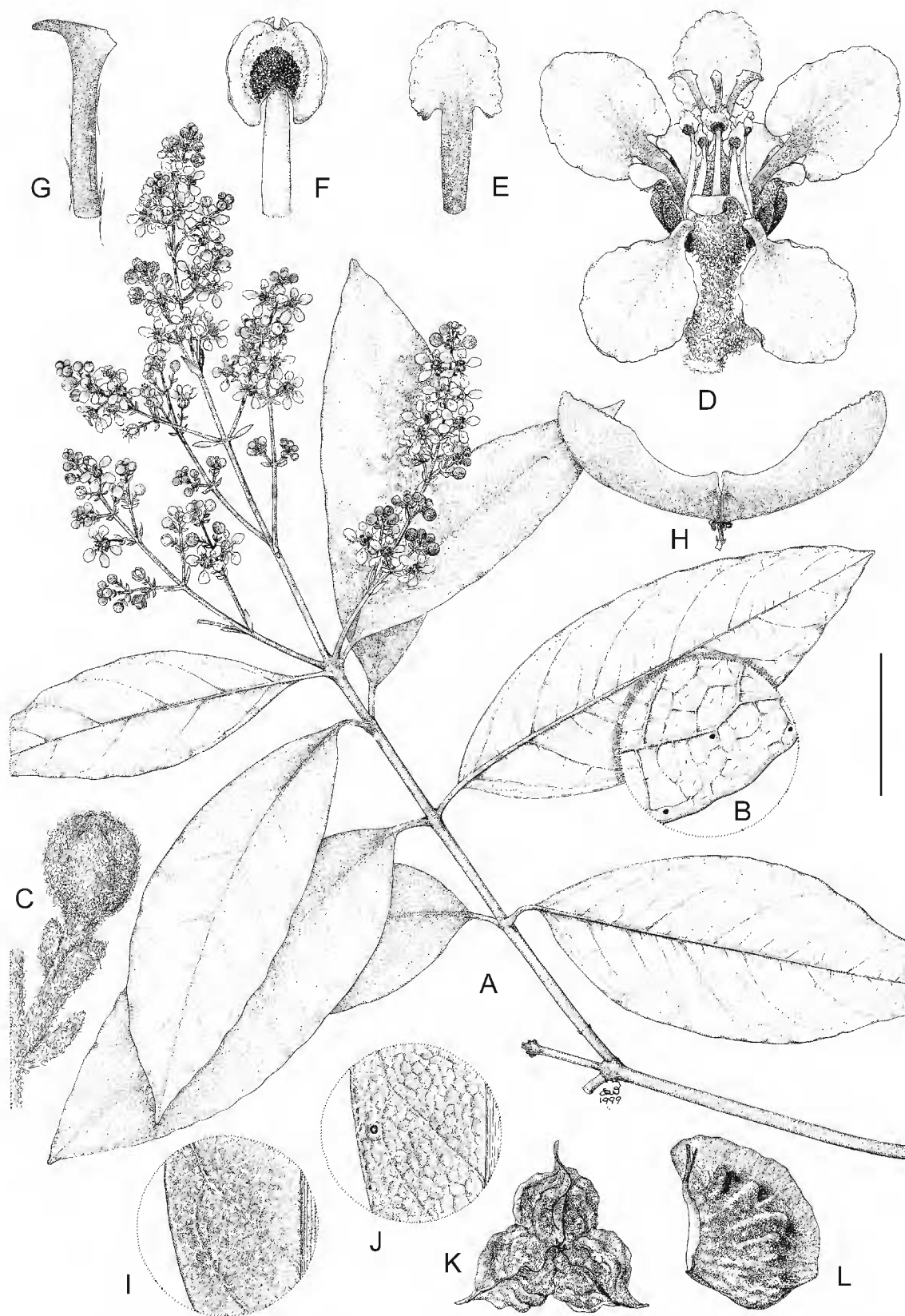


Fig. 17. *Heteropterys*. A–H, *H. laurifolia*. A. flowering branch; B. abaxial leaf surface, enlarged to show venation and glands; C. flower bud; D. flower, posterior petal uppermost; E. posterior petal, adaxial view; F. anther, abaxial view; G. distal portion of style; H. fruit with two samaras developed. I–L, *H. lindeniana*. I. adaxial leaf surface; J. abaxial leaf surface, enlarged to show finely reticulate venation and gland; K. intact fruit from above, with all three mericarps developed; L. mericarp, lateral view. Scale bar equivalents: A, 3 cm; B, 6 mm; C, 3.75 mm; D, E, 3 mm; F, G, 1 mm; H, 2 cm; I, J, 4 mm; K, L, 1 cm. Based on: A–C, *McVaugh 10176*, MICH; D–G, *Lott 1020*, MICH; H, *Téllez 10439*, MICH; I, J, *Gentle 1309*, MICH; K, L, *Whitefoord 2546*, MICH.

***H. barclayana* Benth. and *H. reclinata* Jacq.:** these are sister species with four-flowered umbels, distinguished from each other by different leaf vestiture; they grow in both mesic and tropical deciduous forests. *H. reclinata* occurs in northwestern South America, throughout Central America, and in southern Mexico from the Yucatán Peninsula and Veracruz to Jalisco; *H. barclayana* is found from Nicaragua in Central America to Mexico, where it occurs from Chiapas and Veracruz to Nayarit and Sinaloa. They seem most likely to have diverged in Central America and invaded Mexico independently, in which case they represent two Mexican lineages, but it is possible that they diverged in Mexico and should be considered one Mexican lineage.

***H. fagifolia* (DC.) A. Juss.:** this is another species with four-flowered umbels but morphologically quite distinct from the *H. reclinata* complex (C. Anderson, pers. comm.); it is widespread in South and Central America, and known in southeastern Mexico from the Yucatán Peninsula, Chiapas, Oaxaca, and Veracruz. In Mexico and Central America it grows mostly along rivers and in moist forests.

***H. smilacina* Standl. (Fig. 18):** this species has multiflowered umbels and belongs to a large South American complex; it is known from northwestern South America (Ecuador and Colombia), Central America, and southeastern Mexico (Tabasco, Chiapas, Oaxaca, and Veracruz), growing in moist forests.

***Lasiocarpus* (Figs. 19, 20):** approximately four species endemic to tropical deciduous woods in Mexico from Sinaloa to Chiapas; shrubs and trees, wind-dispersed by bristly mericarps. *Lasiocarpus* is sister to the morphologically and ecologically similar genus *Ptilochaeta* of southern South America (Brazil, Paraguay, Argentina, and Bolivia); nothing resembling those two genera or closely related to them is found anywhere between them (Davis & Anderson, 2010). The 2010 phylogenetic tree shows us that the sister to the *Lasiocarpus/Ptilochaeta* clade is the morphologically very different *Dinemagonum/Dinemandra* clade of Chile. More compelling, perhaps, is the fact that in *Ptilochaeta* the flowers are functionally bisexual as in most Malpighiaceae (including *Dinemagonum* and *Dinemandra*), whereas in *Lasiocarpus* the flowers are functionally unisexual and the species functionally dioecious (W. R. Anderson, unpublished data), so there can be little doubt that *Ptilochaeta* is the less derived of the two genera and the ancestor of *Lasiocarpus* must have migrated from South America to Mexico.

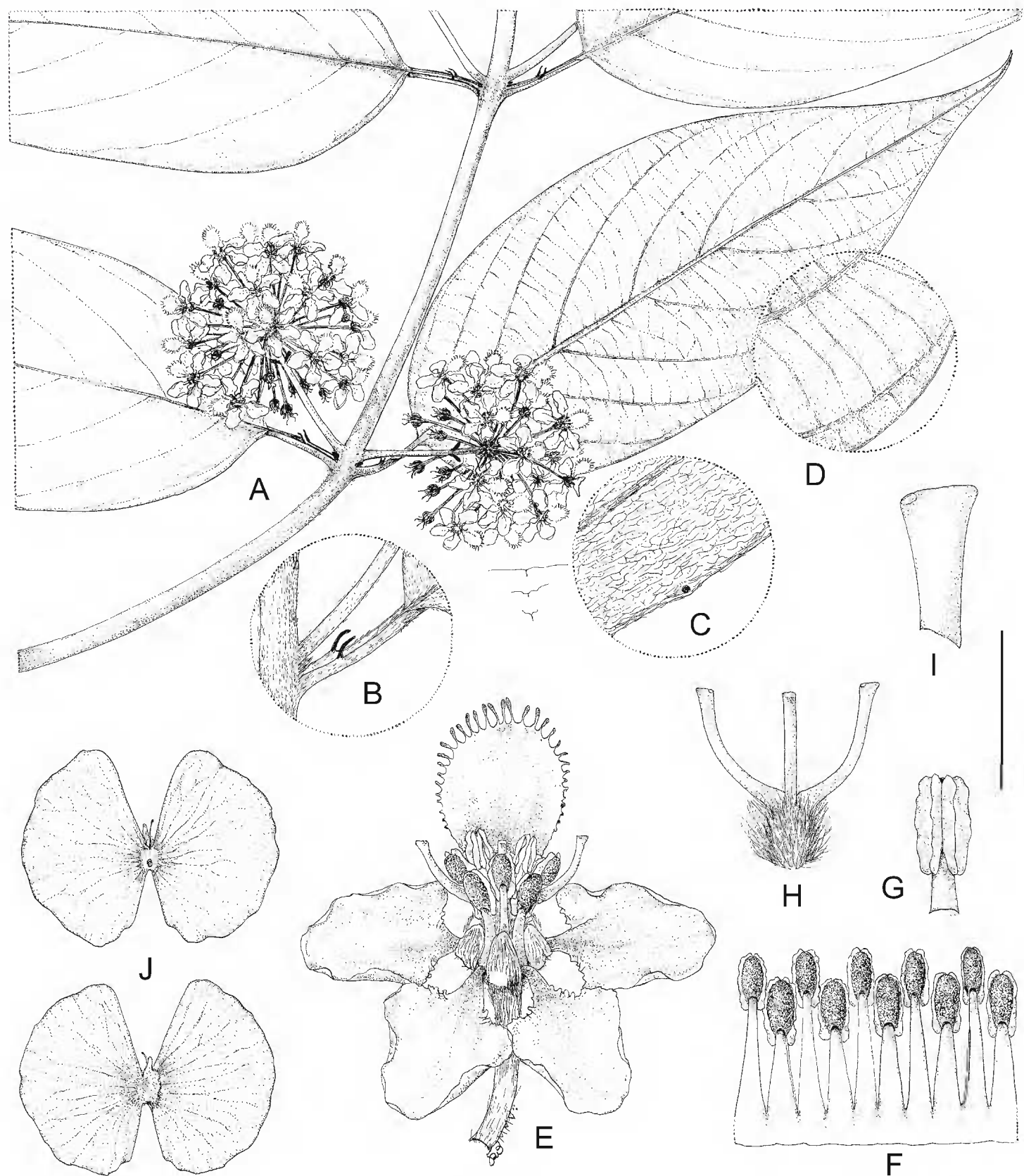


Fig. 18. *Hiraea smilacina*. A. flowering branch; B. petiole with stipules; C. abaxial margin of lamina, showing hairs and marginal gland; D. parallel tertiary veins, abaxial view of lamina; E. flower, posterior petal uppermost; F. androecium laid out, abaxial view, stamen above the letter "F" opposite posterior petal; G. anther, adaxial view; H. gynoecium, anterior style in center; I. distal portion of style; J. samaras, adaxial view (above) and abaxial view (below). Scale bar equivalents: A, 4 cm; B, 2 cm; C, 4 mm; D, 1.3 cm; E, 5.7 mm; F, 4 mm; G, 2 mm; H, 4 mm; I, 1 mm; J, 2.7 cm. Based on: A–I, *Foster 2365*, MICH; J, *Foster 2372*, DUKE.

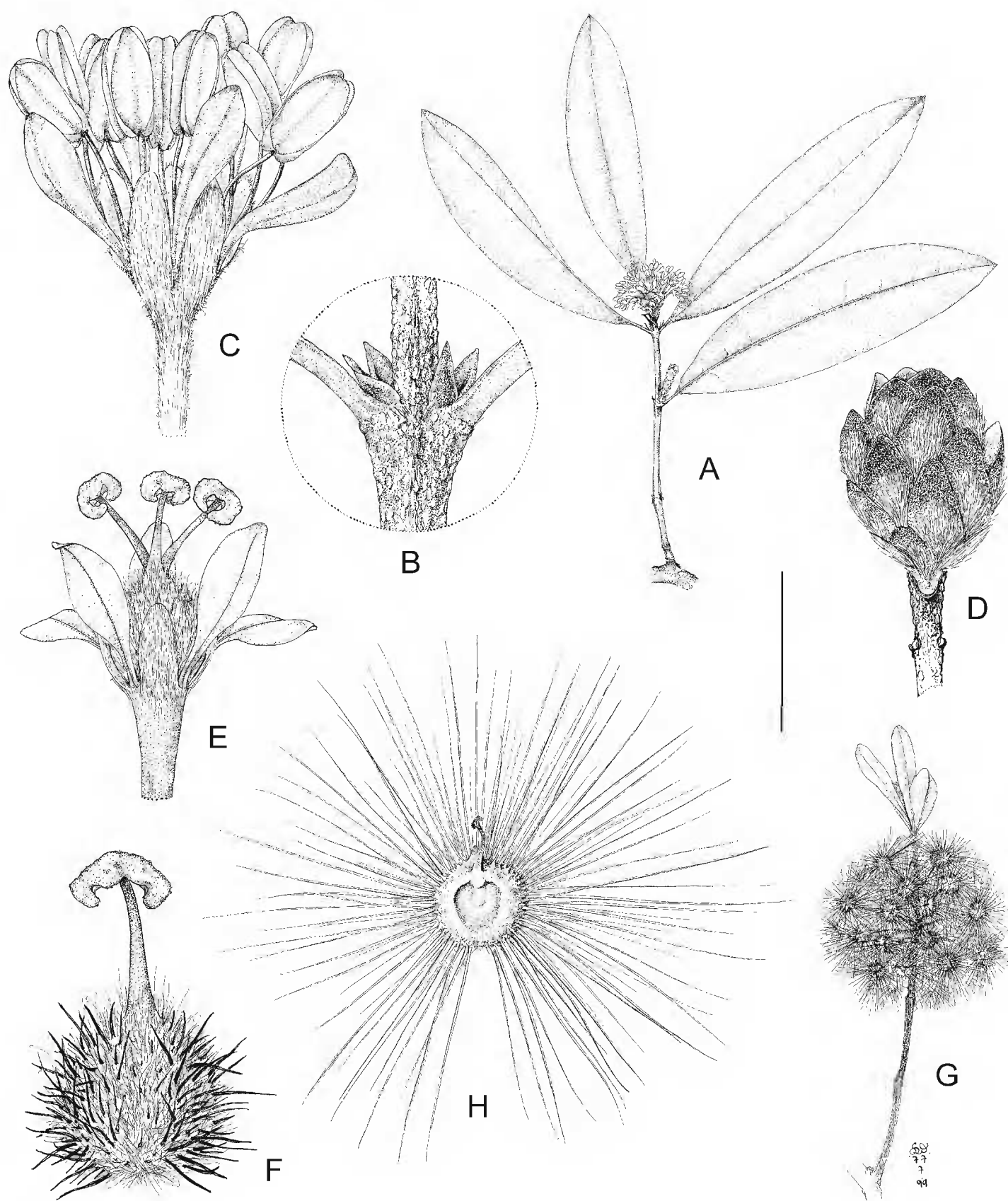


Fig. 19. *Lasiocarpus ferrugineus* H. S. Gentry. A. staminate flowering branch; B. node to show intrapetiolar stipules; C. staminate flower; D. inflorescence in bud with imbricated scales; E. pistillate flower; F. one carpel, abaxial view; G. fruiting branch; H. one mature mericarp, adaxial view. Scale bar equivalents: A, 4 cm; B, 4 mm; C, 2.7 mm; D, 4 mm; E, 2.7 mm; F, 2 mm; G, 4 cm; H, 8 mm. Based on: A–C, *McVaugh 25933*, MICH; D, *Anderson & Anderson 6162*, MICH; E, F, *McVaugh 25862*, MICH; G, H, *Anderson & Anderson 6157*, MICH.

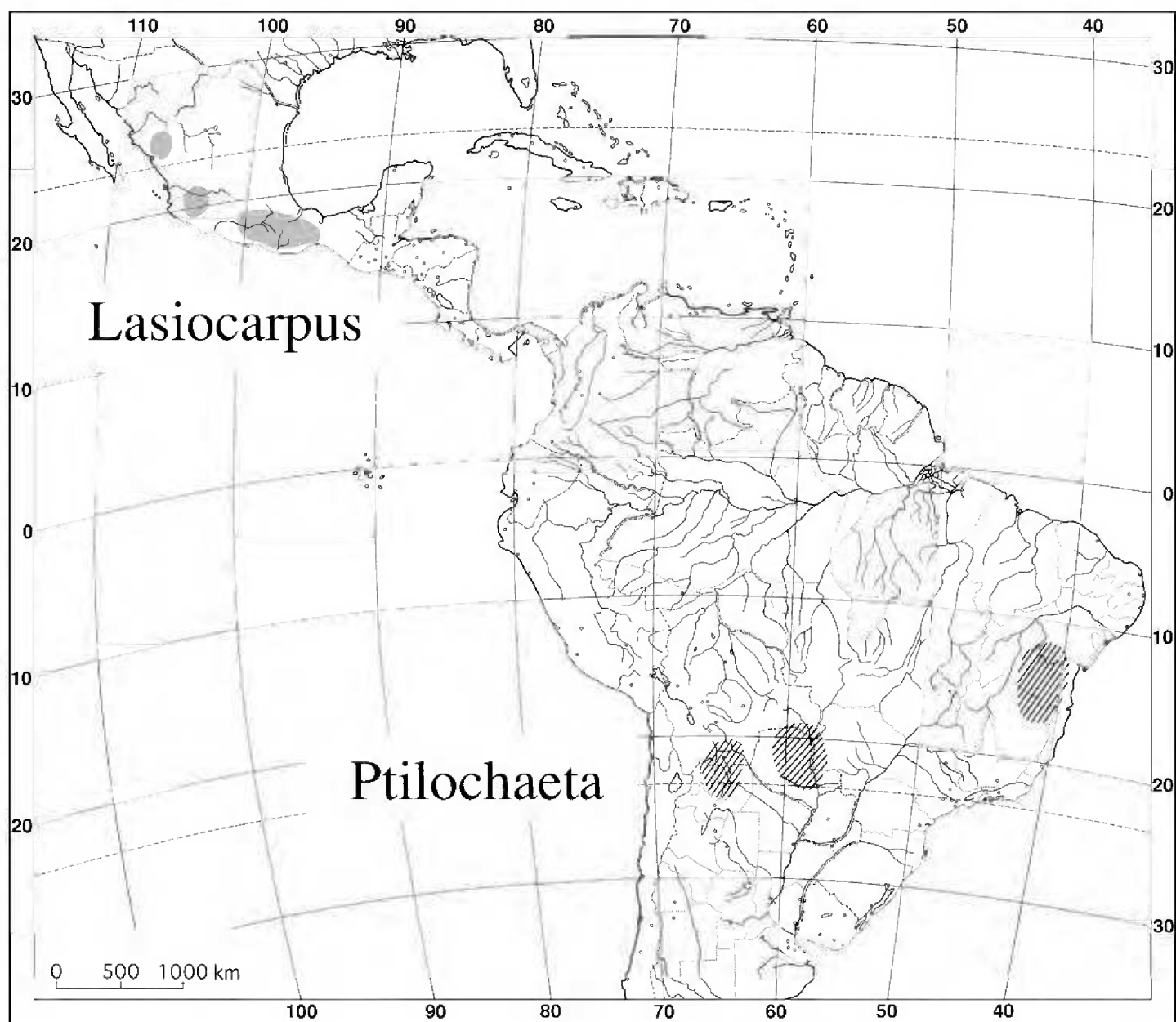


Fig. 20. Distribution of *Lasiocarpus* and *Ptilochaeta*.

***Malpighia* (Fig. 21):** 50 or more species, shrubs and small trees, all but one bird-dispersed by fleshy drupe-like fruits; about half the species grow in Mexico and Central America and the other half in the West Indies, with almost no species occurring in both areas, the one notable exception being the widespread *M. glabra* L. In Mexico the species grow mostly in seasonally dry habitats like tropical deciduous woodland, but some grow also in mesic or even wet forests. The species of Mexico and Central America that have been sequenced form a single clade (Davis & Anderson, 2010). Of approximately 19 species in Mexico, 12 are endemic and seven occur also in Central America; there are four Central American species that do not occur in Mexico. Four Mexican/Central American species extend into northwestern South America. Where *Malpighia* originated is not

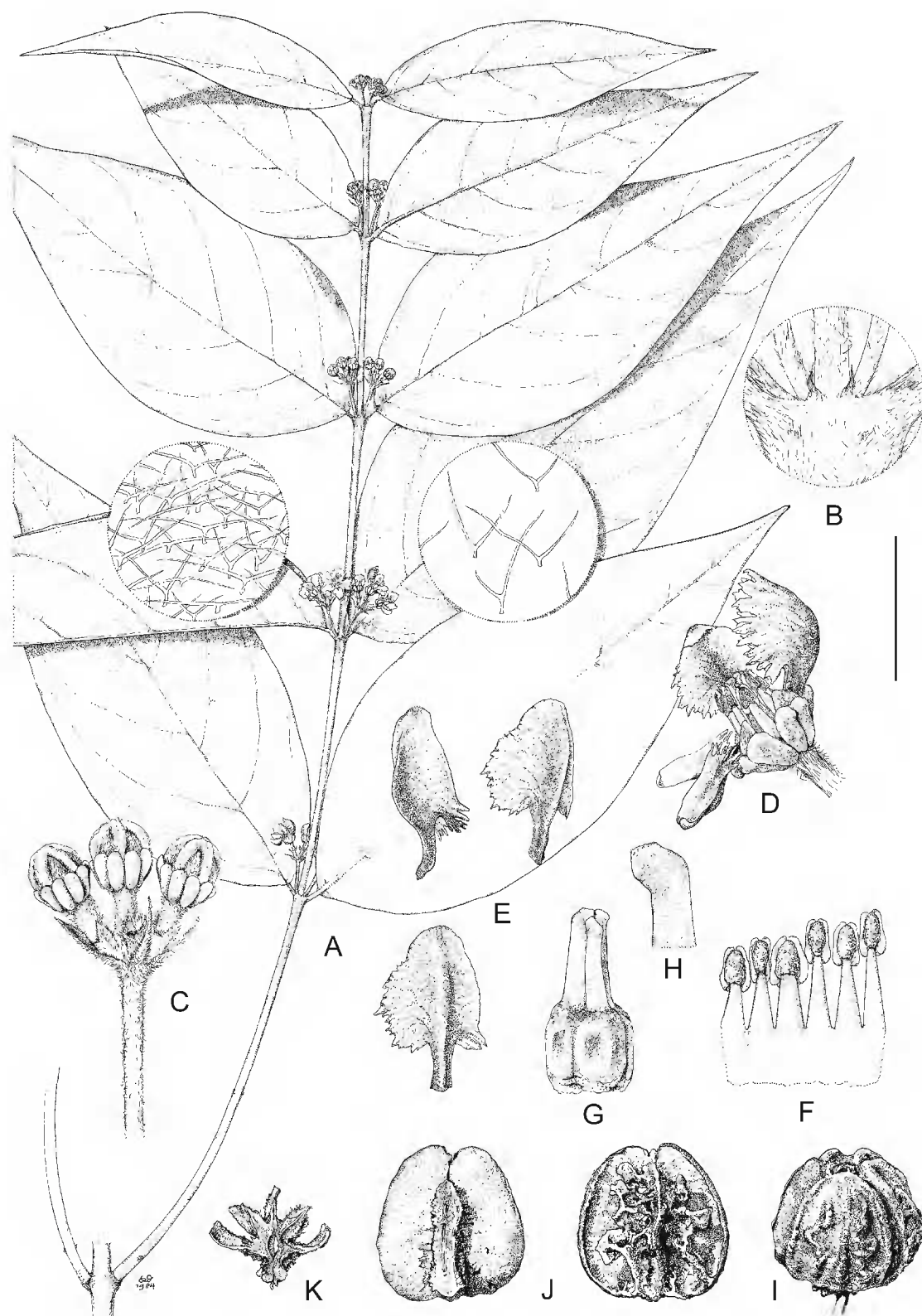


Fig. 21. *Malpighia rzedowskii* W. R. Anderson. A. flowering branch, with enlarged hairs from abaxial surface of lamina (left circle) and adaxial surface (right circle); B. node with interpetiolar stipules; C. umbel of flower buds, one of four removed; D. flower, lateral view, posterior petal erect, one posterior-lateral petal removed; E. petals, above left an anterior-lateral petal, the other two posterior-lateral petals; F. partial androecium laid out, abaxial view, the stamen at left opposite posterior petal; G. gynoecium, anterior style in middle; H. apex of style; I. fruit, dried but intact; J. one pyrene of fruit with flesh removed, adaxial view (left) and abaxial view (right); K. cross-section of one pyrene of fruit with flesh removed. Scale bar equivalents: A, 4 cm (0.8 mm); B, 4 mm; C, 8 mm; D, 6.7 mm; E, 5 mm; F, G, 3.3 mm; H, 2 mm; I–K, 1.3 cm. Based on: A–H, *Rzedowski & McVaugh 1409*, MICH; I–K, *McVaugh 16037*, MICH.



established by the 2010 phylogeny, but one possibility is that it evolved in dry vegetation of central Mexico, home to the Mexican endemic *Calcicola*, which is sister to *Malpighia* and to a large group of Old World genera (Davis & Anderson, 2010); see the discussion above under *Calcicola*. It is also of interest that *M. albiflora* (Cuatrec.) Cuatrec., a species of southern Central America and adjacent Colombia, is sister to the rest of the Mesoamerican species (Davis & Anderson, 2010), because its fruit, while fleshy as in most species, breaks apart into separate mericarps at maturity, as in *Calcicola* and *Mascagnia*. Finally, the perplexing species *Malpighia leticiana* (W. R. Anderson) W. R. Anderson & C. Davis, known only from its type, deserves special comment. Its immature fruit bears coriaceous, probably succulent lateral wings, which originally led to its being described in *Mascagnia*. The latest phylogeny (Davis & Anderson, 2010) shows it to be embedded among the Mexican species of *Malpighia*, for which reason it was reassigned to *Malpighia*. Its fruit presumably represents some kind of reversal to an ancestral condition; further comment is not possible until it is better known. See the discussion of this species and of the problem of distinguishing *Malpighia* from *Mascagnia* in Anderson & Davis, 2005.

***Mascagnia*:** approximately 40 species of woody vines wind-dispersed by winged samaras, found in South America, Central America, and Mexico, with that range soon to be enlarged to include the West Indies when the five species currently assigned to *Triopterys* are absorbed into *Mascagnia* (Anderson & Davis, 2013 [in press]). *Mascagnia* as a whole (including *Triopterys*) is strongly supported in our latest tree (Davis & Anderson, 2010), but major branches within the genus are unsupported. Nevertheless, it seems likely that the genus originated in South America, where its closest sister *Amorimia* is endemic. *Mascagnia* in South America includes many species with the petals pink, lavender, or white and a smaller number of species with yellow petals; both colors are present in Mexico. The five Mexican species represent three or possibly only two lineages.

***M. lilacina* (S. Watson) Nied. and *M. polybotrya* (A. Juss.) Nied. (Fig. 22):** endemic to Mexico, both with petals blue or lavender; they grow in seasonally dry habitats, *M. lilacina* limited to northern Mexico (Coahuila, Durango, Nuevo León, Tamaulipas, and San Luis Potosí) and *M. polybotrya* to western and southern Mexico (from Michoacán to Oaxaca). The phylogeny in Davis & Anderson, 2010, shows these to be sister taxa, presumably derived from a common Mexican ancestor, but the lack of resolution at higher nodes in that tree makes it impossible

to say more about the source of that ancestor at this time (but see note below under *M. vacciniifolia* and *M. almedae*). The ecology and distribution of *M. lilacina* suggest that a similar plant may have been ancestral to *Calcicola* (see discussion above).

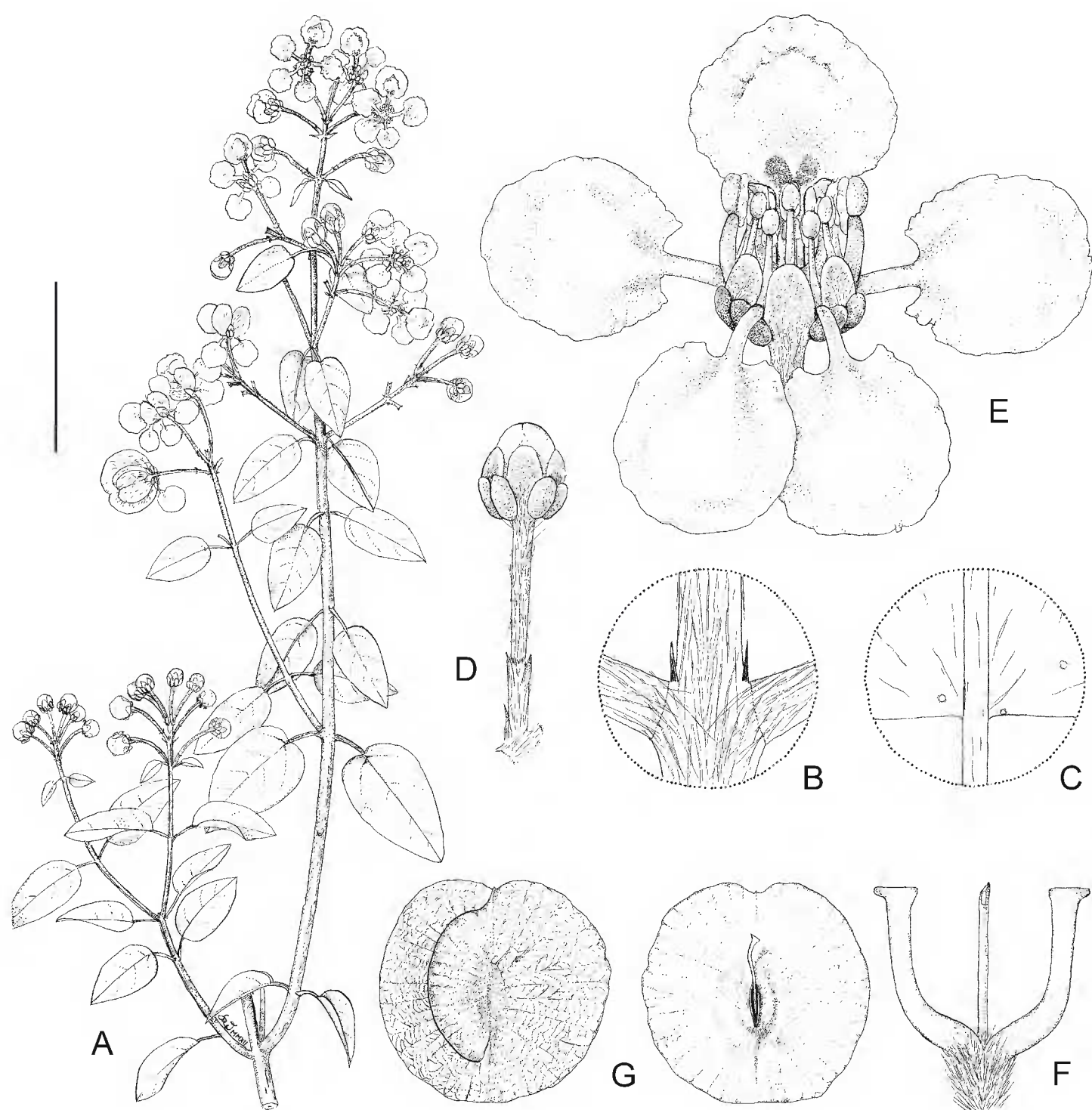


Fig. 22. *Mascagnia lilacina*. A. flowering branch; B. node showing interpetiolar stipules; C. abaxial base of lamina to show glands; D. flower bud; E. flower, posterior petal uppermost; F. gynoecium, anterior style in center; G. samaras, abaxial view (left), adaxial view (right). Scale bar equivalents: A, 4 cm; B, 2 mm; C, 5.7 mm; D, 8 mm; E, 5.7 mm; F, 4 mm; G, 2 cm. Based on: A–F, *Johnston 8514*, GH; G, *Johnston 9001*, GH.

***M. tomentosa* C. E. Anderson:** C. Anderson (2001) described this yellow-flowered species to accommodate plants distributed from Nicaragua to Chiapas, Oaxaca, and Veracruz. Its sister species (Davis & Anderson, 2010) are South American, and *M. tomentosa* seems most likely to have originated in Central America from an immigrant from South America and spread northward to southeastern Mexico.

***M. vacciniifolia* Nied. and *M. almedae* W. R. Anderson:** petals lavender or pink; mostly found in mesic forests. *M. vacciniifolia* occurs from Costa Rica to southeastern Mexico (Chiapas, Oaxaca, and Veracruz), while *M. almedae* is known only from two collections in Chiapas; the latter is morphologically very close to *M. vacciniifolia* and probably a local derivative of the more widespread species. The phylogeny in Davis & Anderson, 2010, places *M. vacciniifolia* without support as sister to the rest of *Mascagnia*, but that placement seems unlikely to be correct, given that these species have triangular samaras without a dorsal winglet and at least *M. vacciniifolia* climbs by means of adventitious roots, which is unique in the family. When the phylogeny within *Mascagnia* is better resolved it is possible that all four of the Mexican species with lavender or pink petals will come together in a single lineage, presumably derived from some unknown immigrant from South America.

***Psychopterys* (Fig. 23):** eight species of southern Mexico and adjacent Belize and Guatemala, woody vines growing in matorral, tropical deciduous forests, and wet forests, wind-dispersed by winged samaras (Anderson & Corso, 2007). This distinctive lineage is embedded in the mostly South American *Hiraea* clade (Davis & Anderson, 2010), but its position in that group is not well resolved and it resembles other genera of the clade only in the butterfly-shaped samaras. The species probably all descended from a single immigrant from South America; nothing like it is known from farther south in Central America.

***Stigmaphyllon*:** 116 species, with a large group (subg. *Stigmaphyllon*) in the New World (mostly in South America) and a much smaller group (subg. *Ryssopterys*) in Asia (C. Anderson, 1997 & 2011). *Stigmaphyllon* reached Mexico six times.

***S. bannisterioides* (L.) C. E. Anderson (Fig. 24):** shrubs or woody vines in beach and mangrove vegetation along the Atlantic coast from Ceará, Brazil, to Veracruz, Mexico; also in the West Indies and coastal West Africa. Unlike most

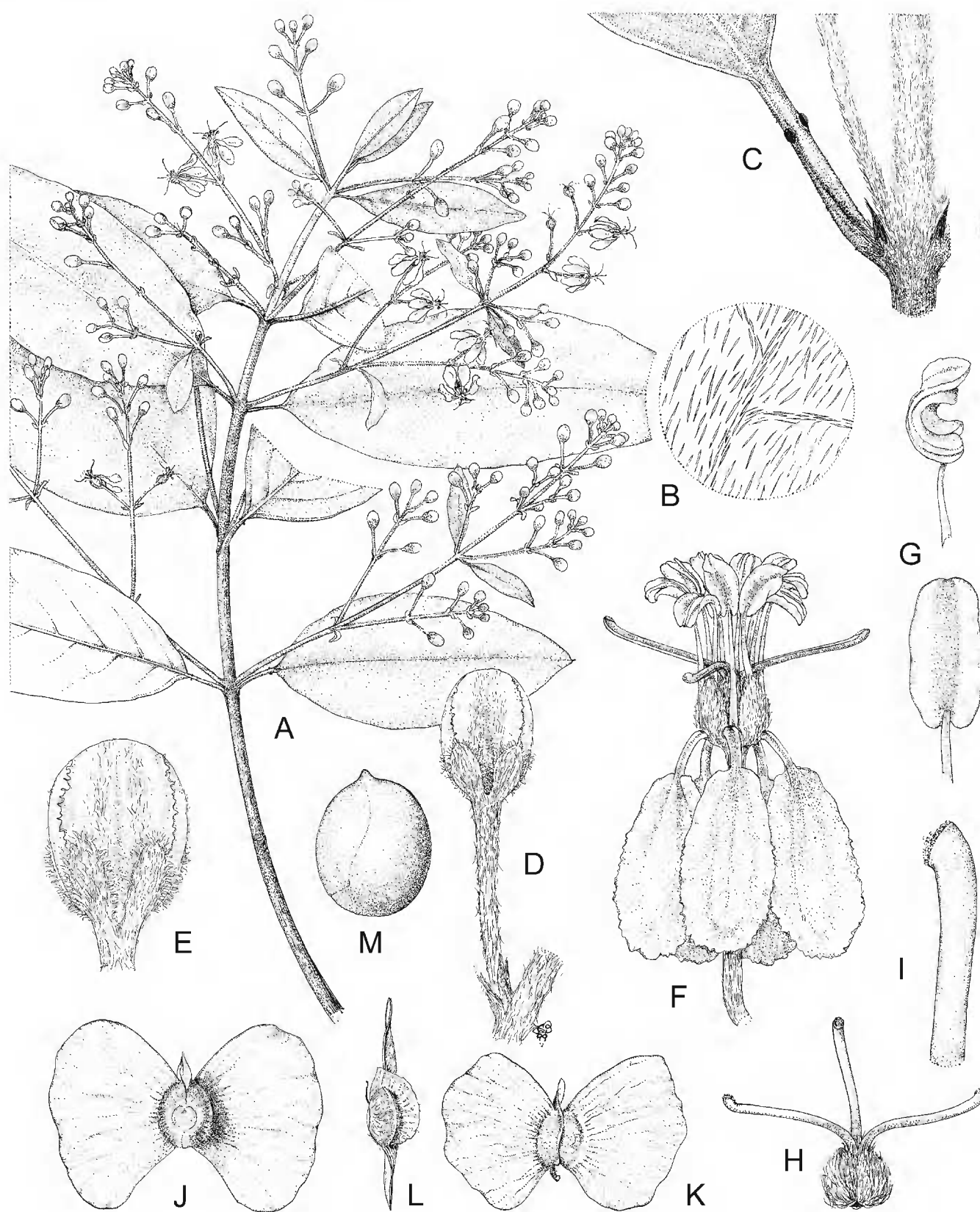


Fig. 23. *Psychopterys dipholiphylla* (Small) W. R. Anderson & S. Corso. A. flowering branch; B. enlargement of abaxial surface of lamina; C. node and base of leaf; D. flower bud with pedicel, bracteoles, bract, and portion of inflorescence axis; E. enlarged flower bud; F. flower; G. abaxial view of young anther (below) and twisted old anther (above); H. gynoecium; I. distal portion of style and stigma; J. samara, adaxial view; K. samara, abaxial view; L. samara with one lateral wing cut away, lateral view to show dorsal wing; M. embryo. Scale bar equivalents: A, 4 cm; B, 2 mm; C, 8 mm; D, 5 mm; E, 3.3 mm; F, 5 mm; G, 2 mm; H, 5 mm; I, 1 mm, J–L, 2 cm; M, 8 mm. Based on: A–I, *Anderson 13819*, MICH; J, K, M, *Hahn s.n.*, P; L, *Hinton 7523*, NY.

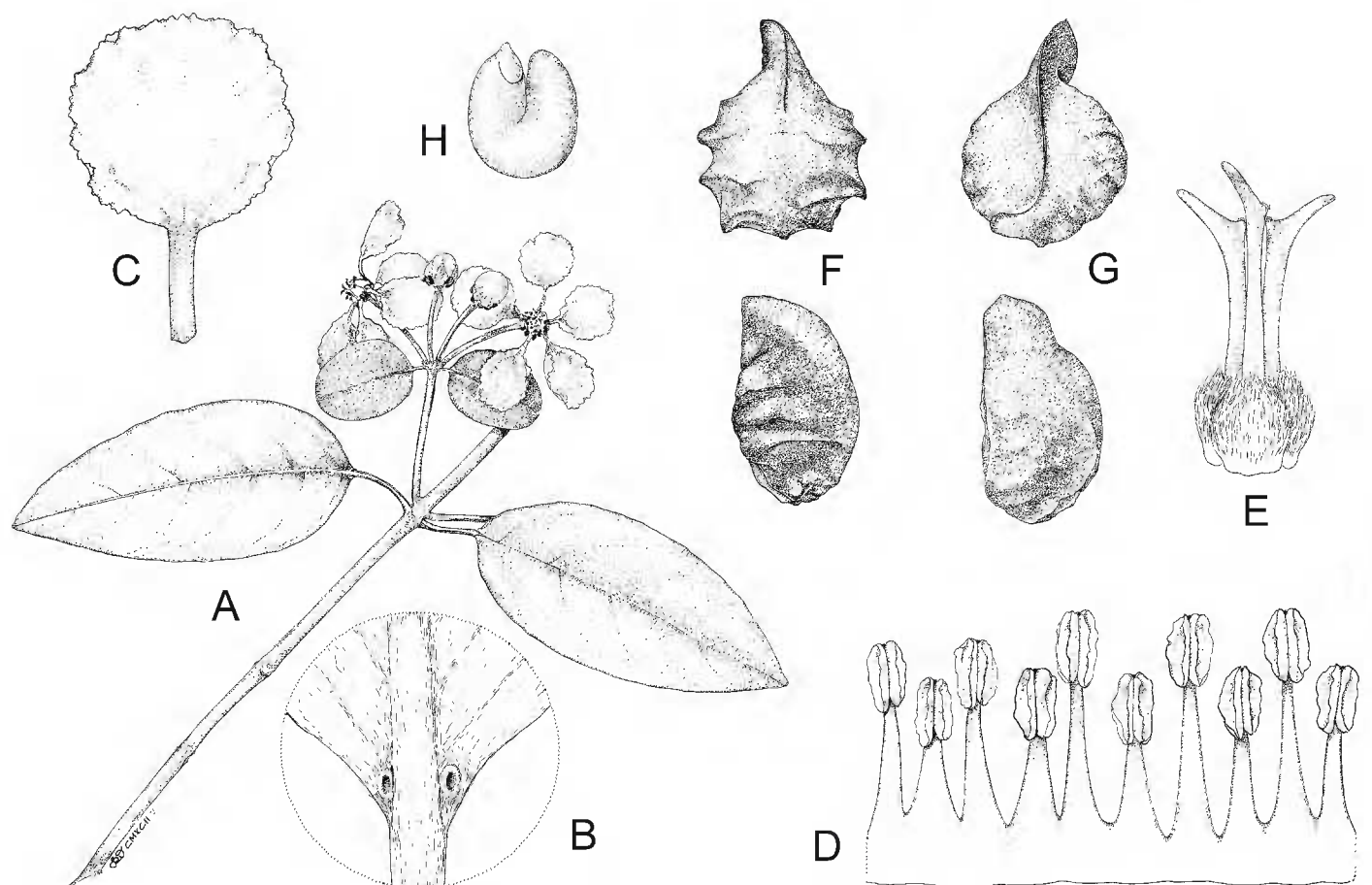


Fig. 24. *Stigmaphyllon bannisterioides*. A. flowering branch; B. base of lamina, abaxial view; C. posterior petal; D. androecium laid out, adaxial view, the stamen second from left opposite posterior petal; E. gynoecium, the anterior style in center; F, G. samaras, abaxial views (above) and lateral views (below), illustrating variation in size and shape of dorsal wing and lateral ornamentation; H. embryo. Scale bar equivalents: A, 4 cm; B, 4 mm; C, 1 cm; D, E, 4 mm; F–H, 1.3 cm. Based on: A, B, *Crosby 42*, MICH; C–E, *Cremers 7812*, MICH; F, H, *Feuillet 898*, MICH; G, *Zanoni et al. 20185*, MICH.

species in the genus, this one is presumably dispersed by water, the wing of the mericarp being reduced to a rudimentary dorsal crest (Fig. 24). Unfortunately this species was not included in the last phylogeny of the family (Davis & Anderson, 2010), but its present distribution and lack of similarity to other species in Mexico makes it most likely to have arrived in Mexico independently of the other Mexican lineages (C. Anderson, pers. comm.).

***S. ellipticum* (Kunth) A. Juss.:** vines wind-dispersed by winged samaras, very common from northwestern South America throughout Central America to southeastern Mexico (the Yucatán Peninsula, Chiapas, Oaxaca, and Veracruz); often in dry disturbed vegetation, but also growing in more mesic forests. The morphology of this species is unlike other Mexican species and suggests an independent arrival in Mexico (C. Anderson, pers. comm.).

***S. lindenianum* A. Juss. and *S. retusum* Griseb.:** both woody vines wind-dispersed by winged samaras. They are morphologically similar and probably sisters (C. Anderson, 1997) and have similar but not identical ranges: *S. lindenianum* occurs from northwestern Colombia throughout Central America to southeastern Mexico (the Yucatán Peninsula, Chiapas, Oaxaca, and Veracruz); *S. retusum* occurs in Central America from Costa Rica northward and penetrates into Mexico as far as Puebla, Querétaro, and San Luis Potosí. Both grow in a wide variety of habitats, from seasonally dry matorral to wet forests. *Stigmaphyllon lindenianum* is embedded in a South American clade (Davis & Anderson, 2010), and *S. retusum* can be expected to be placed in the same clade, so they must represent the result of at least one immigration to Mexico; more likely they reached Mexico independently and should be counted as two Mexican lineages.

***S. pseudopuberum* Nied.:** vines wind-dispersed by winged samaras, endemic to Chiapas and adjacent Guatemala, in montane rain forests and other mesic vegetation; it is morphologically similar to *S. puberum* (Rich.) A. Juss., a species widespread in northern South America, the West Indies, and Central America reaching Guatemala and Belize but not reported from Mexico (C. Anderson, 1997). It seems likely that *S. pseudopuberum* originated in its present area from an immigrant that resembled *S. puberum*.

***S. selerianum* Nied. (Fig. 25):** vines wind-dispersed by winged samaras, endemic to tropical deciduous forests in Oaxaca and Chiapas; morphologically isolated, unlike any species in Central America, presumably derived from an immigrant from South America (C. Anderson, 1997 & pers. comm.).

***Tetrapterys*:** In the broad sense still in use this is a genus of approximately 70 species of woody vines (sometimes shrubby), wind-dispersed by winged samaras, centered in South America but with species in Central America, Mexico, and the West Indies. Unfortunately, *Tetrapterys* is clearly not monophyletic, as shown in the phylogeny in Davis & Anderson, 2010. The Mexican species represent five lineages, which will be discussed here in subgroups:

***Tetrapterys* s. str.:** three species that clearly belong together in the same genus but that arrived independently in Mexico:

***T. discolor* (G. Mey.) DC.:** a variable but distinctive species or species complex, widespread in South America, that presumably migrated north

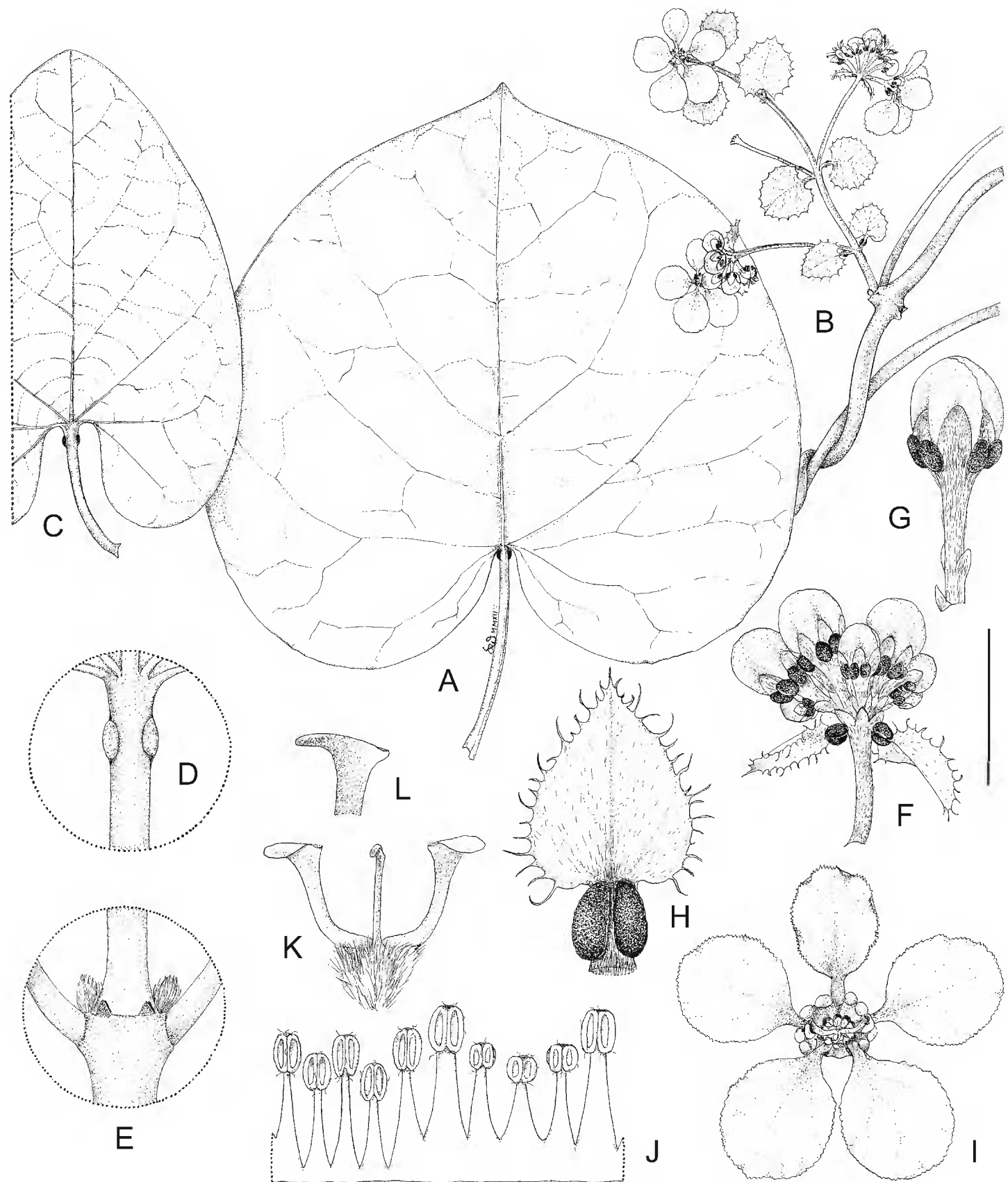


Fig. 25. *Stigmaphyllon selerianum*. A. large leaf; B. flowering branch; C. leaf; D. petiole with glands; E. node with stipules; F. inflorescence; G. flower bud; H. bract from below inflorescence, abaxial view; I. flower, posterior petal uppermost; J. androecium laid out, adaxial view, third stamen from right opposite posterior petal; K. gynoecium, anterior style in center; L. apex of anterior style, lateral view. Scale bar equivalents: A–C, 4 cm; D, E, 8 mm; F, 1.3 cm; G, 1 cm; H, 4 mm; I, 1.3 cm; J, K, 4 mm; L, 2 mm. Based on: A, I–L, *Anderson & Anderson 5555*, MICH; B–H, *Reyes García 333*, MICH.

into Central America, where it occurs mostly in wet forests in most countries, and thence into southeastern Mexico (Tabasco, Chiapas, Oaxaca, and Veracruz).

***T. schiedeana* Schltdl. & Cham. (Fig. 26):** throughout Central America from Costa Rica (with one collection from adjacent Panama) northward, very common in Mexico south of Sinaloa and Tamaulipas; mostly in wet or mesic forests but also in tropical deciduous forests. The relationships of this species within *Tetrapterys* s. str. are not obvious, and the representation of the genus in our 2010 phylogeny is too poor to help with that problem, so for now we will have to be content with saying that its ancestor probably came from South America, but whether the species originated in Mexico and migrated south or originated in Central America and migrated north into Mexico is unknown.

***T. tinifolia* Triana & Planch.:** widespread in northern South America and throughout Central America into southeastern Mexico (Chiapas, Oaxaca, and Veracruz), in wet forests; sister to *T. goudotiana* Triana & Planch. of Central America and Colombia and many similar species of South America.

***Tetrapterys* s. l. 1 (Fig. 27):** six species that occur in Mexico and/or northern Central America: *T. argentea* Bertol.: mesic forests of southeastern Mexico (Chiapas), Guatemala, and El Salvador; *T. cotoneaster* A. Juss.: endemic to tropical deciduous forests of southern Mexico (Guerrero, Morelos, Oaxaca); *T. heterophylla* (Griseb.) W. R. Anderson: tropical deciduous forests of southern Mexico (Guerrero, Oaxaca, Chiapas), Guatemala, and El Salvador; *T. mexicana* Hook. & Arn.: endemic to pine-oak forests and tropical deciduous forests of northwestern and southern Mexico from Sinaloa to Oaxaca; and *T. sp. nov. ined.*, endemic to oak woodlands in east-central Mexico (Hidalgo, Querétaro, San Luis Potosí, and Veracruz). Those five species, plus a sixth undescribed species that is endemic to Honduras, form a clade that resembles *Tetrapterys* s. str. in some characters but differs in others (especially the strictly marginal leaf glands). Unfortunately, none of these species was included among those sequenced for our recent phylogeny (Davis & Anderson, 2010), so the phylogenetic placement of this clade remains to be determined, but for the purpose of this paper it is enough to say that this clade is surely a single lineage in Mexico. Nothing like these plants occurs farther south in Central America or in northern South America; the closest possible



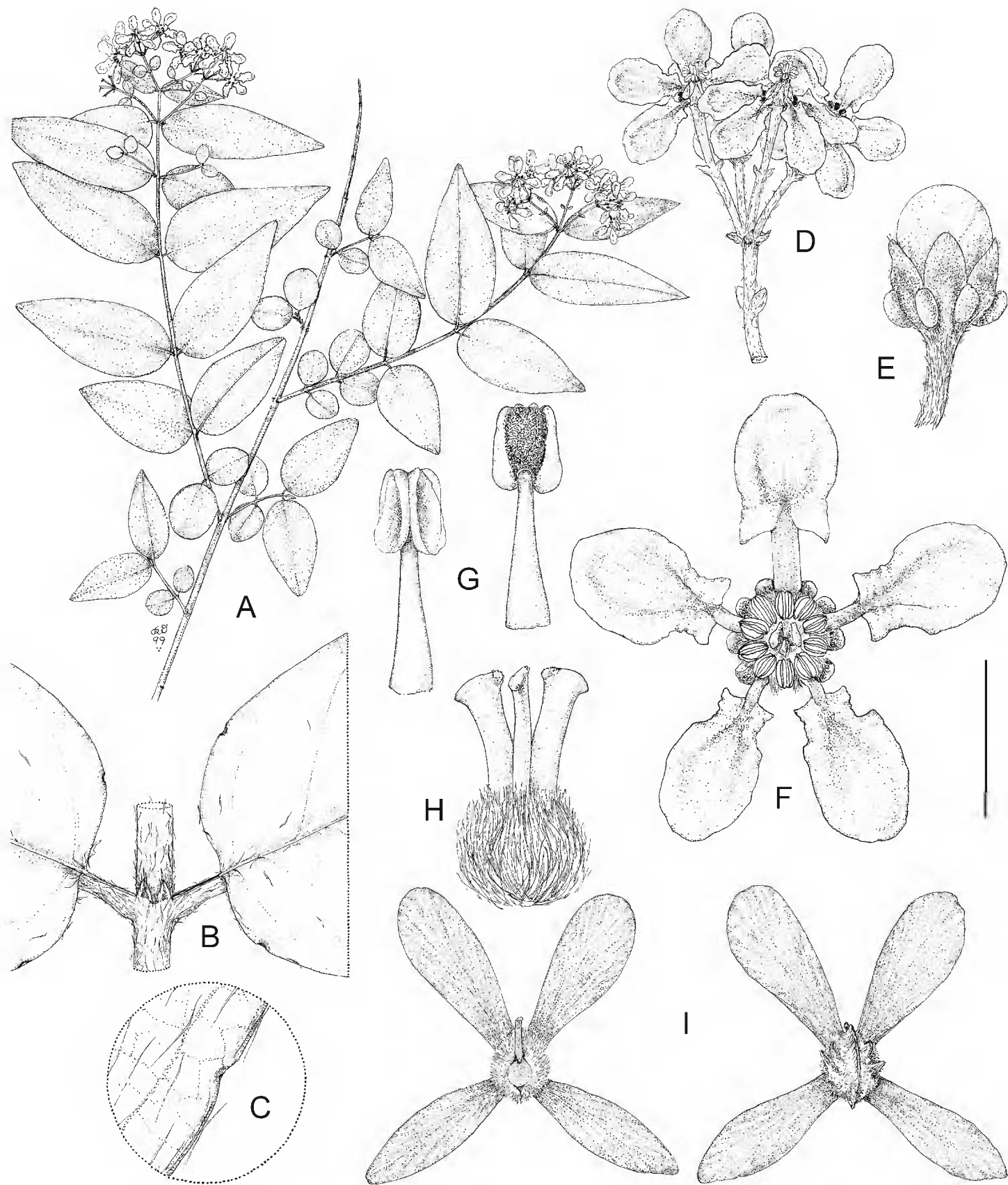


Fig. 26. *Tetrapteryx schiedeana*. A. flowering branch; B. node with stipules and adaxial view of leaf bases; C. marginal leaf gland, abaxial view; D. umbel; E. flower bud; F. flower, posterior petal uppermost; G. stamens, adaxial view (left) and abaxial view (right); H. gynoecium, anterior style in center; I. samaras, adaxial view (left) and abaxial view (right). Scale bar equivalents: A, 4 cm; B, 4 mm; C, 2 mm; D, 1 cm; E, F, 4 mm; G, H, 2 mm; I, 1.3 cm. Based on: A–H, *McVaugh 19046*, MICH; I, *McVaugh & Koelz 1305*, MICH.

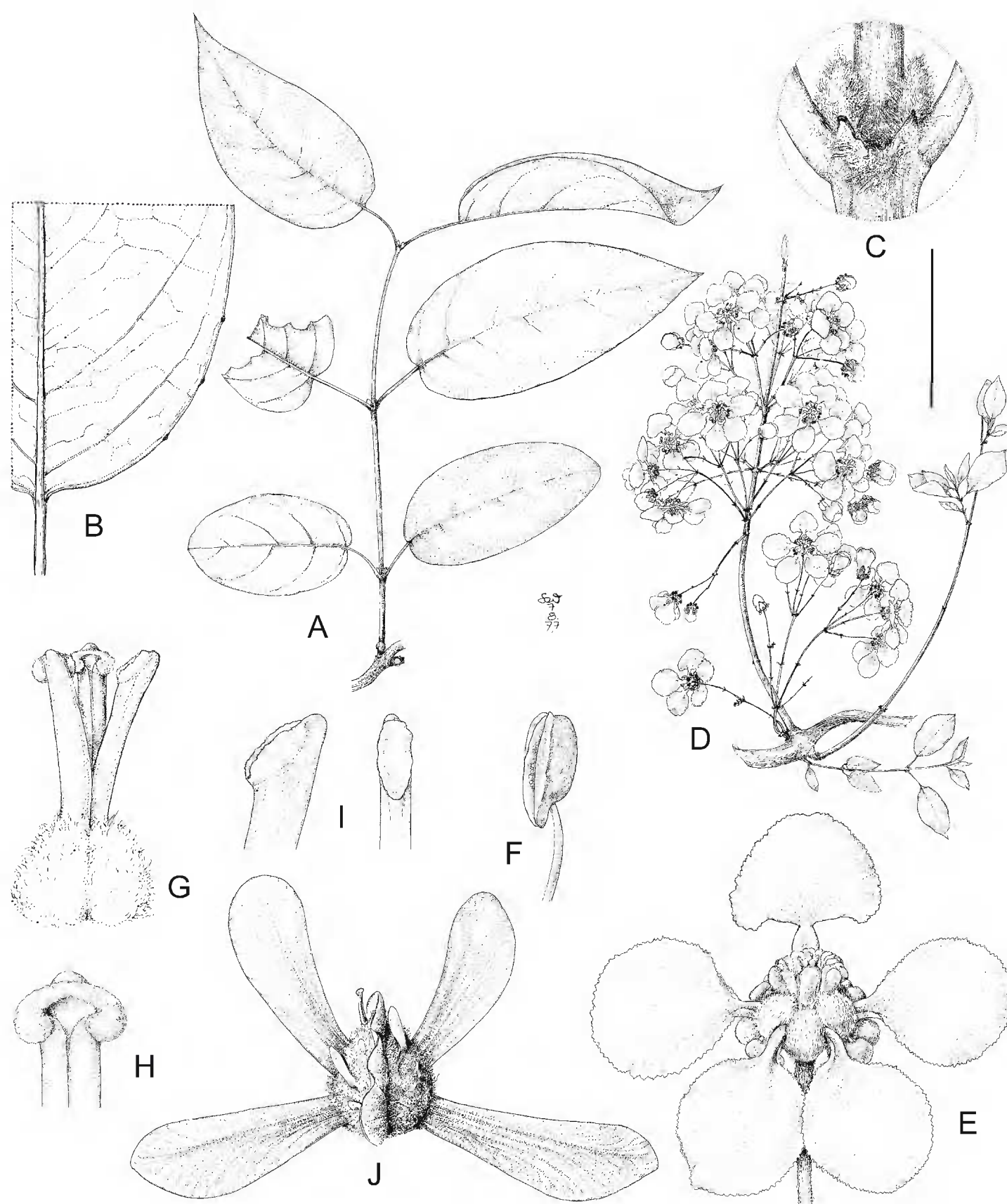


Fig. 27. *Tetrapteryx mexicana*. A. leafy branch; B. base of leaf, abaxial view, to show marginal glands; C. node to show interpetiolar stipules; D. flowering branch; E. flower, posterior petal uppermost; F. anther, lateral view; G. gynoecium, anterior style to right; H. distal portion of posterior-lateral style, adaxial view; I. distal portion of anterior style, lateral view (left) and adaxial view (right); J. samara, abaxial view. Scale bar equivalents: A, 4 cm; B, 1.3 cm; C, 4 mm; D, 4 cm; E, 8 mm; F, 2 mm; G, 2.7 mm; H, I, 1.3 mm; J, 8 mm. Based on: A–C, J, *McVaugh 11931*, MICH; D–I, *Anderson & Anderson 6137*, MICH.

relatives are probably *T. buxifolia* Cav. on Hispaniola and *T. bracteolata* Griseb. in southeastern Brazil. Whatever the ancestor of this clade may have been, it must have reached northern Central America or Mexico from some considerable distance.

***Tetrapteryx* s. l. 2 (Fig. 28):** two sister species (*T. arcana* C. V. Morton and *T. seleriana* Nied.) in diverse habitats (dry scrub to forest) from Nicaragua to the Yucatán Peninsula, Oaxaca, and Veracruz. Those species belong to a clade that is very strongly supported in our phylogeny (Davis & Anderson, 2010), where they are represented by *T. arcana*; it is morphologically quite distinct from *Tetrapteryx* s. str. and all the other species are South American, so it seems clear that the Mexican plants represent a single lineage derived from South American plants that moved north into Central America; such species were presumably similar to *T. styloptera* A. Juss., which is widespread in northern South America and reaches in Central America to Nicaragua.

**Summary of Mexican lineages of Malpighiaceae:** *Adelphia*, 1; *Aspicarpa/Gaudi-chaudia*, 1; *Banisteriopsis*, 2; *Bronwenia*, 2; *Bunchosia*, 1, possibly more; *Byrsonima*, 2; *Calcicola*, 1; *Callaeum*, 1, possibly 2; *Carolus*, 1; *Christianella*, 1; *Cottsia*, 1; *Diplopteryx*, 1; *Echinopteryx*, 1; *Galphimia*, 1, possibly 2; *Heteropteryx*, 4; *Hiraea*, 4, possibly 3; *Lasiocarpus*, 1; *Malpighia*, 1; *Mascagnia*, 3, possibly 2; *Psychopteryx*, 1; *Stigmaphyllon*, 6; *Tetrapteryx*, 5. TOTAL: 42, possibly several more or fewer.

#### ADAPTATIONS FOR DISPERSAL IN MEXICAN LINEAGES OF MALPIGHIACEAE

Almost all the Malpighiaceae that reached Mexico had some kind of effective adaptation for dispersal. The majority of the species in Mexico now have wind-dispersed mericarps (winged or bristly), or probably evolved from wing-fruited ancestors by loss of the wing in Mexico (*Aspicarpa* spp.). Three genera have fleshy, bird-dispersed fruits, with *Bunchosia* and *Byrsonima* undoubtedly dispersed from South and Central America by means of such fruits; *Malpighia*, which seems to be of Mexican origin, may be derived from an ancestor with a mascagnoid samara (see the discussion above).

Two Mexican species grow near water and have mericarps with reduced wings that are surely dispersed by water. One, *Heteropteryx lindeniana*, seems

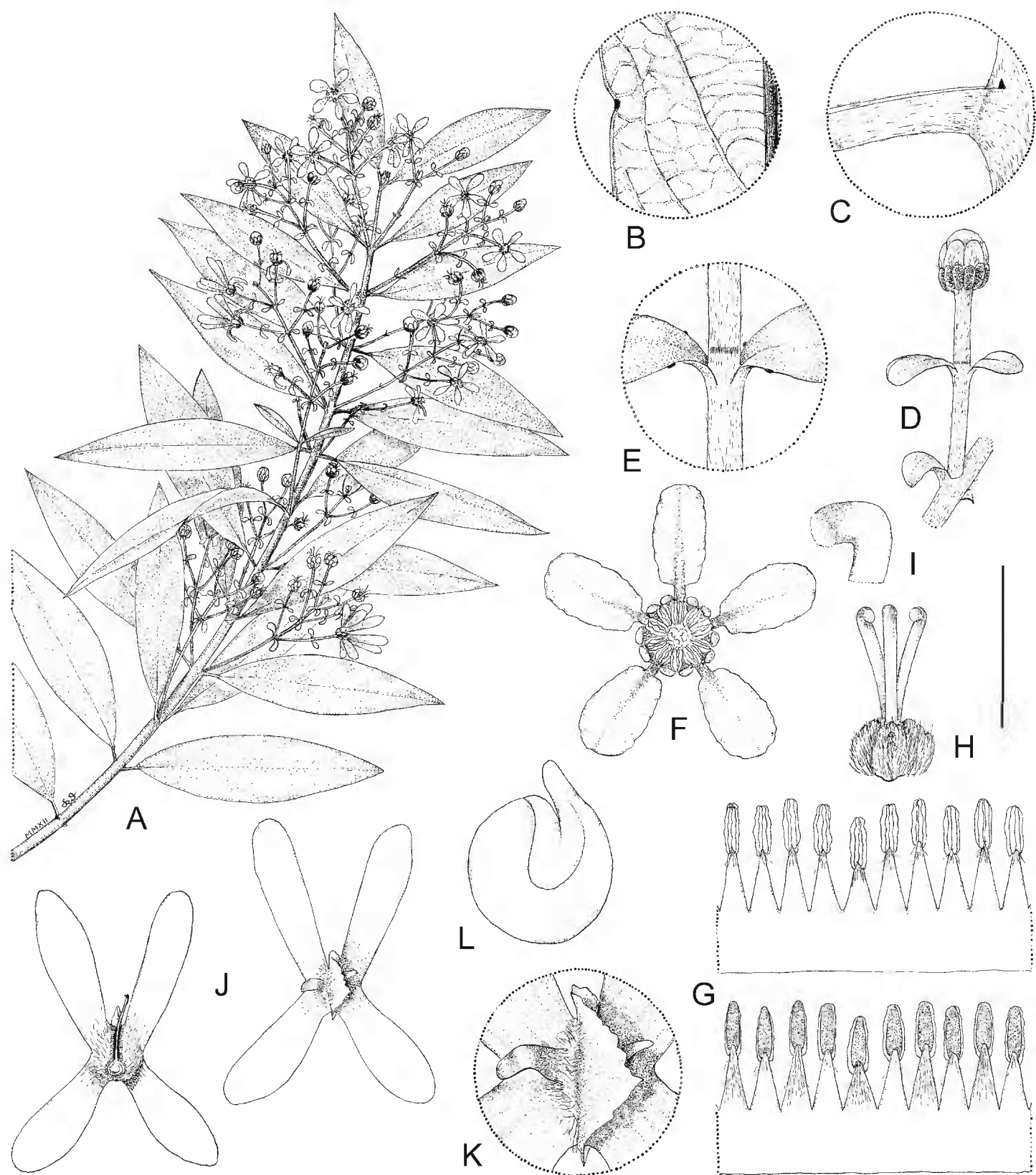


Fig. 28. *Tetrapteryx seleriana*. A. flowering branch; B. marginal leaf gland, abaxial view; C. minute stipule beside base of petiole; D. flower bud on pedicel subtended by peduncle with subapical bracteoles, the peduncle in turn subtended by a bract; E. bracteoles with marginal glands near base; F. flower, posterior petal uppermost; G. androecium laid out, adaxial view above, abaxial view below, the stamen fifth from left opposite posterior petal; H. gynoecium, anterior style in center; I. distal portion of style; J. samaras, adaxial view (left) and abaxial view (right); K. enlargement of dorsal wings on samara; L. embryo. Scale bar equivalents: A, 4 cm; B, C, 4 mm; D, 8 mm; E, 4 mm; F, 6.7 mm; G, H, 2.7 mm; I, 0.8 mm; J, 1 cm; K, 4 mm; L, 2.2 mm. Based on: A–I, *Cabrera C. 5549*, MICH; J–L, *Matuda 3099*, MICH.

likely to have evolved from *H. laurifolia* in the Yucatán Peninsula or adjacent Central America, while the other, *Stigmaphyllon bannisterioides*, is widespread in the Caribbean region and probably followed the Atlantic coast from Brazil to Mexico.

One Mexican species, *Diplopterys mexicana*, is unknown in fruit. Its fruit seems most likely to be a winged samara, but it could also be adapted for dispersal by water like several related species in South America.

That brings us to *Galphimia*, possibly the most intriguing clade of Malpighiaceae in Mexico. The cocci of this genus (like those of its sister, *Verrucularia*) have no obvious adaptation for dispersal (Fig. 15), unless the persistent dried petals of some Mexican species aid in local dispersal (see discussion above). No South American species of *Galphimia* now occurs north of the Amazon or west of Bolivia, although one of the two species of *Verrucularia* does occur in Amazonas, Brazil, just south of Venezuela (W. Anderson, 1981). Moreover, the only species of *Galphimia* in Central America (*G. speciosa*) is not basal in the genus and is probably the result of extension of the range of a Mexican species southward. The genus *Galphimia* is clearly monophyletic (Davis & Anderson, 2010), and the strongly supported clade of *Galphimia+Verrucularia* is well-supported as sister to the *Lophanthera+Spachea* clade, a group of South America, Panama, and Costa Rica (Davis & Anderson, 2010). I see no way to escape the conclusion that the cocci of the ancestor of *Galphimia* traveled by long-distance dispersal from South America to Mexico, in spite of their unadorned exocarp, and there is no modern evidence that that dispersal was accomplished via a series of intermediate populations in northwestern South America or Central America.

#### POSSIBLE SOURCES OF MALPIGHIACEAE NOW IN MEXICO

The evidence available indicates that the Malpighiaceae originated and underwent their early diversification in South America, probably at a time when dissemination from South America to other continents was difficult (W. Anderson, 1990; Cameron et al., 2001; Davis et al., 2001; Davis & Anderson, 2010), so it is not really surprising to find that the *ultimate* source for all the Mexican lineages described above was South America. That statement, however, is an oversimplification that could lead to misinterpretation. The reality seems to be that the approximately 42 lineages of Malpighiaceae now found in Mexico can be arranged on a gradient from ones that represent nothing more than an extension of the range of a South

American species north into Mexico (e.g., *Heteropterys macrostachya*) to ones with roots presumably in South America but without any close relative in South America at this time (e.g., *Echinopterys*). The paragraphs below put the Mexican lineages into four groups that represent the two extremes of that gradient and two intermediate stations on the gradient.

1. Seventeen of the Mexican lineages of Malpighiaceae represent a straightforward range extension of a South American species or group of species that is embedded in a South American clade, leaving no basis for doubt that the Mexican plants originated in South America. 11 of these lineages have penetrated no farther than southeastern Mexico (defined here as all of Mexico from Veracruz and Oaxaca eastward) while the other six are more widespread in Mexico.

*Adelphia hiraesa*: South America to Tabasco and Chiapas

*Banisteriopsis elegans*: South America to Chiapas

*Banisteriopsis muricata*: South America to Chiapas and Oaxaca

*Bronwenia acapulcensis*: South America to Oaxaca and Guerrero

*Bronwenia cornifolia*: South America to southeastern Mexico

*Byrsonima crassifolia*: South America to southern Mexico

*Carolus sinemariensis*: South America to southern Mexico

*Heteropterys brachiata* group: South America to central and southern Mexico

*Heteropterys laurifolia* group: South America to southern Mexico

*Heteropterys macrostachya*: South America to Chiapas

*Hiraea reclinata*: South America to southern Mexico

*Hiraea fagifolia*: South America to southeastern Mexico

*Hiraea smilacina*: South America to southeastern Mexico

*Stigmaphyllon bannisterioides*: South America to Veracruz

*Stigmaphyllon ellipticum*: South America to southeastern Mexico

*Tetrapteryx discolor*: South America to southeastern Mexico

*Tetrapteryx tinifolia*: South America to southeastern Mexico

2. The following nine species or species groups are Central American and Mexican lineages that do not or barely occur in South America but have unmistakable roots in South American clades of the same genus. Seven of these lineages have reached only southeastern Mexico, while the other two are more widespread in southern Mexico:

*Christianella mesoamericana*: Central America to Chiapas

*Heteropteryx panamensis*: Central America to Chiapas

*Hiraea barclayana*: Central America to northwestern Mexico  
*Mascagnia tomentosa*: Central America to southeastern Mexico  
*Mascagnia vacciniifolia* group: Central America to southeastern Mexico  
*Stigmaphyllon lindenianum*: Central America and adjacent Colombia to southeastern Mexico  
*Stigmaphyllon pseudopuberum*: Guatemala and Chiapas  
*Stigmaphyllon retusum*: Central America to southern Mexico  
*Tetrapterys seleriana* group: Central America to southeastern Mexico

3. The following nine lineages are Mexican, some also in Central America; they have congeners but no obvious close relatives in South America:

*Bunchosia* spp. group: Central America to Mexico, with one species also in the West Indies  
*Byrsonima bucidifolia*: northern Central America and the Yucatán Peninsula of Mexico  
*Callaeum* spp. group: Central America to Mexico  
*Diplopterys mexicana*: Veracruz, Mexico  
*Galphimia* spp. group: Mexico with one species also in Central America  
*Mascagnia lilacina* group: southern to northeastern Mexico  
*Stigmaphyllon selerianum*: southeastern Mexico  
*Tetrapterys mexicana* group: northern Central America and Mexico  
*Tetrapterys schiedeana*: Central America to southern Mexico

4. The following seven lineages seem likely to have evolved in Mexico, although some of them have extended their ranges southward and one (*Malpighia*) is widespread in the West Indies. The claim that their ultimate origin must have been in South America is based on their phylogenetic relationships (Davis & Anderson, 2010), not on their present distribution. For each lineage see the discussion above.

*Aspicarpa/Gaudichaudia*: Mexico and adjacent United States and Central America, with one derived species in northwestern South America  
*Calccicola*: central Mexico  
*Cottsia*: northern Mexico and adjacent United States  
*Echinopterys*: Mexico  
*Lasiocarpus*: southern Mexico  
*Malpighia*: Mexico, Central America, northwestern South America, and the West Indies  
*Psychopterys*: southern Mexico and adjacent Belize and Guatemala

## THE FOSSIL GENUS *EOGLANDULOSA*

Reliably identifiable macrofossils of Malpighiaceae are few, but one fossil of what certainly appears to be a flower of Malpighiaceae dates from the Eocene and was described as *Eoglandulosa warmanensis* Taylor & Crepet (Taylor & Crepet, 1987). The fossil was found in Tennessee, USA, far north and east of Mexico; the family now extends barely north of Mexico, with two species in Arizona and New Mexico and six species in Texas; one Caribbean species is native to southernmost Florida. Two aspects of *Eoglandulosa* are informative about its most likely relationships: 1) All five sepals bear paired abaxial glands, whereas most of the more derived genera of the family have paired glands on the four lateral sepals and the anterior sepal is eglandular (or all the sepal glands are much reduced or absent). 2) The pollen is radially symmetrical and tricolporate, as in the genera near the base of our phylogeny (Davis & Anderson, 2010; Anderson et al., 2012); more derived genera have globally symmetrical pollen with very diverse numbers and distributions of colpi and apertures. Of the genera of Malpighiaceae now in Mexico, only *Byrsonima* has that combination of calyx glands and pollen type. Of the two species of *Byrsonima* currently in Mexico, *B. bucidifolia* is the one whose morphology suggests a possible ancestry in the Caribbean, with one possible sister being *B. lucida*, which is native in southernmost Florida today (see discussion of *Byrsonima* above). Lacking information on the age of *Byrsonima*, we cannot say with any confidence that *Eoglandulosa* was a *Byrsonima* or something related to *Byrsonima*, but it is tempting to speculate that *Eoglandulosa* may indicate an early invasion of North America by *Byrsonima*, perhaps travelling via the Caribbean. Beyond that, I cannot see that *Eoglandulosa* sheds much light on the origins of the lineages of Malpighiaceae currently in Mexico.

## CONCLUSIONS

The Malpighiaceae in Mexico today represent approximately 42 lineages, all with their *ultimate* roots in South America, so this family, at least, gives strong support to Rzedowski's generalization (1991) about the affinities of the Mexican flora with plants of South America. Some of those lineages probably arrived recently, diverging little in Mexico and, in many cases, not or hardly penetrating beyond the relatively mesic vegetation of southeastern Mexico into the seasonally dry vegetation types that abound to the west and north. Other lineages (e.g., *Aspicarpa/Gaudi-*



*chaudia* and *Galphimia*) probably reached Mexico long ago, if one can judge from their ecological success and phyletic diversification throughout much of Mexico. Indeed, several lineages must have originated in Mexico from unknown ancestors whose South American source can be inferred only from interpretation of a phylogenetic tree. Most of the Malpighiaceae that reached Mexico have (or originally had) effective adaptations for dispersal, the one notable exception to that statement being the genus *Galphimia*; that is as one would expect in a suite of plants that had to migrate short to long distances to reach Mexico. Even so, one of the most interesting conclusions I can draw from the data presented above is that in a number of cases there is no evidence that the ancestors now in Mexico reached that country by means of gradual extension of terrestrial ranges (“stepping-stone” dispersal). The evidence now available indicates that there have been a number of long-distance dispersal events from South America to Mexico; for discussion of the importance of long-distance dispersal in Neotropical plant lineages, see Christenhusz & Chase, 2013.

#### ACKNOWLEDGEMENTS

The beautiful drawings in this paper are all from the talented pen of Karin Douthit. I am indebted to Christiane Anderson and Charles Davis for many years of collaboration and exchange of information and ideas. Socorro González Elizondo very kindly helped by translating my abstract from English into Spanish.

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Recibido en febrero de 2013.

Aceptado en abril de 2013.