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The systematics of *Serjania* section *Platycoccus* (Sapindaceae)

Acevedo-Rodríguez, Pedro, Ph.D.

City University of New York, 1989

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THE SYSTEMATICS OF SERJANIA SECTION PLATYCOCCUS
(SAPINDACEAE)

by

PEDRO ACEVEDO-RODRIGUEZ

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

1989

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

THE SYSTEMATICS OF SERJANIA SECTION PLATYCOCCUS. (SAPINDACEAE)

by

Pedro Acevedo-Rodríguez

Chairman: Scott A. Mori.

Serjania section Platycoccus is characterized by its membranous samaroid fruits with flat cocci. As previosly delimited, section Platycoccus contained 24 species, of which only 12 are recognized in this revision. Five names where reduced to synonomy, nine species were transferred to other sections, and three recently described species were incorporated into Platycoccus.

The infrageneric classification of Serjania as proposed by Radlkofer in 1874 is modified, and only five of his twelve sections are recognized in this work. The creation of a new section (Confertiflora) is proposed in order to accomodate a group of species previously included in section Platycoccus, but distinctive from species of other sections of Serjania.

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Finally I would like to dedicate this work to my parents for their support and encouragement throughout its duration.

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INTRODUCTION

Serjania Miller, is a large genus of more or less woody vines, native to tropical and subtropical areas of the New World. Its essentially climbing habit, the presence of stipules, modified peduncles as tendrils, and nectary disk modified into four protruding glands, places Serjania with five other genera into the tribe Paullinieae Kunth.

A comprehensive revision of the genus was done by Radlkofer in 1875, which he expanded in his treatments of Sapindaceae for Martius' **Flora Brasiliensis** (1892-1900) and Engler's **Das Pflanzenreich** (1931-1934). The latter is the culmination of his work in the Sapindaceae which spanned nearly half of a century. He described 144 species in Serjania, and recognized a total of 201 species. In his monograph of Serjania, he created 12 sections based on fruit morphology. His system is rather difficult to use because there are no quantitative characters defining some of his sections which results in some intergradation. The sectional placement of many species of Serjania is open to question, principally because many of them are only known from one or few collections bearing inadequate fruiting material.

Identification of Serjania species is particularly difficult because many of them are vegetatively very similar, not only to other Serjanias but also to species in other genera of the Paullinieae. The presence of fruits is essential to establish the identity of the genera, especially for those taxonomists not familiar with the group.

Section Platycoccus, as previously delimited, contained 24 species, of which only 12 are recognized in this revision. Five names were reduced to synonymy, nine species were transferred to other sections, and three recently described species were incorporated into section Platycoccus. A new section (Confertiflora) is created here to accommodate a group of species previosly included in Platycoccus, and distinctive from species of other sections of Serjania.

The systematics of Serjania is still in a rather chaotic stage, and a complete revision of the genus is needed. There is also need for more field work, which should increase knowledge of the poorly known species, as well as the biology of this interesting group of lianas.

TAXONOMIC HISTORY

The first published description of Serjania was provided by Plumier in 1703. It consisted of a Latin diagnosis and a dedication to Rev. Father Philippe Sergeant, a physician and French botanist. The genus is considered to be validly published in Miller's Garden Dictionary (1754), because this is the first published description after 1753. Although the name Serjania was originally published with this orthography by Plumier and Miller, some variations of its spelling have been recorded. Burmann (1757), Willdenow (1799), Sprengel (1825), Schott (1825) and Schlechtendal and Chamisso (1830) published various species under the name Seriana. Schumacher (1794) and Humboldt, Bonpland and Kunth (1821) used the name *Seriania*. Another variation is recorded from Martius (1837) as *Serjana*.

Schumacher (1794) published *S. divaricata*, *S. lucida*, *S. lupulina*, *S. racemosa*, *S. sinuata*, and *S. spectabilis* as the first binomials for the genus. *Serjania sinuata*, collected from the island of Hispaniola, was the species illustrated by Plumier, as *Serjania scandens triphylla* & *racemosa* (published by Burmann, 1757). Therefore, this species represents the original concept of the genus, and it has been designated as the type by Croat (1976a).

Linnaeus (1753) and Jussieu (1789) did not recognize *Serjania* as different from the closely related *Paullinia*. In 1799, Willdenow transferred some species of *Paullinia* into *Serjania* [*S. caracasana* (Jacq.) Willd., *S. mexicana* (L.) Willd.], in this way contributing to a better understanding of the then developing generic delimitation of these taxa.

Willdenow (1799) published two more species in the genus, namely *S. angustifolia* and *S. triternata*. Poiret in 1804 published *S. subdentata*. In 1821, Humboldt, Bonpland and Kunth, contributed eight more names, viz. *S. acapulcensis*, *S. emarginata*, *S. glabrata*, *S. mollis*, *S. oxyphylla*, *S. paniculata*, *S. parvifolia*, and *S. pubescens.* In 1824 Saint Hilaire described *S. lethalis*.

De Candolle (1824), provided the first infrageneric classification for *Serjania*. He treated all the species of *Serjania* known at that time, and published three new names, *S. paucidentata*, *S. heterophylla* and *S. ossana* (the latter two considered synonyms by

Radlkofer). The 21 species treated by him were placed into four categories according to foliar characters, viz. ternate, biternate, triternate, or imparipinnate leaves (Table I).

In 1825, Sprengel published S. australis, S. dubia, and S. plumeriana (all which were considered synonyms by Radlkofer), and Schott wrongly described a species of Toulicia (Sapindaceae) as S. stans.

Three years later, Cambessèdes in Saint Hilaire **Flora Brasiliae Meridionalis** (1828), described 11 new species, viz. S. clematidifolia, S. communis, S. cuspidata, S. elegans, S. laruotteana, S. meridionalis, S. multiflora, S. noxia, S. paludosa, S. reticulata, S. velutina, and four other names, which I consider synonyms, viz. S. dombeyana, S. grandiflora, S. hirsuta, and S. lanceolata.

In 1829 Vellozo described a non Sapindaceous plant as S. aquatica. Schlechtendal and Chamisso described two new species for Mexico, one in 1830 (S. cambessedeana) and another in 1831 (S. cardiospermoides).

Martius (1837) published S. guarumina (here cosidered a synonym of S. cuspidata Cambess.) and, in 1839, described S. mansiana. Macfadyen (1837) described S. equestris in his **Flora of Jamaica**.

Serjania membranacea was described from Surinam by Splitgerber in 1842. In 1843, many other species were described: S. deflexa by Gardner; S. dibotrya, S. inflata and S. nutans by Poeppig and Endlicher; and S. marginata by Casaretto. In 1844 eight species

TABLE I

Treatment of *Serjania* by A. P. de Candolle

Foliis ternatis

- *S. sinuata*
- *S. mollis*
- *S. acapulcensis*
- *S. emarginata*

Foliis biternatis

- *S. divaricata*
- *S. caracasana*
- *S. oxyphylla*
- *S. racemosa*
- *S. lucida*
- *S. spectabilis*
- *S. paucidentata*
- *S. glabrata*
- *S. pubescens*
- *S. paniculata*
- *S. mexicana*
- *S. angustifolia*
- *S. ossana*
- *S. lupulina*

Foliis (tri)ternatis

- *S. triternata*

Foliis imparipinnatis

- *S. parviflora*
- *S. heterophylla*

were described, one by Bentham (S. brevipes) and seven by Schlechtendal (S. grossi, S. regnellii, S. salzmanniana, S. schiedeana, S. monogyna, S. moritziana, and S. rubens, the latter two are here considered synonyms).

Bentham (1851) described three new species from Brazil, S. hebecarpa, S. platycarpa, and S. nitidula (the latter considered a synonym of S. caracasana (Jacq.) Willd. by Radlkofer). Two years later Seemann (1853) described S. grandis from Panama.

Turczaninow added two more names to the genus, S. megalocarpa (basionym of Toulicia megalocarpa) in 1858 and S. cornigera in 1859. Grisebach described S. samydea (considered a synonym for S. mexicana (L.) Willd. by Radlkofer) in 1858 and S. crenata in 1861. Torrey (1859) published S. incisa from Mexico, and few years later, Triana and Planchon (1862) added six more names to the genus (S. acuta, S. ampelopsis, S. clematidea, S. seemanni, S. floribunda, and S. mariquitensis, the latter two considered synonyms by Radlkofer).

Grisebach (1866) in his **Catalogus Plantarum Cubensium**, described S. albopunctata (here considered a synonym of S. subdentata Juss.). In 1873 Sauvalle and Wright described S. atrolineata in Sauvalle's **Flora Cubana**. In 1874, Grisebach described two more species, S. foveata and S. fulta (the latter here considered a synonym of S. glabrata Kunth).

Since De Candolle (1824), no other infrageneric treatment for Serjania had been proposed until 1874, when Radlkofer published his **Conspectus Sectionum Specierumque Generis Serjaniae**, which appeared prior to his **Monographie der Sapindaceen-Gattung Serjania**(1875). In this summary, he divided the genus into 12 sections, based mostly on fruit characters. Therein, 145 species of Serjania were treated, including the 86 new species to be published a few months later (1875), and six species were transferred from closely related genera. In 1878, he published S. californica, and S. decemstriata, and in 1883 S. cystocarpa. Watson in 1882 published S. inflata (a preocupied name) a synonym of S. cystocarpa. A few years later (1886), Radlkofer published a supplement to his monograph, in which he described six new species. In a series of papers (1891, 1892-1900, 1893, 1895a-d, 1898, 1899, 1901, 1903a-b, 1905, 1909, 1910, 1913a-b, 1914a-b, 1916, 1921) Radlkofer described an additional 39 species. A total of 133 species were described by him, most of which were placed in the sections he established in 1874, and a few remained in uncertain position. The sectional placement of species of Serjania known by him is presented in Table II.

In 1889, Watson published S. palmeri from Mexico. In 1923, Standley described S. heterocarpa (Cardiospermum sp.?), S. oaxacana (here considered a synonym of S. triquetra Radlk.), S. pacifica (here considered a synonym of S. racemosa Schum.), and S. rekoi. Britton (1923) added a new synonym to S. caracasana (Jacq.) Willd. by publishing S. ierensis from the island of Trinidad.

Hoehne (1925) added S. tricostata and S. fusca from Brazil. In 1930, Urban described S. nipensis from Cuba and Standley published

TABLE II

Treatment of *Serjania* by Radlkofer. Species described by Radlkofer; *=1875, +=1886, all other individual dates shown in the table. Species followed by names in parenthesis represent transfers made by Radlkofer.

Section Platycoccus

S. *chartacea**
S. *leptocarpa**
S. *trichomisca**
S. *confertiflora**
S. *squarrosa**
S. *dumicola**
S. *tenuis**
S. *stenopterygia**
S. *areolata*+
S. *viridissima*(+)
S. *brachyptera*(1905)
S. *grandidens*(1905)
S. *inscripta*(1906)
S. *platypetala*(1916)
S. *communis*
S. *regnellii*
S. *cuspidata*
S. *hirsuta*
S. *decemstriata*
S. *foveata*
S. *ampelopsis*
S. *paludosa*
S. *minutiflora*(1921)
S. *cardiospermoides*

Section Ceratococcus

S. *aluligera*(1893)
S. *calligera*(1916)
S. *setigera* (1921)
S. *cornigera*
S. *mollis*

Section Eurycoccus

S. *acoma**
S. *altissima* (P.& E.)*
S. *corrugata* *
S. *cuneolata**
S. *diversifolia** (Jacq.)
S. *dura**
S. *eucardia**
S. *glutinosa**
S. *gracilis**
S. *laxiflora**
S. *macrostachya**

TABLE II (cont.)

S. *paleata**
S. *paradoxa**
S. *pedicellaris**
S. *comata**
S. *subimpunctata**
S. *depauperata*+
S. *platycarpa*
S. *velutina*
S. *rubicunda* (1913)
S. *elegans*
S. *salzmanniana*
S. *lateritia* (1893)

Section Eucoccus

S. *dentata* (Vell.)*
S. *faveolata**
S. *aculeata**
S. *pyramidata**
S. *sphaerococca**
S. *lamprophylla**
S. *adusta**
S. *lateritia* (1893)
S. *laruotteana*
S. *caracasana*
S. *grandiflora*
S. *seemanni*
S. *crenata*

Section Pachycoccus

S. *erecta* *
S. *piscatoria*
S. *reticulata*
S. *marginata*
S. *dibotrya*

Section Holcoccus

S. *exarata**
S. *grandifolia**
S. *plicata**
S. *thoracoides**
S. *grandiceps* (1898)
S. *glabrata*
S. *membranacea*

Section Dictyococcus

S. *polyphylla* (L.)*
S. *crassinervis**
S. *scatens**
S. *sinuata*
S. *subdentata*
S. *paniculata*
S. *angustifolia*

TABLE II (cont.)

Section Simococcus

- _S. tenuifolia_*
- _S. amplifolia_*
- _S. fuscifolia_*
- _S. ovalifolia_*
- _S. oblongifolia_*
- _S. subrotundifolia_+
- _S. pannifolia_ (1905)
- _S. clematidifolia_
- _S. crassifolia_ *
- _S. pinnatifolia_ *

Section Oococcus

- _S. acutidentata_*
- _S. ichthyoctona_*
- _S. lamprophylla_*
- _S. obtusidentata_*
- _S. oxytoma_*
- _S. perulacea_*
- _S. scopulifera_*
- _S. lamelligera_+
- _S. nutans_
- _S. multiflora_
- _S. paucidentata_

Section Phacococcus

- _S. brachycarpa_*
- _S. grammatophora_*
- _S. longipes_*
- _S. mexicana_
- _S. brevipes_
- _S. brachycarpa_
- _S. rubicaulis_ Benth. ex*

Section Physococcus

- _S. macrococca_*
- _S. mucronulata_*
- _S. rigida_*
- _S. sordida_*
- _S. striata_*
- _S. subtriplinervis_*
- _S. albida_ (1895)
- _S. psilophylla_ (1891)
- _S. sphenocarpa_*
- _S. vesicosa_*

TABLE II (cont.)

S. rufisepala (1891)
S polystachya(Turcz.)*
S. punctata (1895)
S. corindifolia (1903)
S. fuscostriata (1905)
S. ochroclada (1921)
S. flaviflora (1923)
S. grosii
S. incisa
S. cystocarpa (1883)
S. acuta
S. parvifolia

S. brachylopha (1895)
S. fuscopunctata (1895)
S. rutaefolia (1895)
S. longistipula (1905)
S. striolata (1905)
S. unguiculata (1921)
S. racemosa
S. emarginata
S. palmeri
S. californica (1878)
S. oxyphylla
S. inflata

Section Syncoccus

*S. brachystachya**
S. curassavica (L.)*
*S. dasyclados**
*S. filicifolia**
*S. insignis**
*S. orbicularis**
*S. rhombea**
*S. serrata**
*S. trachygona**

*S. cissoides**
*S. deltoidea**
*S. diffusa**
*S. goniocarpa**
*S. nigricans**
*S. purpurascens**
*S. rufa**
*S. sufferruginea**
S. triquetra (H.M.)*

TABLE II (cont.)

_S. tristis_*
S. rachyptera (1891)
S. trifoliolata (1895)
S. columbiana (1905)
S. acupunctata (1913)
S. trirostris (1914)
S. meridionalis
S. suborbicularis (1892)
S. pernambucensis (1893)
S. mansiana
S. schiedeana
S. impressa *
S. noxia
S. peruviana+
S. adiantoides (1898)
S. chaetocarpa (1895)
S. eriocarpa (1910)
S. microcephala (1914)
S. punctulata (1921)
S. cambessedeana
S. truncata (1893)
S. hebecarpa
S. grandis
S. laevigata
S. clematidea

Sedis Dubiae

_S. acuminata_*
_S. circumvallata_*
_S. inebrians_*
_S. setulosa_*
S. didymadenia (1893)
S. leucosepala (1913)
S. punctulata (1921)
_S. brachyphylla_*
_S. hamuligera_*
_S. piscatoria_*
S. nodosa (Jacq.)*
S. humifusa (1909)
S. incana (1903)

S. yucatanensis from Yucatan. Macbride (1931) published *S. elongata* from Peru. Jones (1933) published *S. papilio* (here considered a synonym for *S.schiedeana* Schlecht.), Rusby (1934) published *S. lyrata* (here considered a synonym of *S. diffusa* Radlk.) and Diels (1937) described *S. ptelifolia* from Ecuador.

Standley (1935) published *S. pterarthra* and in 1937 he added *S. pteropoda*, and *S. valerii*. In 1940 he published *S. cissifolia* (here considered a synonym of *S. grandis* Seem.). A few years later Standley and Steyermark published *S. lobulata* and *S. macrocarpa* in 1943, and *S. hispida* and *S. phaseoloides* (the latter here considered a synonym of *S. cardiospermoides* Schlecht. & Cham.) in 1944.

Johnston (1949) published *S. nesites* (a synonym for *S. mexicana* (Jacq.) Willd.). Standley and Williams (1950) described *S. tallioniana* from Guatemala, and Cuatrecasas (1952) described two new species from Colombia (*S. calimensis* and *S. schultesii*, the latter here considered a synonym of *S. leptocarpa*).

Macbride (1956), in his Flora of Peru, described *S. alsmithii* (= *S. communis* var. *alsmithii*) and *S. killipii* (here considered a synonym of *S. subrotundifolia* Radlk.).

Barkley (1957), relying on trivial characters proposed three new species, which I consider synonyms of previously described species, viz. *S. araquei* (= *S. erecta* Radlk.), *S. descolei* (= *S. glutinosa* Radlk.), and *S. meyeri* (= *S. perulacea* Radlk.).

Eighteen years elapsed until the appearance of more names assigned to *Serjania*. Lippold (1974), described three new species from the island of Cuba (S. linnearifolia, S. microphylla, and S. occidentalis) for which I have not yet seen material.

In 1976, Croat described five new species, one for Mexico (S. lundellii) (1976b) and four for Panama in his treatment of the Sapindaceae for the **Flora of Panama** [S. allenii, S. darcyi, S. decapleura, and S. pluvialiflorens (1976a)]. I consider S. allenii and S. pluvialiflorens as synonyms of S. membranacea Splitg., and S. decapleura as a synonym of S. pyramidata Radlk.

Ferrucci (1981a), provided the new name S. herteri for S. australis (St. Hil.) Herter, a latter homonym of S. australis Spreng. (considered a synonym of Dodonea pinnata Smith by Radlkofer). In 1983, she published two new species, S. hatschbachii from Brazil and S. tripleura from Argentina, and in 1985(a) she published S. bahiana from Bahia, Brazil.

More recent names published are those by Acevedo Rodríguez in 1987 (S. fluminensis and S. unidentata from Brazil) and in 1988 (S. magnistipulata, and S. morii from Brazil and S. schunkei from Perú).

The most recent names were published by Sommer (1988a-b) for species from the Brazilian states of Rio de Janeiro (S. grazielae, S. itatiatensis and S. carautae) and Espírito Santo (S. bradeana, S. espiritosantensis). I have not seen the types of these species.

A total of 286 names have been validly published under Serjania, of these I tentatively accept 226 as biological entities. The authors and number of species described by them in Serjania are provided in Table III.

TABLE III

Number of names of *Serjania* proposed by different authors.

Radlkofer, L.	133	Hoehne, F.C.	2
Cambessèdes, J.	15	Martius, C.F.P.	2
Standley, P.	10	Schlechtendal & Chamisso	2
Kunth, C.S.	8	Britton, N.L.	1
Schlechtendal, D.F.L.	7	Casaretto, G.	1
Schumacher, C.F.	6	Diels, F.L.E.	1
Triana & Planchon	6	Gardner, G.	1
Acevedo-Rodríguez, P.	5	Johnston, I.M.	1
Croat, T.B.	5	Jones, M.E.	1
Grisebach, A.H.R.	5	Jussieu, A.L.	1
Sommer G. V.	5	Macfadyen, J.	1
Barkley, F.A.	4	Rusby, H.H.	1
Bentham, G.	4	Saint Hilaire, A.	1
Ferrucci, M.S.	4	Schott, H.W.	1
Lippold, H.	4	Seemann, B.	1
Willdenow, C.L.	4	Smith, J.E.	1
De Candolle, A.P.	3	Splitgerber, F.L.	1
Macbride, F.	3	Standley & Williams	1
Poeppig and Endlicher	3	Torrey, J.	1
Sprengel, K.	3	Urban, I.	1
Standley & Steyermark	3	Vellozo, J.M.	1
Turczaninow, N.S.	3	Watson, P.W.	1
Cuatrecasas J.	2	Wright, W.	1

TABLE IV

Infraspecific taxa of *Serjania* published by Radlkofer

- S. atrolineata
  - f. genuina
  - f. lancifolia
- S. communis
  - var. glabra
  - var. mollis
  - var. pilosula
- S. confertiflora
  - var. hooibrenki
  - var. dasycephala
    - f. glabriuscula
    - f. subincana
- S. diversifolia
  - var. parvula (Griseb.)
    - subvar. multifoliolata
- S. glabrata
  - f. mollior
  - f. mollissima
- S. caracasana
  - f. genuina
  - f. subincisa
  - f. puberula
  - f. nitidula
  - f. flavoviridis
- S. cuspidata
  - f. dissecta
- S. cardiospermoides
  - f. leptothyrsa
  - f. subjubata
- S. racemosa
  - f. glabriuscula
  - f. hirta
  - f. pubescens
- S. reticulata
  - f. microcarpa
  - f. platyptera
  - f. rubens

TABLE IV (cont.)

- S. glutinosa
  - f. multisecta
  - f. genuina
- S. hebecarpa
  - f. amblycephala
  - f. oxycephala
  - f. platycephala
- S. incana
  - f. glabriuscula
  - f. genuina
- S. marginata
  - f. paucidentata
  - f. isopterygia
  - f. pluridentata
- S. paradoxa
  - f. glanduligera
  - f. molliuscula
  - f. pilosa
  - f. subglabra
  - f. subtomentosa
  - f. subvelutina
- S. rigida
  - f. hirta
  - f. glabra
- S. rufisepala
  - f. genuina
  - f. bicolor
- S. salzmanniana
  - f. pubescens
  - f. puberula
  - f. glabrata
- S. sinuata
  - f. plumeriana
    - subf. serrato-dentata
  - f. ilicifolia
    - subf. anomala
- S. subdentata
  - f. subcrenato-dentata
  - f. angustifolia

A total of 63 infraspecific names have been published for *Serjania*. Between 1875 and 1931, Radlkofer published 49 infraspecific names without consistency of application of the infraspecific categories. These names were designated as forms, varieties, subforms, or subvarieties without an explanation for selecting a particular category. The infraspecific names he published are presented in Table IV.

In 1866, Grisebach published two varieties in *S. lupulina*, (vars. *parvula* and *angustifolia*), and in 1879, he reduced *S. foveta* Griseb. to a variety of *S. meridionalis* Cambessèdes. Kuntze (1891), published a variety of *S. mexicana*, (var. *pubescens*), and in 1898, the form *radlkoferi* for *S. caracasana* (L.) Radlk. Huber (1915) described var. *acuminata* in *S. clematidea* Tria. & Planch. Schultes (1949) described *S. dasyclados* Radlk. var. *sibundaya* from Colombia.

In 1957 Barkley described three varieties in *S. meridionalis* Cambess. (vars. *cuezzoi*, *borsiniae* and *o'donellii*). In 1976(b), Croat described var. *glabricarpa* in *S. macrocarpa* Stand. & Steyerm.

GENERIC RELATIONSHIPS

The genus *Serjania* is very similar to five other genera in the Sapindaceae (*Paullinia* L., *Cardiospermum* L., *Urvillea* Kunth, *Houssayanthus* Hunz., and *Lophostigma* Radlk.). Distinction of the different genera, based on vegetative characters, is very difficult and usually requires previous experience with the group. However, they are easily distinguished by the type of fruit. These six genera certainly constitute a natural group within the Sapindaceae, being distinctive enough to be placed in their own tribe, the Paullinieae.

The development of the modern concept of the Paullinieae can be traced back to 1821 when Kunth proposed the section Paullinaceae within the Sapindaceae. This "section" was defined by the presence of climbing habit, tendrils, and nectary disks modified into four protruding glands. It included the genera Cardiospermum, Urvillea, Serjania, and Paullinia.

A few years later, De Candolle (1824) designated the group as a tribe, providing the termination -ieae. In his work, he recognized the same genera as Kunth and provided descriptions of all of the species known in these genera at that time. In 1888, Radlkofer provided a classification scheme for the Sapindaceae, dividing the family into 14 tribes. In this treatment, he divided the Paullinieae into two subtribes (the Eupaullinieae and Thinouieae), and added the genus Thinouia Trian. & Planch. into the latter subtribe. Although the inclusion of Thinouia in the Paullinieae (sensu Kunth) expanded the limits of the tribe, the tribe was not emended until 1931 when Radlkofer characterized the two subtribes. According to Radlkofer, the Eupaullinieae includes the genera with zygomorphic flowers and a nectary disk modified into four prominent glands (Serjania, Paullinia, Cardiospermum, Urvillea, and Lophostigma, the latter added by Radlkofer in 1897). The monotypic Thinouieae possess actinomorphic flowers.

In 1978, Hunziker created the genus Houssayanthus and placed it in the Paullinieae, bringing to seven the total number of genera in the tribe. Houssayanthus was segregated from Urvillea because of its schizocarpic (not loculicidal) fruits. Recently, other species segregated from Paullinia and Serjania have been added to that genus. Houssayanthus has been found to have a particular distribution along flooded margins of forests, peripheral to the Amazon basin (Ferrucci, 1987).

Other workers did not recognize the validity of the Paullinieae in the Sapindaceae. Spach (1834), Meisner (1837), and Lindley (1846) placed the genera Paullinia, Cardiospermum, Urvillea, and Serjania, along with other genera, into the tribe Sapindeae. Bentham and Hooker (1862) included them in the subfamily (subordo) Sapindoideae along with many other genera.

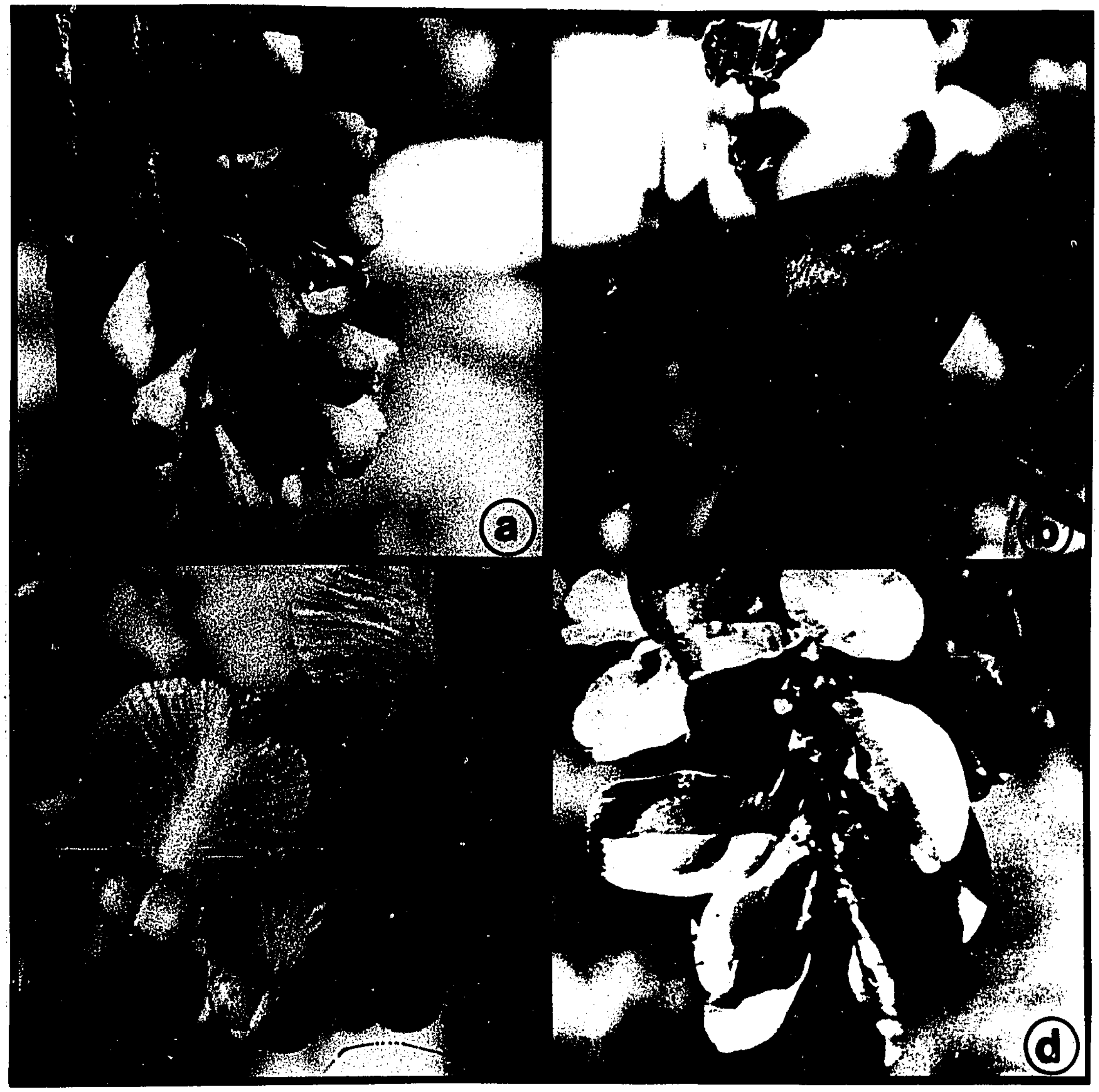
The Paullinieae sensu Kunth appears to constitute a natural group and seems preferable to the systems proposed by other workers. I do not consider the Paullinieae sensu Radlkofer to be a natural group because of the inclusion of Thinouia. Thinouia was included in the Paullinieae because of its climbing habit. However, it seems that the climbing habit is not a homologous character (in the cladistic sense) for Thinouia and the Paullinieae. In a phylogenetic analysis more weight should be given to floral and pollen characters. The actinomorphic flowers and spherical pollen grains found in Thinouia are widely distributed throughout the Sapindaceae, but are absent in the Paullinieae and only a few taxa of the Thouinieae have spherical pollen grains. This suggests that Thinouia belongs to a different tribe, perhaps the Sapindeae, where these characters are widely distributed.

Serjania is particularly close to Houssayanthus because of their schizocarpic fruits (Fig. 18a), however, it differs from Houssayanthus by the presence of samaroid (not sem-inflated) merocarps (Fig. 1c). Houssayanthus, because of its water dispersed fruits, seems to be more derived than Serjania. It also has a more restricted distribution and a smaller number of species.

Serjania is also closely related to Paullinia, but is distinguished from it by the presence of schizocarpic (not loculicidal capsules) fruits (Figs. 1a & c; 18a & b) and demitricolporate (not triporate) pollen grains. In the demicolporate pollen the secondary colpi enclose a pore. Serjania seems to be more primitive with respect to these characters. Schizocarpic fruits are present in all members of the closely related Thouinieae (out-group of Paullinieae), suggesting that this character is primitive or plesiomorphic for the Paullinieae. The triporate pollen present in Paullinia was regarded by Muller and Leenhouts (1976) as being directly derived from the demitricolporate condition by the reduction of the colpi, however, their survey included only a small sample of the genera.

Cardiospermum, Urvillea, and Lophostigma seem to be closer to Paullinia than to Serjania. Cardiospermum and Urvillea have loculicidal fruits (Figs. 1b, d & 18b) as does Paullinia. However

Figure 1. Type or fruits in the Paullinieae. A. Loculicidal thick, woody capsular fruits in _Paullinia_ _alata_ G.Don (_Acevedo et al. 1581_). B. Loculicidal, thin, inflated capsular fruits in _Cardiospermum_ _halicacabum_ L. (_Acevedo 2501_). C. Schizocarpic fruits with samaroid merocarps (_Serjania_ _fluminensis_, _Acevedo & Farney 1424_). D. Loculicidal, thin, semi-winged capsules in _Urvillea_ _villosa_ Radlk. (_Acevedo et al. 1481_).


a
b
d

they differ from Paullinia by having a reduced chromosome number of $n=11$ (not $n=12$), shorter life cycle, papery fruits, and herbaceous habit. It seems that the reduction of chromosome number is accompanied by a less woody habit and shorter life cycles. Lophostigma, although incompletely known, seems to be closer to Paullinia because of its biporate pollen grains, a condition apparently derived from triporate pollen (Muller & Leenhouts, 1976). The placement of Lophostigma close to Paullinia is provisional because pollen grains are not known for many species of Paullinieae.

Cladistic Analysis

The phylogenetic relationships of the Paullinieae (sensu Radlkofer) and the Thouinieae were analyzed cladistically using the computer program PAUP (Phylogenetic Analysis Using Parsimony, ver. 2.4; Swofford, 1985). Thirty-one characters were selected for this analysis (Table V) and character state polarities were established using the method of out-group comparison (Donoghue & Cantino, 1984; Watrous & Wheeler, 1981). The genera of Paullinieae and Thouinieae were compared to the tribe Sapindeae, which is believed to be closely related to both tribes, due to their overall similarity. A discussion of the characters and their polarization follows (Table V).

TABLE V

Characters used in the cladistic analysis of the genera of Paullinieae and Thouinieae.

Code	Character	Plesiomorphic	Apomorphic
1.	ovule/carpel	two or more(0)	one(1)
2.	fruit	schizocarp(0)	capsule(1)
3.	embryo	biplicate(0)	incurved(1)
			substraight(2)
4.	terminal leaflet	absent(0)	present(1)
5.	life form	trees, shrubs(0)	climbers(1)
6.	cambium	normal(0)	s. anomalous(1)
			p. anomalous(2)
7.	leaves	pinnate(0)	ternate(1)
			simple(2)
8.	phyllotaxy	alternate(0)	opposite(1)
9.	flower symmetry	actinomorphic(0)	zygomorphic(1)
10.	scales	bifid(0)	reflexed(1)
11.	seed coat	hard(0)	sarcotesta(1)
			red. sarcot(2)
12.	dissepimentum	narrow(0)	wide(1)
13.	nectary disc	annular(0)	unilat(1)
			4-lobed(2)
			4-glds(3)
			2-glds(4)

TABLE V (cont.)

14.	styloid crystal	absent(0)	present(1)
15.	ovary	three carpels(0)	two carpels(1)
16.	calyx	5-merous(0)	4-merous(1)
17.	sclereid ring	present(0)	absent(1)
18.	mucilaginous c.	present(0)	absent(1)
19.	pollen	A type(0)	C2 type(1) C3 type(2) D type(3)
20.	resin	absent(0)	present(1)
21.	torus	absent(0)	developed(1)
22.	habit	woody(0)	herbaceous(1)
23.	anther append.	absent(0)	present(1)
24.	stigma	papillose(0)	plumose(1)
25.	anthers attach	dorsifixed(0)	basifixed(1)
26.	chromosome no.	n> 12(0)	n=12(1), n=11(2)
27.	Fruit texture	woody(0)	papery(1) fleshy(2)
28.	fruit shape	various (0)	inflated (1)
29.	stipules	absent(0)	present(1)
30.	coccus position	central(0)	proximal(1) distal(2)
31.	partitioning wall	persistent(0)	degrading(1)

1. Ovule. One ovule per carpel (1) is restricted to the subfamily Sapindoideae, therefore it is considered a derived condition. Two or more ovules per carpel (0) seems to be the primitive condition for the Sapindaceae because it is present inits out-group as well as in other families of the Sapindales (sensu Cronquist, 1981). Although the presence of one ovule per carpel is uninformative for this analysis, it is important when choosing the out-groups of the Paullinieae, because this character places the Paullinieae in the subfamily Sapindoideae.

2. Fruit. Capsular fruits (1) are considered derived within the Paullinieae because they are not present in the sister-group, and their distribution is restricted to a few genera of the Paullinieae. Indehiscent, schizocarpic fruits (0) are considered plesiomorphic for the Paullinieae because they are found throughout the sister-group (Thouinieae) and the more distant out-group, the Sapindeae.

3. Embryo. The incurved embryo (1), where both cotyledons are bent toward the fruit axis, and where the adaxial cotyledon is larger and covers the abaxial one, is restricted to Bridgesia (Thouinieae) and is not present in the out-group. Within the Paullinieae, the embryo with straight cotyledons which are bent at the apex [substraight (2)] is a condition restricted to Houssayanthus. Its absence from the out-groups indicates that it is a derived character. The condition in which the embryo's adaxial cotyledon is bent over the biplicate abaxial one [biplicate (0)] is

widespread in the Paullinieae as well as in the out-groups Thouinieae and Sapindeae, it is also very common throughout the Sapindaceae and the Sapindales. For this reason it is considered the primitive state.

4. Terminal leaflet. The presence of a terminal leaflet (1) seems to be the derived condition (synapomorphic) for the genera of Paullinieae and Thouinieae when compared to the Sapindeae and other tribes of the subfamily Sapindoideae. The absence of a terminal leaflet (0) seems to be primitive because it is present in many members outside of the Sapindoideae.

5. Life form. Climbing habit (1), and associated characters such as tendrils, is the dominant growth form in the Paullinieae. In contrast, climbers are absent in the out-groups of the Paullinieae, therefore this condition is considered derived. Its occurrence in two other genera (<u>Allosanthus</u> and <u>Thinouia</u>) within the Sapindoideae seems to be due to convergence. Trees or shrubs (0) are common throughout the remaining tribes of Sapindaceae, as well as in other families of Sapindales, which suggest that these growth forms are primitive in the Sapindaceae.

6. Anomalous cambium. The differentiation of discrete cambial layers within the primary body of the plant [primary anomalous growth (2)] is unique within the plant kingdom to some elements of the climbing genera of Paullinieae, indicating its derived condition. The differentiation of cambial zones within the secondary body of the plant [resulting in anomalous secondary growth

(1)] is restricted to some species of the climbing genera of Paullinieae and the lianescent genus Thinouia. This character is not present in any other member of Sapindaceae, therefore it is considered derived. The production of a single, continuous cambial layer (0), which results in normal secondary growth, is present in all of the remaining members of Sapindaceae, and also in all other families of the Sapindales, indicating its primitive state.

7. Leaf. Polarity of leaf composition is difficult to establish because much variation is present throughout the Sapindaceae. The ternately compound condition (1) is unique to the Paullinieae and the Thouinieae within the subfamily Sapindoideae. For that reason, it is considered a derived character which (synapomorphic) defines the Thouinieae and the Paullinieae. The occurrence of simple leaves (2) is restricted to a few genera of Thouinieae, while it is absent from the remaining tribes of the Sapindoideae, thereby indicating that simple leaves represent a derived condition. Pinnately compound leaves (0) are widespread in many species of Sapindaceae, as well as in many families of the Sapindales. For this reason, pinnately compound leaves are considered primitive.

8. Phyllotaxy. Opposite leaves (1) are restricted to a few genera of the Thouinieae. For this reason they are considered to be derived. Alternate leaves (0) are common throughout the Sapindaceae as well as in the remaining families of Sapindales.

9. Flower symmetry. Within the subfamily Sapindoideae, zygomorphic flowers (1) are restricted to the tribes Paullinieae and

Thouinieae. For this reason, zygomorphic flowers are considered derived. Actinomorphic flowers (0) are common in the remaining genera of the subfamily Sapindoideae as well as in other Sapindaceae. Outside of the Sapindaceae, actinomorphic flowers are prevalent, thereby indicating their primitive state.

10. Petal scales. Reflexed, hood-shaped scales are restricted to the Paullinieae and the Thouinieae within the subfamily Sapindoideae, which suggest that they are derived. Bifid scales (0) occur in the remaining genera of the subfamily Sapindoideae as well as in other Sapindaceae. In a comparative study, Leinfellner (1958) considered the bifid type as more primitive than the reflexed, hood-shaped type.

11. Seed coat. The presence of a sarcotesta (fleshy seed coat) (1) in the Paullinieae is restricted to Paullinia. The fact that it is absent in the sister-group suggests that it is a derived character. The subsequent loss of the sarcotesta (2), as shown by the presence of a "remnant" aril-like structure in Cardiospermum and Urvillea, is suggestive of a further derived state limited to a few members of the Paullinieae. A hard seedcoat (0) is widespread in the Paullinieae as well as in the out-groups, and is therefore considered primitive.

12. Dissepimentum. A wide dissepimentum (1) is restricted to a few genera of Paullinieae and is absent in its sister-group which suggests that it is derived. A narrow dissepimentum (0), although not common in the Paullinieae, is present in the out-groups.

13. Nectary disk. A unilateral disk (1) is restricted to the Paullinieae and the Thouinieae in the subfamily Sapindoideae. Therefore, its presence is considered to represent an advanced state. A four-lobed, unilateral disk (2) is restricted to Guindillia and Bridgesia which indicates its derived condition within the Thouinieae. Unilateral disks modified into four glands (3) represent a further derived condition restricted to most members of Paullinieae and to some Thouinieae but absent in their out-group. Developmentally, it seems that this state is derived from ancestors with unilateral disks. A unilateral disk with two glands (4) is restricted to a few genera of Paullinieae and is absent in their out-groups, and, for this reason is considered a further derived state. An annular disc (0) is common in the remaining genera of the subfamily Sapindoideae, as well as for many of the remaining members of Sapindaceae, which suggests its primitive condition.

14. Styloid crystals. Within the Sapindaceae, the presence of styloid crystals (1) in the bark has been regarded as unique to the genus Diatenopteryx (Solereder, 1908). Therefore, it is considered an autoapomorphic character for Diatenopteryx. The absence of styloid crystals (0) is considered primitive.

15. Ovary. The bicarpellar ovary (1) is restricted to a few members of the Thouinieae and it is absent in the out-group of the Paullinieae and Thouinieae. Therefore, it is considered the derived condition. The tricarpellar ovary (0) is considered primitive

because it is present in the out-groups of the Paullinieae and Thouinieae. It is also the commonest condition in other Sapindaceae.

16. Calyx. The possession of a four-merous calyx (1) is thought to be derived because it is restricted to a few genera of the Thouinieae and because it is absent in the out-group (Sapindeae). The five-merous calyx (0) is considered primitive because of its widespread occurrence in the out-group as well as in other Sapindaceae.

17. Sclereid ring. Isolated groups of primary phloem fibers not forming a ring (1) are found only in <u>Guindilia</u>. For this reason they are felt to represent a derived character within the Sapindaceae. The presence of a ring of sclereids (0) at the inner limit of the cortex is considered primitive because it is a common feature in all members of the Paullinieae, the Thouinieae, their out-group, and other Sapindaceae (Solereder, 1908).

18. Mucilaginous cells. <u>Athyana</u> is unique because it lacks mucilaginous cells (1). Mucilaginous cells (0) in the epidermis are present in the remaining members of the Thouinieae, its out-group, and other Sapindaceae.

19. Pollen grains. Type C pollen (1,2) is a common feature of the Paullinieae and is found in a few members of its sister-group, the Thouinieae. In the more distant out-group (tribe Sapindeae), this condition is absent, suggesting its derived nature. In this analysis, I follow Muller and Leenhouts (1976) who, in a comparative

study, considered type C3 [isopolar, triporate (2)] as necessarily derived from type C2 [heteropolar, demitricolporate (1)]. Type D [biporate (3)] is restricted to Lophostigma and a few species of Allophylus. For this reason it is considered to be more derived. Type A [spherical, tricolporate (0)] is present in the remaining members of the Thouinieae, in its out-group, and in the remaining members of the subfamily Sapindoideae. For this reason type A pollen is considered primitive.

20. Resin. The presence of a whitish resin (1) is a derived state for the Paullinieae because it is absent from its sister-group as well as from the rest of the family.

21. Torus. A well developed torus (1) is restricted to a few genera of Paullinieae and to Diatenopteryx in the Thouinieae. The distribution of this character (absent in out-group) suggests that it is derived from ancestors without a torus.

22. Habit. The herbaceous habit (1) is restricted to very few members of the Paullinieae. Its absence from the out-group and the remaining members of Sapindaceae indicates that this is a derived condition. The woody (0) habit is predominant within the Paullinieae, the Thouinieae, their out-group, other Sapindaceae, and the remaining families of Sapindales which indicates its primitive condition.

23. Anther appendages. The presence of a terminal appendage (1) at the anther tip is restricted to a few species of the Paullinieae, and is completely absent from the sister-group (Thouinieae). This

suggests that this character is derived. This character is absent in the more distant out-groups which suggests that the absence of an anther appendage (0) is primitive.

24. Stigma. The presence of a plumose (1) stigma is considered derived, because it is restricted within the Paullinieae to the monotypic Lophostigma. A papillose (0) stigmatic surface is widespread within the Paullinieae, the Thouinieae, and their out-group. Consequently, papillose stigmas are considered as primitive.

25. Anther attachment. Basifixed (1) anthers are restricted within the Paullinieae to Lophostigma. They are absent in the sister- and out-groups, and are therefore considered to be derived. Dorsifixed (0) anthers are found throughout the Paullinieae and in its sister-group, the Thouinieae. They are also present in their out-group, and therefore, are considered to be primitive.

26. Chromosome number. N=12 (1) is restricted to species of the Paullinieae. This number is absent from the sister- and out-groups suggesting that is the more derived state. Within the Paullinieae, n=11 (2) is a further derived state because it is restricted to a few genera. N= >12 (0) is widely distributed in the Thouinieae and Sapindoideae, suggesting that numbers greater than 12 are primitive.

27. Fruit texture. Papery fruits (1) are restricted to few genera of Paullinieae, and are absent in the out-groups. Therefore, they are considered as representing an advanced state. Fleshy

fruits (2) seem to be derived within the Thouinieae because the out-group has mostly woody fruits. Woody fruits (0) are predominant in the Paullinieae as well as in the sister-group (Thouinieae) and the more distant out-group (Sapindeae). Therefore, they are considered to be primitive.

28. Fruit shape. Within the Paullinieae and the Thouinieae inflated fruits (1) only occur in _Cardiospermum_. The widespread occurrence of non-inflated fruits (0) throughout the Paullinieae and Thouinieae, and in their more distant out-group, the Sapindeae, suggests that this condition is primitive.

29. Stipules. True stipules (1) are present in the Paullinieae and in _Thinouia_, but they are absent from the rest of Sapindaceae and from most of the Sapindales, which indicates their derived condition. Pseudostipules, which occur in many Old World genera, are not homologous to true stipules (Weberling, 1976). Therefore, taxa with pseudostipules are considered as exstipulate (0). Exstipulate plants are a widespread condition not only in Sapindaceae but also in the Sapindales.

30. Coccus. The distal (1) position of the seed-bearing portion (coccus) of the fruit is restricted within the Paullinieae to _Serjania_. Similarly, the coccus in a proximal (2) position is restricted to _Thouinia_ and _Thinouia_ but absent in the Sapindeae (out-group of the Thouinieae). A central position of the fruit coccus (0) is widespread in the Paullinieae as well as in its sister and out-groups. Consequently, distal and proximal positions

of the coccus are thought to be directly derived from ancestors with the fruit coccus a in central position.

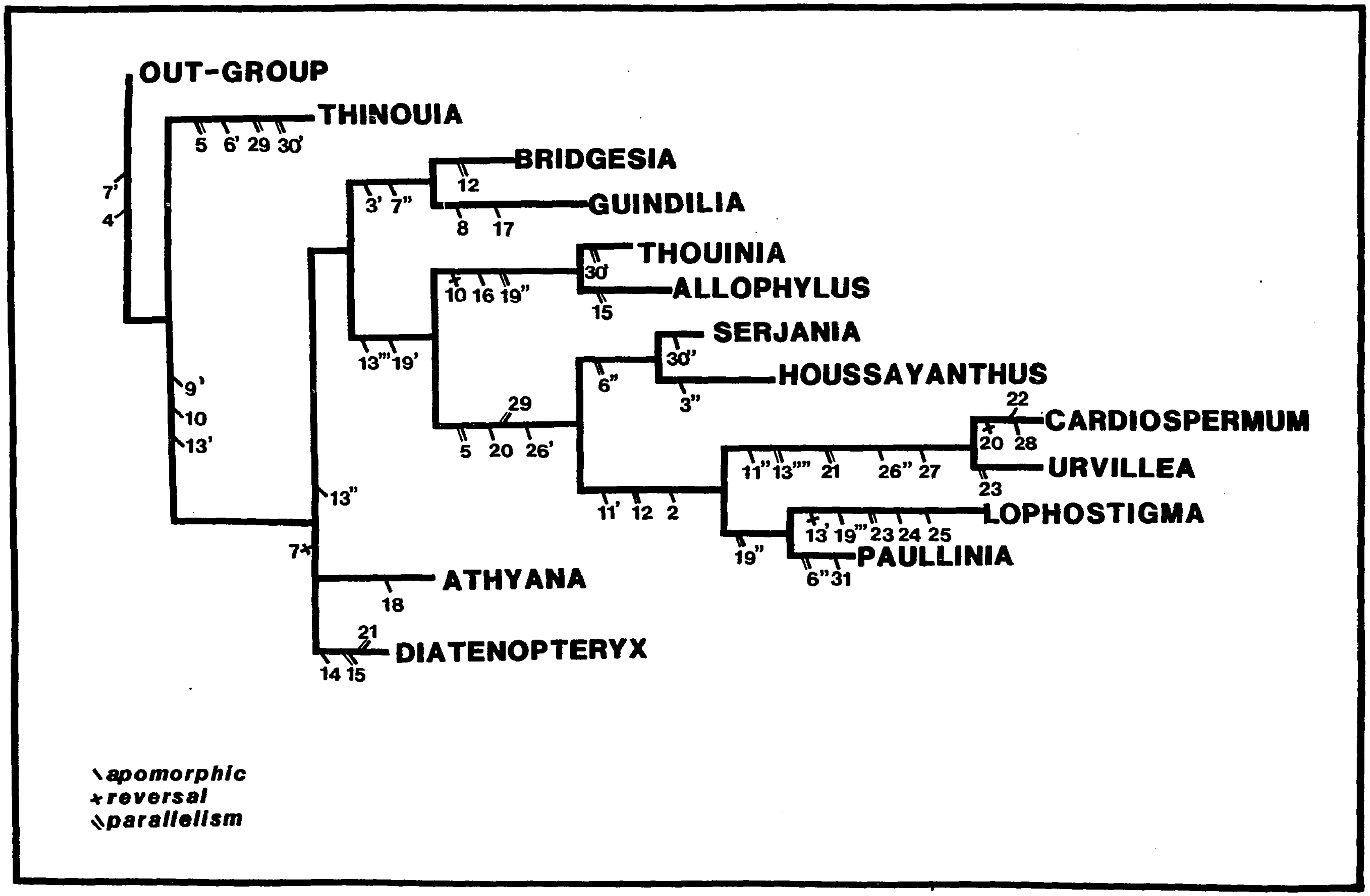
31. Partitioning fruit wall. This character is restricted to the taxa of Paullinieae with loculicidal fruits. As this character does not occur in the sister-group, it is difficult to polarize it by using the out-group comparison method. Ontogenetically, the taxa having this character pass through a common developmental sequence. The wall is initiated (0) in early stages, but it disintegrates (1) in Paullinia only after the fruits reach maturity. The disintegration of the fruit wall constitutes an additional step in fruit development, therefore it is considered an apomorphic state.

The following PAUP options were used for the performance of the cladistic analysis: 1) trees were rooted to a designated out-group (Sapindeae); 2) the "closest" addition sequence were selected; 3) global branch swapping was employed; 4)"mulspar" was used to search for equally parsimonious trees; 5) "Farris" optimization was selected; and 6) extra weight was applied to character 19 (weight of 2).

Results

Two cladistic analyses were performed. In the first, all characters were equally weighted and in the second different weight was assigned to one of the characters. The first analysis produced several equally parsimonious trees differing in the number and position of parallelisms or reversals. Those trees differ from the

Figure 2. Cladogram of genera traditionally included in the tribes Paullinieae (Serjania, Paullinia, Cardiospermum, Urvillea, Lophostigma, Houssayanthus, and Thinouia) and Thouinieae (Athyana, Diatenopteryx, Bridgesia, Guindilia, Thouinia, and Allophylus). Generated by PAUP from the data matrix in Table VI and drawn directly from the computer output. The cladogram is completely resolved. The lengths of the branches have no significance. Number without primes correspond to "0"; prime, double prime and triple prime correspond to states "1", "2" and "3" respectively in the data matrix.


OUT-GROUP
THINOUIA
5 6' 29 30'
7'
4
BRIDGESIA
12
GUINDILIA
3' 7"
8 17
THOUINIA
30'
ALLOPHYLUS
10 16 19"
15
SERJANIA
30'
HOUSSAYANTHUS
6"
3"
13'"19'
9'
10
13'
29
5 20 26'
22
CARDIOSPERMUM
20 28
URVILLEA
11" 13"" 21
26" 27
23
13"
11' 12 2
LOPHOSTIGMA
13' 19'" 23 24 25
19"
PAULLINIA
6" 31
7
ATHYANA
18
21
DIATENOPTERYX
14 15
apomorphic
reversal
parallelism

trees produced in the second analysis in the position of Lophostigma (at the base of the Paullinieae rather than close to Paullinia), a taxon for which many characters remain unknown.

In the second analysis, extra weight was applied to character 19 (pollen morphology, weight of 2) because it is a variable character known for every genera of the Paullinieae. In my opinion, this analysis better reflects the position of Lophostigma which has many apomorphic characters that suggest a rather derived position within the Paullinieae. Two equally parsimonious trees resulted from this analysis but only one is shown (Fig. 2) because it has one less parallelism than the alternative tree. The position of Lophostigma is open to question because many of its characters remain unknown. However, I feel more confident keeping Lophostigma closer to Paullinia than to the base of the Paullinieae because of its high number of derived characters.

The cladistic analysis shows a major clade in which all genera of Paullinieae and Thouinieae, as well as the genus Thinouia, are not separable into discrete groups. This is the result of using character 4 and 7 (terminal leaflet and ternately compound leaves) as synapomorphies. However, it is necessary to point out that these characters are perhaps more variable than previously believed, and the suggested relationship might not hold true for all of the genera. In any case, the clade defined by characters 13''' and 19' (Thouinia, Allophylus, Serjania, Houssayanthus, Cardiospermum, Urvillea, Paullinieae, and Lophostigma) will stand as a natural

TABLE VI

Data matrix for the cladistic analysis of the genera of Paullinieae and Thouinieae.

	Characters															
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Out-group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<u>Thinouia</u>	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
<u>Bridgesia</u>	0	0	1	1	0	0	2	0	1	1	0	1	2	0	0	0
<u>Guindilia</u>	0	0	1	1	0	0	2	1	1	1	0	0	2	0	0	0
<u>Diatenopteryx</u>	0	0	0	1	0	0	0	0	1	1	0	0	1	1	1	0
<u>Athyana</u>	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0
<u>Thouinia</u>	0	0	0	1	0	0	1	0	1	0	0	0	3	0	0	1
<u>Allophylus</u>	0	0	0	1	0	0	1	0	1	0	0	0	3	0	1	1
<u>Serjania</u>	0	0	0	1	1	2	1	0	1	1	0	0	3	0	0	0
<u>Houssayanthus</u>	0	0	2	1	1	2	1	0	1	1	0	0	3	0	0	0
<u>Cardiospermum</u>	0	1	0	1	1	0	1	0	1	1	2	1	4	0	0	0
<u>Urvillea</u>	0	1	0	1	1	0	0	1	1	2	1	1	4	0	0	0
<u>Lophostigma</u>	0	9	9	1	1	0	0	1	1	9	1	9	1	0	0	0
<u>Paullinia</u>	0	1	0	1	1	2	1	0	1	1	1	1	3	0	0	0

For characters see Table V.

9= unknown character.

TABLE VI (cont.)

	Characters														
Taxa	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Out-group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thinouia	0	0	0	0	0	0	0	0	0	9	0	0	1	1	0
Bridgesia	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0
Guindilia	1	0	0	0	0	0	0	0	0	9	0	0	0	0	0
Diatenopteryx	0	0	0	0	1	0	0	0	0	9	0	0	0	0	0
Athyana	0	1	0	0	0	0	0	0	0	9	0	0	0	0	0
Thouinia	0	0	2	0	0	0	0	0	0	9	0	0	0	1	0
Allophylus	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Serjania	0	0	1	1	0	0	0	0	0	1	0	0	1	2	0
Houssayanthus	0	0	1	9	0	0	0	0	0	1	0	0	1	0	0
Cardiospermum	0	0	1	1	1	1	0	0	0	2	1	1	1	0	0
Urvillea	0	0	1	1	1	1	0	0	0	2	1	0	1	0	0
Lophostigma	0	0	3	9	0	0	1	1	1	9	0	0	1	9	0
Paullinia	0	0	2	1	0	0	0	0	0	1	0	0	1	0	1

group because it is defined by truly apomorphic characters.

One of the major results of this analysis is the demonstration that *Thinouia* is not closely related to the genera of Paullinieae (sensu Kunth), and that their similarity is due to convergent evolution, especially of the climbing habit and related traits.

MORPHOLOGY and ANATOMY

Habit

Species of *Serjania* are mostly perennial, woody climbers with tendrils. However, in the absence of support they may become arching shrubs or trailing vines. There are few species with the shrubby habit (e.g., *S. erecta* and *S. trichomisca*). The most weedy species are usually small and essentially herbaceous. A number of species are branched from the base, producing many principal stems, while others present a single main stem with lateral branches throughout their extension.

There are no published reports on the architecture of *Serjania*. However, other members of the Paullinieae, such as *Paullinia pinnata* (Cremers, 1974; pers. observ.) and *Cardiospermum halicacabum* (pers. observ.), have monopodial growth. The first leaves produced are opposite and simple in *P. pinnata* and opposite and ternately compound in *C. halicacabum*. Subsequent leaves produced are alternate and the stem has long internodes. In *C. halicacabum*, five consecutive leaves are produced on an orthotropic stem which lacks tendrils. At this stage of development the stem is still erect but somewhat arched. After the sixth leaf is produced, a short axillary branch carrying two tendrils is produced syllectically with the main axis. Supernumerary buds are present in the leaf axils. These will later develop into lateral branches, which usually terminate in an inflorescence.

Stems

Although most species of Serjania are shorter than 10 m, some species have stems that may reach up to 30 m in length and ca 6 cm in diam. In many species, a watery or milky sap (resin) is produced when the stem is cut. Adventitious roots are produced at the internodes of some species with creeping stems (S. polyphylla and S. reticulata), or on plants growing in areas subject to flooding (S. inscripta). The general appearance of the stem may vary from smooth or rough to densely lenticellate and from terete to angled and furrowed. Some species, such as S. mexicana, S. rubicaulis, S. aculeata, and S. hatschbachii, possess aculeate projections.

Cross sections of young stems show an **epidermis** with wavy anticlinal walls (Figs. 7c; 15f). The **cortex** consists of a parenchymatous zone approximately ten cells wide in cross section. Parenchyma containing druses or prismatic crystals were common in all examined species. Tannin idioblasts (Figs. 7d, 9a) and secretory canals (Fig. 7d, 9a-b) are very common in the cortex.

These canals seem to originate schizogenously and are surrounded by epithelial cells. Their contents appear cloudy in sectioned material (Fig. 9a). Secretions from freshly cut stems are frequently milky, however, they usually dry crystal clear with an amber color. This fact, along with the structure (a canal surrounded by epithelial cells) of the secretive tissue, suggests that they are resin canals. A **sclerenchyma ring**, usually seven to ten cells wide, encloses the vascular cylinders. This layer occurs in the inner zone of the cortex, and, in many species, consists of pure fibers (Fig. 6c, 7a, 9b) or fibers and brachysclereids (Fig. 9a). The steles are ectophloic **siphonosteles**. The outer layers of cells of the **pith** consist of collenchyma in many species (Fig. 6c, 7a).

Serjania section Platycoccus posses all these characters except for resin canals in the cortex.

Wood Anatomy

The wood anatomy of the Paullinieae, particularly of Serjania, has attracted the attention of many workers because of the anomalies present in many of its species. Gaudichaud (1841) was the first to describe a type of anomaly unique to the stems of Serjania. In this type, the stem is made up of five to seven radially disposed vascular cylinders and there is no central vascular cylinder. Nägeli (1868), studied the anatomy of various species of Serjania and Paullinia with respect to the ontogenic development of the anomalous structures. Radlkofer (1874, 1876, 1886, 1931) investigated these anomalies with regard to their systematic value and used them in the construction of keys and as supplementary characters in sectional and specific delimitation. In 1884, Haberlandt discussed some of the anomalies present in *Serjania* in relation to their adaptive significance to the climbing habit. Schenck (1893), in his classical work on the biology and anatomy of lianas, discussed the different wood anomalies present in Sapindaceae. Pfeiffer (1926) presented a key for the species of *Serjania* based on wood anatomy. He also classified the anomalies present in the stems of the Paullinieae under seven different types, six of them occurring in *Serjania*. Meijer (1932) studied the stem and leaf anatomy of *S. curassavica*. Solereder (1908) and Metcalfe and Chalk (1957, 1979) presented general peculiarities of the wood anatomy of *Serjania*. Johnson and Truscott (1956) studied the path of the bundles in *S. mexicana* and in *S. subdentata*. Cutter (1971), in her discussion of anomalous secondary growth, mentioned some of the peculiarities occurring in *Serjania*.

Macroscopic Characteristics.

In cross section, the stems of different species of *Serjania*, present one to many vascular cylinders separated by ground tissue. This is a feature easily observed without the aid of a microscope or a hand lens. For this reason, the anomalous patterns shown by the species of *Serjania* are considered macroscopic characters. They have been classified by Radlkofer (1875, 1876, 1886, 1931) under the terms **simple, compound, divided, corded, and cleft xylem masses.** This character is very important in the description of species because of its diagnostic value.

A simple vascular cylinder (undivided and cylindric xylem) is the normal condition present in many families of dicotyledons as well as in most Sapindaceae. This condition is present in 96 species of *Serjania* (ca. 42% of the species), in 90% of *Paullinia*, and in all species of *Cardiospermum* and *Urvillea*. The stems may be terete (Fig. 3d) or lobed (Fig. 3e) due to the unequal production of secondary xylem. Another type of anomaly present in some species of *Serjania* and *Thinouia* with a single vascular cylinder is the production of vascular bundles within the cortex or bark. This is the **corded** type of Radlkofer (Figs. 3f). These vascular bundles are produced after a few years of normal growth and are stated (Radlkofer, 1876; Solereder, 1908; Metcalfe & Chalk, 1957, 1979) to be connected to each other, but not with the central vascular cylinder. Another anomaly found in some species of *Serjania* with a single vascular cylinder is what Pfeiffer (1926) termed a **parted xylem mass** (Fig. 4a & 4f). The xylem becomes fractured into various complexes or islands which are the consequence of the delayed development of parenchymatous tissue within the xylem (Pfeiffer, 1926). The **cleft xylem**, described by Gaudichaud (1841) and Radlkofer (1876) for *Urvillea ulmacea* H.B.K. and *Serjania* *piscatoria*, is also produced within the secondary body. A cross section of the mature stem shows the xylem radially fractured in three parts. This anomaly results from the unequal production of xylem in three areas of the stem. The stem at first becomes lobed, but later breaks through the areas where less xylem is produced. Carlquist (1988) considered this anomaly as equivalent to the divided xylem mass, however they differ ontogenetically, therefore, they are different and not equivalent phylogenetically.

The condition in which numerous vascular cylinders are present is known as the **multistelar stem** (**compound xylem** of Radlkofer). In this type of anomaly, a central vascular cylinder is surrounded by three, five or more vascular cylinders (**peripheral cylinders**) that are separated by ground tissue. Nägeli (1868) studied the ontogenic development of this anomaly in *Serjania cuspidata* (= *Urvillea ferruginea*), *S. caracasana*, and *Paullinia alata* G. Don. Most recently, Obaton (1960) and Van der Walt et al. (1973) studied the ontogeny of this anomaly in *Paullinia pinnata* L. and concluded, as did Nägeli, that this anomaly originates within the primary body of the plant. In *S. cuspidata* and *P. pinnata*, three of the primary vascular bundles (occupying three different angles of the stem) differentiate into three vascular cylinders. These are independent from the central bundles, which will give rise to a central vascular cylinder by the activity of an interfascicular cambium. The peripheral cylinders are produced by anomalous differentiation of

Figure 3. Cross sections of stems of Serjania showing multistelar stems (A-C), simple (D-E), and corded (F) vascularization. A. With three peripheral cylinders, Serjania nutans (Acevedo & Vargas 1744). B. With five peripheral cylinders S. glabrata (Baker 6284). C. With three peripheral cylinders, S. paucidentata (Wendt 4093). D. Simple terete vascular cylinder, S. schunkei (Schunke Vigo 12492). E. Simple, lobed vascular cylinder, S. mexicana (Acevedo 509). F. Corded, vascular cylinder, S. meridionalis (Acevedo et al. 1467).

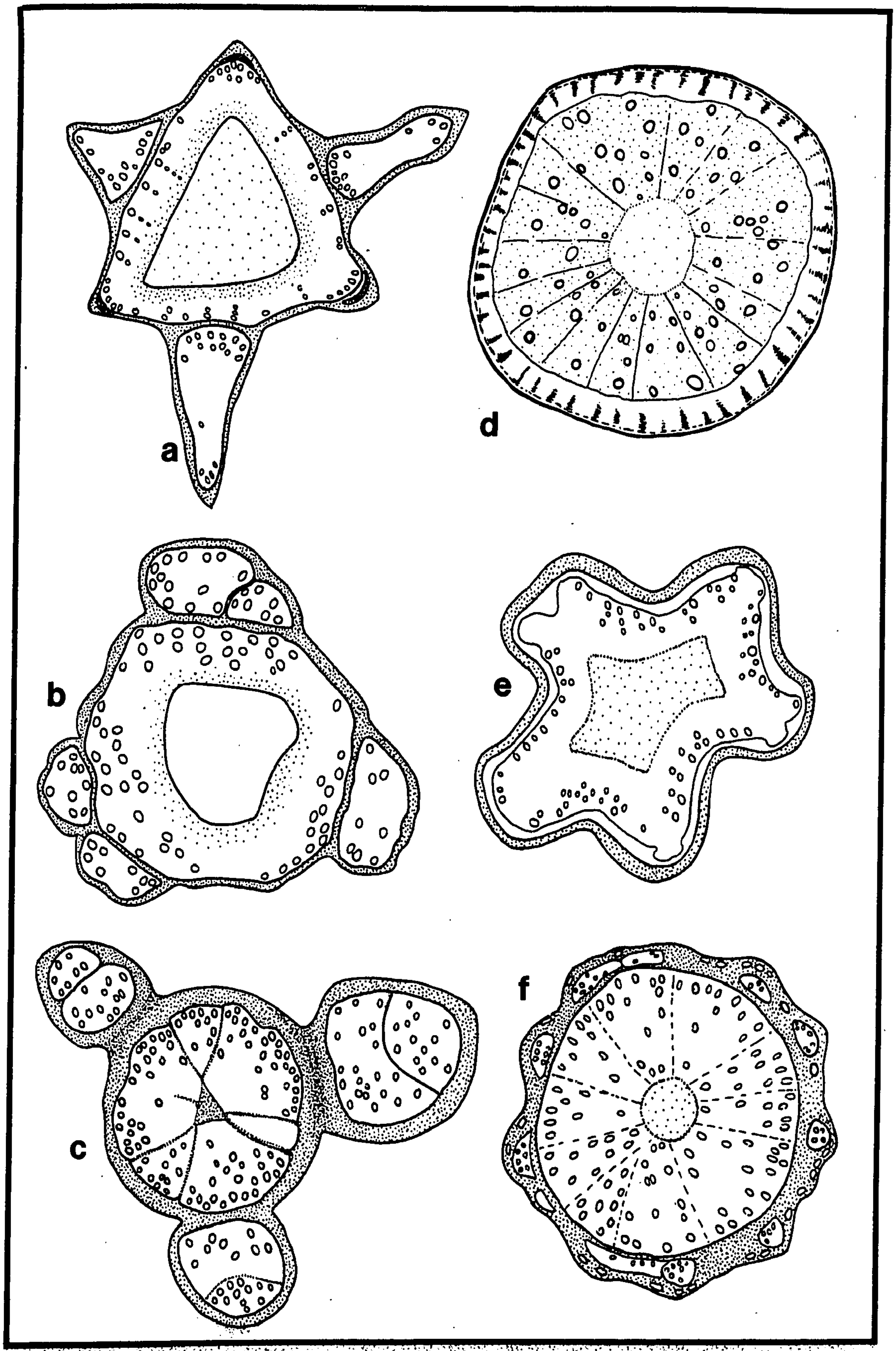
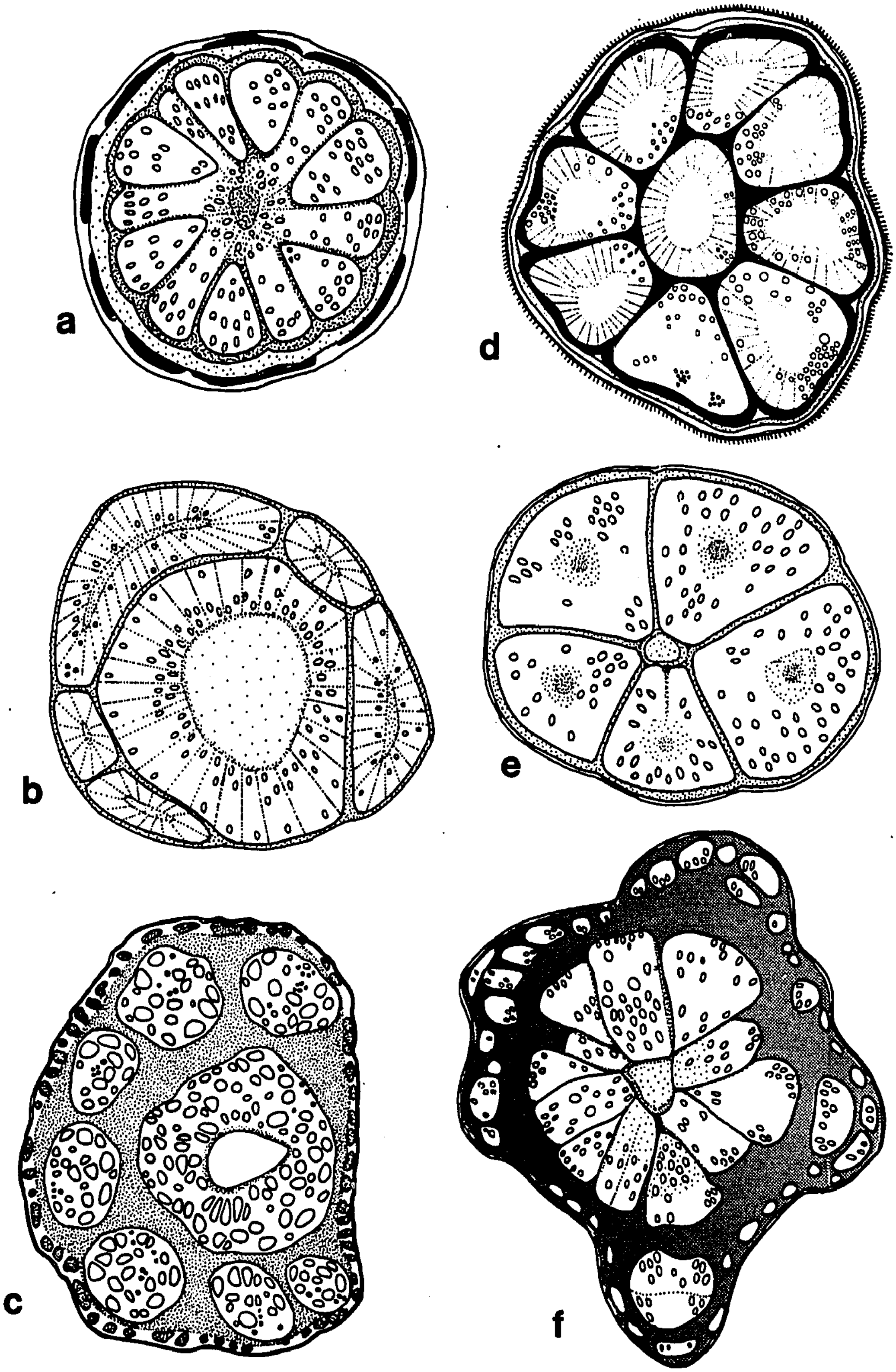

a
d
b
e
c
f

Figure 4. Cross sections of stems of Serjania showing parted (A-F), multistelar (B-D), and divided (E) vascularization. A. Parted vascular cylinder, Serjania laxiflora (Acevedo et al. 1484). B. Multistelar stem with five flattened peripheral cylinders, S. perulacea (Acevedo et al. 1482). C. Multistelar stem with seven peripheral cylinders, S. unidentata (Acevedo et al. 1570). D. Multistelar stem with eight peripheral cylinders, S. fluminensis (Acevedo & Farney 1424). E. Divided vascular cylinder, S. paradoxa (Acevedo et al. 1502). F. Parted vascular cylinder, S. grandifolia (Acevedo & Daly 1619).


a
d
b
e
c
f

the intrafascicular cambium in these peripheral bundles. Each cylinder continues to grow in a normal way, producing xylem toward the inside and phloem toward the outside. The peripheral vascular cylinders are usually three (Fig. 3a & 3c) or five (Fig. 3b) and are arranged in a triangular or, less frequently, in a pentagonal way. The presence of three peripheral cylinders occurs in 79 species of Serjania (34 % of the species), in a few species of the closely related Paullinia (ca. 10 % of the species), and in all three species of Houssayanthus. The presence of five peripheral vascular cylinders occurs in 21 species of Serjania (ca 9 % of the species). Of these, 14 species show a variable number of peripherals, ranging from three to five. This character occurs only in 2-3 % of the species of Paullinia. The presence of eight to ten peripheral vascular cylinders, arranged in a circle around the central cylinder is unique to Serjania (Fig. 4c & 4d), occurring in 25 species (10 % of the species). The shape of the peripheral vascular cylinders varies from species to species. They are usually terete, but they may be also cuneiform, or compressed radially or peripherally (Figs. 3a-c, 4b-d).

This type of anomalous growth (peripheral vascular cylinders around a central cylinder) was regarded as unique, with the doubtful exception of its occurrence in the Fabaceae, to the Paullinieae by Metcalfe & Chalk (1957). In 1979, Metcalfe & Chalk, quoting Leandri (1931), also consider this anomaly to occur in the rhizomes of Gnidia (Thymeliaceae). However this is a different kind of anomaly, consisting of concentric additions of xylem and phloem.

Six species of Serjania present a vascular cylinder radially divided into four or five parts by parenchymatous tissue (divided xylem of Radlkofer). In this type, each part possesses a central medulla (Fig. 4e). This feature is unique to Serjania, but is present only in the "S. paradoxa complex" of section Eurycoccus.

The presence of one versus many vascular cylinders, as well as the number of cylinders and their shape, are good taxonomic characters. It has been argued by Radlkofer (1869, 1886) that, in order to obtain comparable results, a cross section should be made at the middle of the internode. This is due to the fact that the peripheral cylinders are interconnected with the central cylinder in a very complex way at the nodes (Johnson & Truscott, 1956). A certain degree of variation is recorded in species having four or five peripheral vascular cylinders. In the former, all species vary, and produce also three peripheral cylinders. In the latter, two-thirds of the species also present three peripheral cylinders. Two of the most variable species with respect to this character are S. caracasana (Fig. 5a-b), and S. polyphylla (Fig. 5c-e) both having from four to ten peripheral vascular cylinders.

The presence of wide vessels and rays as well as a hollow medulla are some of the features which can easily be seen without the aid of a microscope.

The species of Serjania section Platycoccus have either stems with a simple vascular cylinder, or with a central and three (five to seven in S. hatschbachii) peripheral vascular cylinders. They also have wide vessels which are easily observed with the naked eye.

Anomalous growth has been considered an adaptation to the climbing habit because it increases the mechanical flexibility of stems (Haberlandt, 1884; Schenck, 1893). In the Paullinieae, the anomalous structures present wide areas of parenchymatous tissue between the xylem, conferring flexibility to the stems, which in turn prevents their breakage when they are twisted or bent. The rope-like construction of stems in some species of Paullinieae may confer strength for withstanding the tensile forces resulting from the continuous movement of their supports (branches and trunks of trees). The presence of phloem between vascular cylinders in the anomalous Paullinieae, may constitute a reservoir tissue, from which regeneration can take place when the stems (often subject to damage from friction with supporting trees) are injured (Dobbins & Fisher, 1986).

Microscopic characteristics.

The wood in Serjania is **diffuse-porous**, and the vessels occur in two modes, wide or narrow, without intermediates (Fig. 6c & 6d, Table VII). This feature has been referred to by Carlquist (1985a) as **vessel dimorphism**. The wide vessels allow a much higher conductivity rate and the narrow ones carry out mechanical as well as conductivity functions. In cross section, the vessels are rounded, elliptic or slightly angular in outline, and occur solitary

Figure 5. Cross sections of stems of Serjania showing intraspecific variation of anomalous growth pattern. A-B. Serjania caracasana (Pereira et al. 4092). C-E. S. polyphylla (Zanoni et al. 19739).

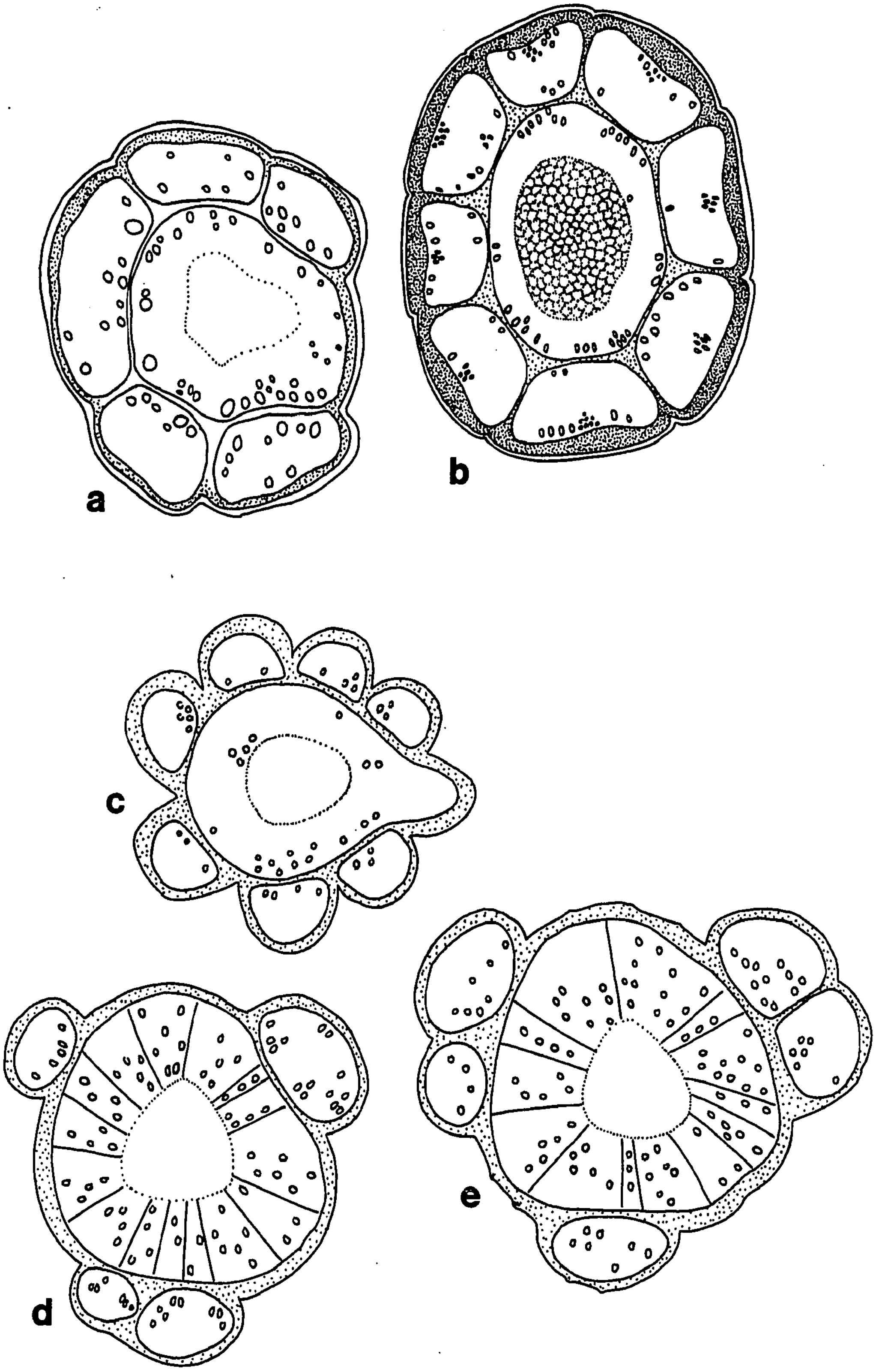

a
b
c
d
e

Figure 6. Wood anatomy of Serjania leptocarpa (Breteler 3495). A. Radial section showing perpendicular endings in wide vessel element, overlapping ending in narrow vessel elements, and alternate pitting. B. Tangential section showing uniseriate rays containing prismatic crystals. C. Cross section showing cortical fibers (1), vessel dimorphism (white arrows), collenchyma at outer region of medulla (black arrow), and solitary and aggregated vessels. D. Detail showing vessel dimorphism.

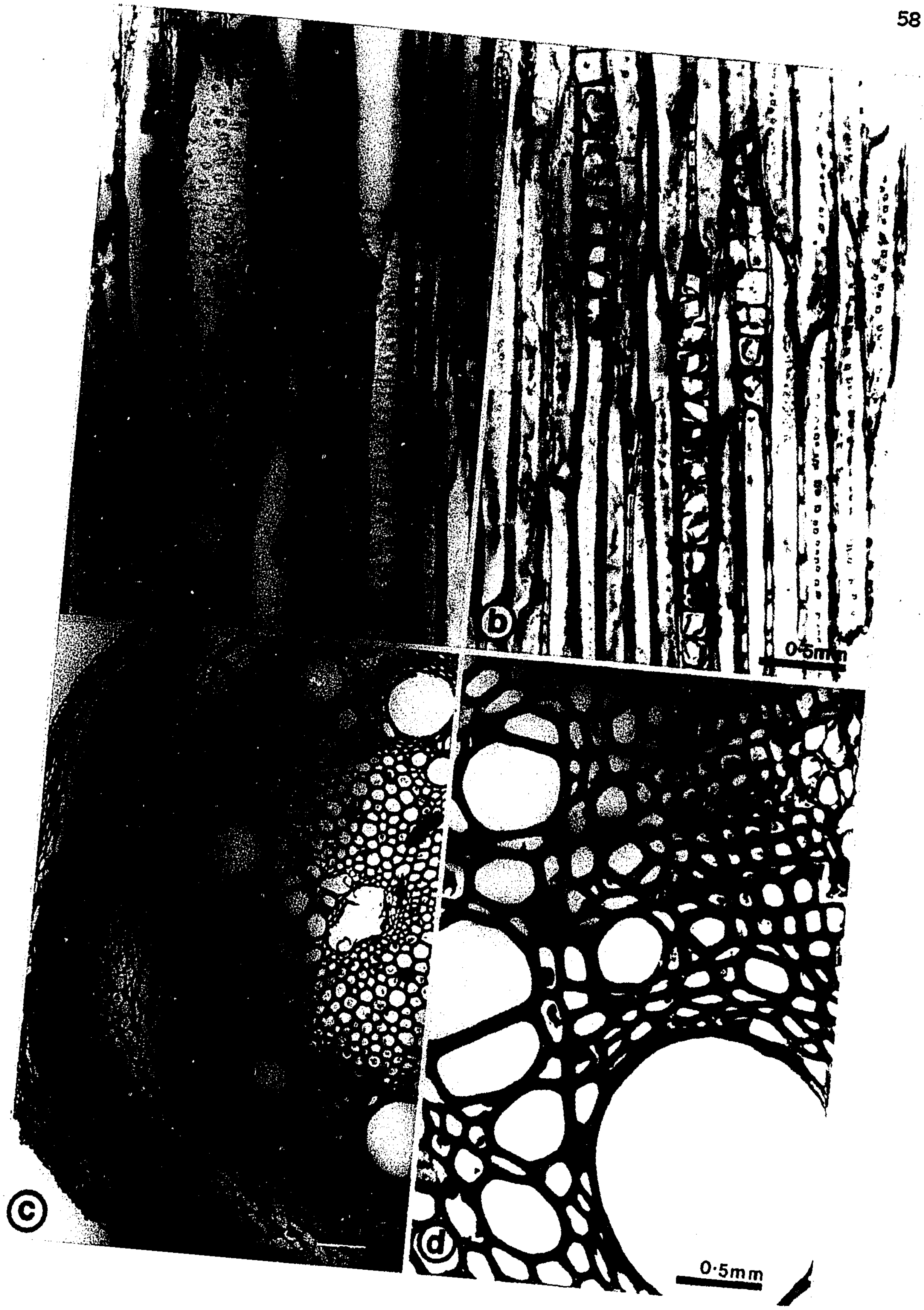

b
0·5mm
c
d
0·5mm

TABLE VII

Wood characteristics of selected species of _Serjania_.

Species	Pore diam.	vessel length	perfor.	inter-vas pitt.	rays
communis	0.7-11.7 um	6.5-37.7 um	simple	alternate	
dumicola	0.7-16.5 um	8.5-71.5 um	simple	alternate	uni/multi
polyphylla	1.0-28.6 um	7.8-35.7 um	simple	alternate	uni/multi
ampelopsis	1.2-13.0 um	9.7-45.5 um	simple	alternate	uni

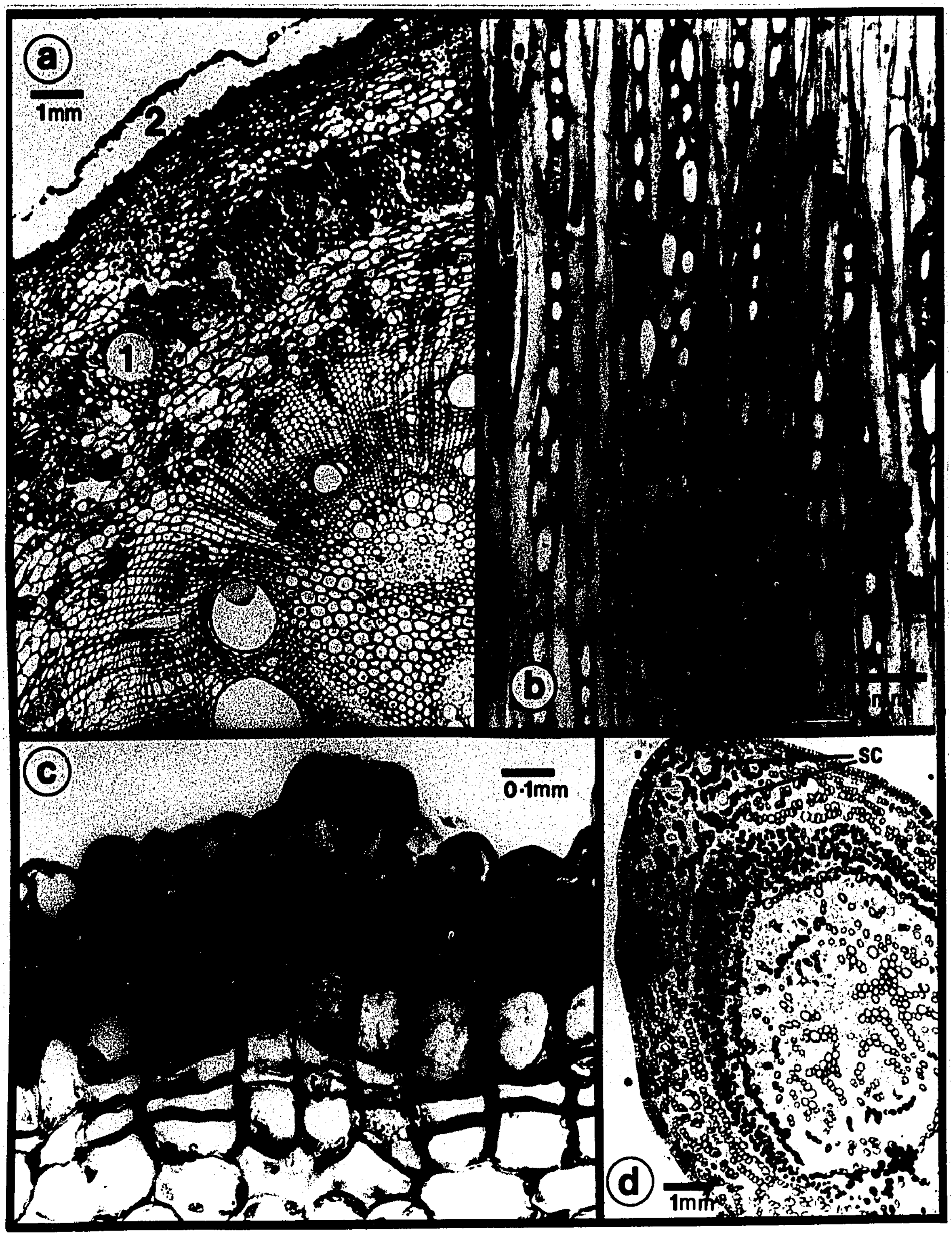
or in groups (Fig. 6c-d, 7a). The perforation plates are simple. The large elements have perpendicular ends (Fig. 6a) and the small elements have oblique overlapping endwalls (Fig. 6a). Intervessel pitting is alternate in all species examined (Fig. 6a). Vasicentric tracheids may be widely distributed in the genus. Carlquist (1985b) has reported them for S. glabrata, and I have observed them in S. dumicola. The ray parenchyma is heterogeneous, uniseriate (Fig. 6b), or multiseriate (up to four cells wide, Fig. 7b), and contains prismatic crystals (Fig. 6b) or accumulates tannins (Fig. 7b). All these features are found in species of Serjania section Platycoccus.

Serjania has many features in common with climbing plants in other families. One of them is the presence of narrow stems with much higher water conductivity than stems in shrubs with equivalent diameters (Putts, 1984). The stems, which rely on external support, are specialized for water conduction at the expense of mechanical elements. The high conductivity in liana stems is the result of the unusually wide vessels present in their stems, but this makes them susceptible to air embolism. Carlquist (1985a & b) has suggested that the occurrence of libriform vessels and tracheids associated with the large vessels constitutes a subsidiary conducting system which operates in case of failure in conduction caused by embolism.

Bark

The phellogen consists of a dark layer of narrow cells, which develops from the hypoderm (Fig. 7c). The phellem is formed in

Figure 7. Anatomical features of Serjania. A. Cross section of Serjania unidentata stem, showing ring of cortical fibers disrupted by secondary growth (1), differentiation of fibers at outer layer of phloem (black arrows), and phellem (2) (Acevedo et al. 1570). B. Tangential section of S. polyphylla stem showing multiseriate rays and ray cells containing tannins (Acevedo 719). C. Cross section of S. dumicola stem showing insertion of phellogen at outer cortex and, epidermal cells with anticlinal wavy walls (Acevedo & Vargas 1759). D. Cross section of a peripheral stele in S. polyphylla showing high concentration of tannin idioblasts in cortex, secretory canals (sc), and inner zone of cortex not yet differentiated into fibers (Acevedo 719).


a
1mm
2
1
b
c
0·1mm
sc
d
1mm

small plates. The phelloderm contains many layers of densely staining parenchyma which, in some species, contains secretory canals. A fiber sheath is developed at the outer portion of the phloem all around the vascular cylinders (Fig. 7a). This layer, which becomes disrupted as a consequence of secondary growth, is continuously repaired by the sclerification of surrounding parenchyma (Fig. 7a). The development of the bark observed in some species of Serjania section Platycoccus corresponds with that described for species of other sections of the genus.

Indument

The indument of Serjania is made up of trichomes that are either glandular or non-glandular. The trichomes present in a particular species may be all of the same kind or a mixture of different types. It is not rare to find plants with glandular and non-glandular hairs on the same organ. Both glandular and non-glandular are unbranched and sometimes the basal cell is swollen and surrounded by a ring of epidermal cells (Fig. 12d, 13d). The non-glandular hairs are by far more common and are more diverse and larger than the glandular hairs. They are usually ferruginous or whitish. The different hairs can be classified into nine types as follows:

1) erect, bristle-like, unicellular (Fig. 8a);
2) erect, bristle-like, multicellular;
3) short, curved, unicellular (Fig. 8b & d);

Figure 8. Indument types in Serjania. A. Unbranched, erect, bristle-like, unicellular (stems, S. cuspidata Holway 1319). B. Unbranched, unicellular, short curly hairs (leaf surface S. sufferruginea Acevedo & Vargas 1726). C. Scale-like, appressed hairs (stem, S. insignis Killip 14324). D. Unicellular, short curly hairs (leaf surface, S. cardiospermoides Purpus 6063. E. Minute, curly, unicellular hairs with wooly appearance (stem, S. fuscifolia Gentry 51973). F. Appressed multicellular (stem, S. columbiana Gentry 34787a).

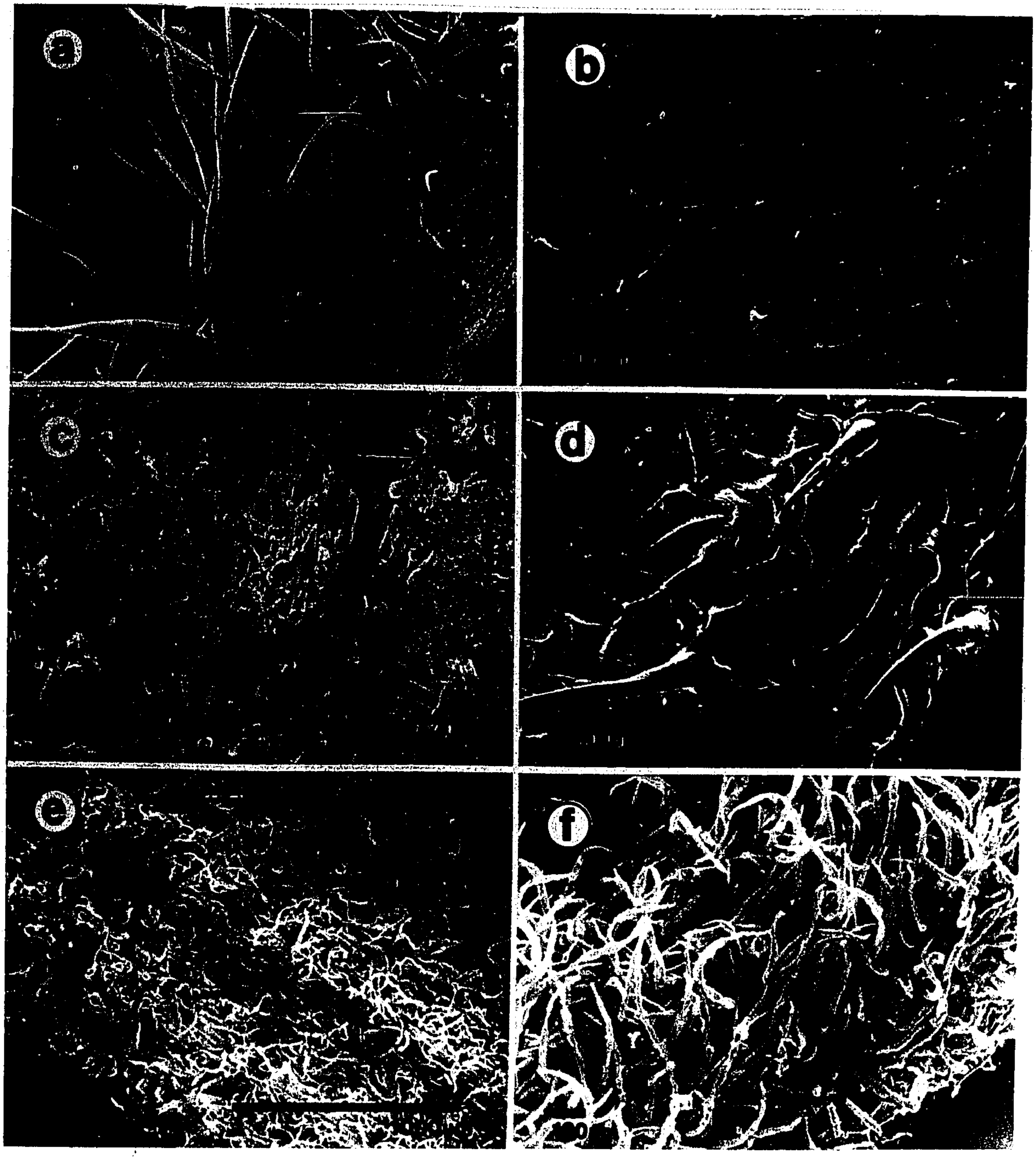
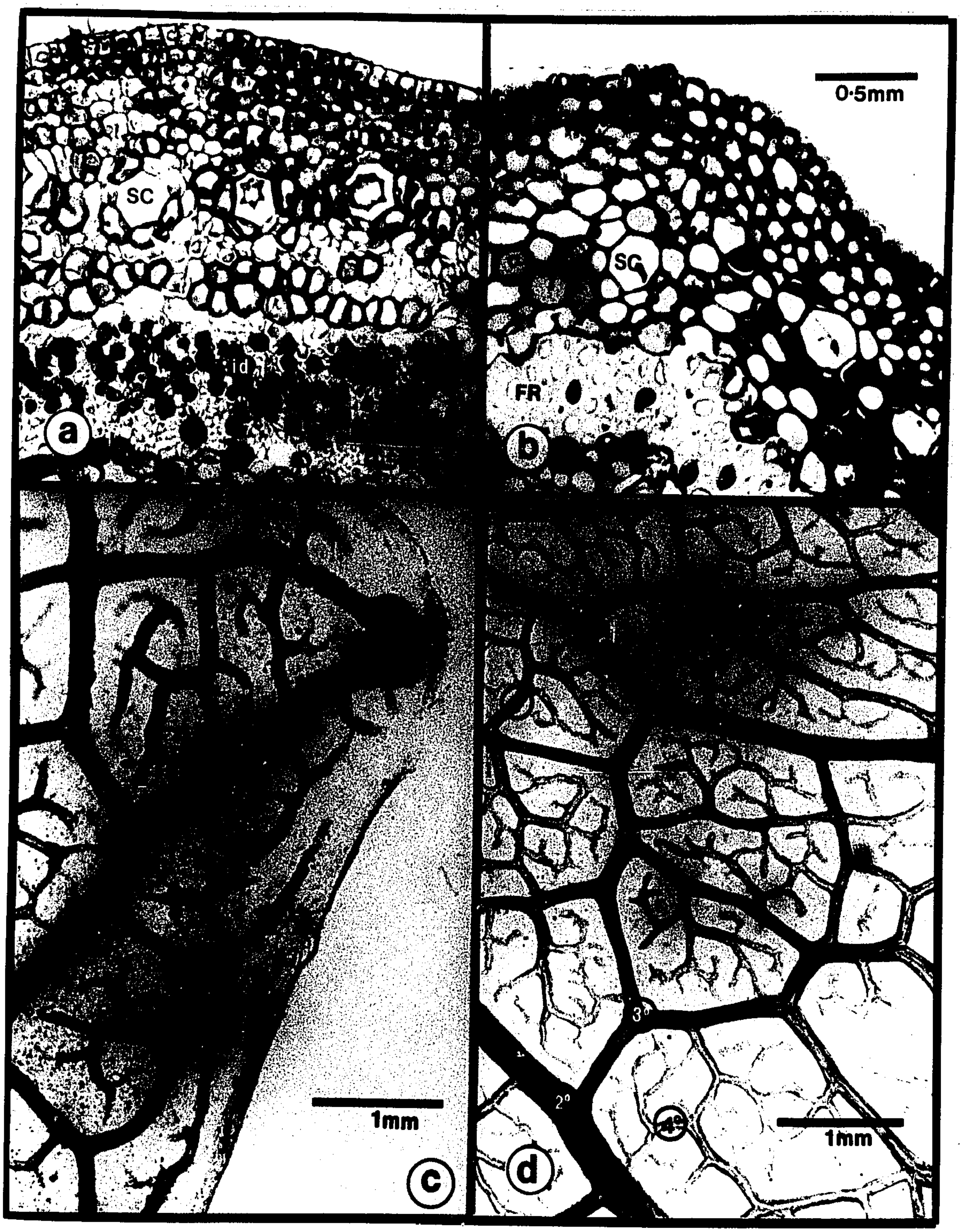

a
b
c
d
e
f
r
100

Figure 9. Stem and leaf features of *Serjania*. A. Cross section of the stem cortex of *S*. *polyphylla* in early stage of development. Tannin idioblasts (id) and resin ducts (sc) with epithelial cells are common (*Acevedo 719*). B. Cross section of the stem cortex of *S*. *polyphylla* in later stage of development, showing inner zone of cortex with a ring of fibers (fr), resin canal (sc), and less tannins in cortex (*Acevedo 719*). C. Glandular tooth of cleared leaflet of *S*. *unidentata* (*Acevedo et al. 1570*). D. Cleared leaflet of *S*. *laruotteana* showing different orders of venation, areoles, and free veinlets (*Acevedo & Badini 1518*).


a
SC
id
b
SC
FR
0·5mm
c
1mm
d
2°
3°
4°
1mm

4) short, curved, multicellular;

5) minute, scale-like, unicellular (Fig. 8c);

6) minute, curly, unicellular, with wooly appearance (Fig.8e);

7) appressed; multicellular (sericeous) (Fig. 8f);

8) glandular, globose, with four apical cells (Fig. 14a); and

9) glandular, elliptic, with one apical cell (Fig. 14b).

Stipules

The stipules of Serjania are usually deltoid or subulate, ca 5 mm long, and early deciduous. Only S. longistipula, S. hispida, and S. magnistipulata are known to have stipules longer than 1 cm. The large, foliaceous stipules of S. magnistipulata are unique in Serjania. The stipules of Serjania contrast with those of Paullinia which are usually larger than 1 cm long, and persistent and variable in shape. The species of section Platycoccus, as do the majority of most species of Serjania in other sections, possess small, deciduous stipules.

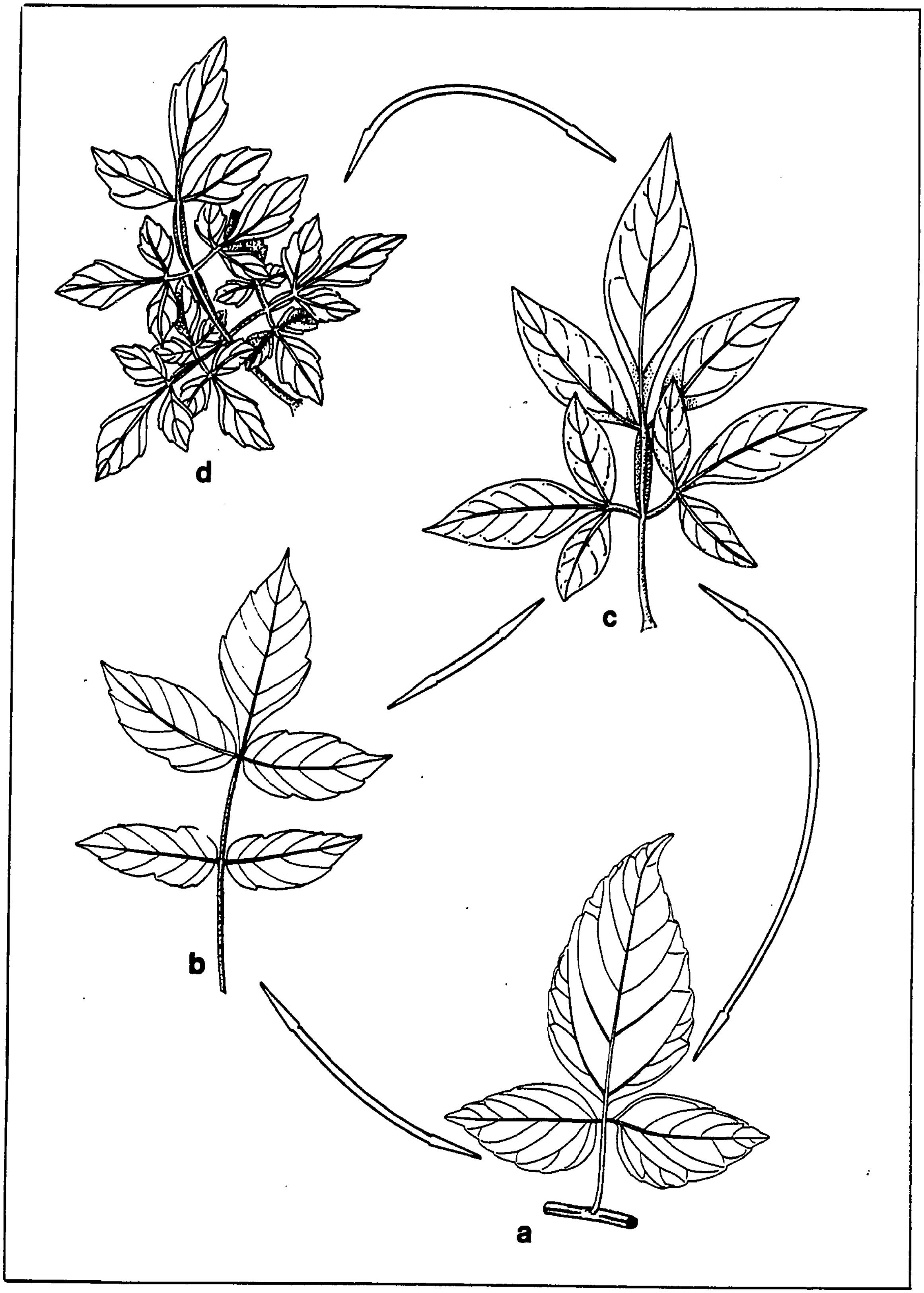
Leaves

The leaves of Serjania are alternate and pinnately compound with a terminal leaflet. The leaves are commonly ternately compound (Fig. 10a) or multiples of ternate, viz. biternate (Fig. 10c) or triternate (Fig. 10d). Five foliolate pinnately compound leaves (Fig. 10b) as well as leaves with intermediate forms (between biternate and triternate) are also found. Ternate leaves occur in all genera of Paullinieae. The occurrence of ternate leaves as an ontogenic pathway in species with more complex leaves (e.g., *Cardiospermum* and *Paullinia*) suggests that ternate leaves have been one of the steps in their leaf evolution. Ternate leaves are also very common in the sister tribe Thouinieae and occur in other genera of Sapindaceae. Therefore, it seems that ternate leaves are a basic type from which other types have been derived. Ternate leaves occur in 41 species (18%) of *Serjania*.

The 5-foliolate, pinnate leaf (Fig. 10b) can be derived from a ternate ancestor by the subdivision of the terminal leaflets into three. This condition is not very common in *Serjania*, occurring only in 21 (9%) of the species, however, it is very common in *Paullinia*.

The biternate (Fig. 10c) form is by far the most common leaf type in *Serjania*, occurring in 145 (63%) species. This condition can be derived from ternate leaves by the subdivision of all leaflets in three, or from 5-pinnately compound leaves by the subdivision of the two proximal leaflets in three. Other forms result from the subdivision of different leaflets. The triternate (Fig. 10d), occurs in eight species of *Serjania* and the 3-4-jugate, imparipinnate and bipinnate forms, occur in less than 10% of the species. The term decompound was utilized by Radlkofer to describe the last to forms mentioned, which are further compound than the ternate form. Most of the species in section *Platycoccus* have ternate or biternate leaves except for *S*. *squarrosa* which has decompound leaves.

Figure 10. Type of leaves in _Serjania_. A. Ternate (_S. schunkei_, _Schunke Vigo 12492)_. B. 5-pinnately compound (_S. magnistipulata_, _Santos et al. 3472_). C. Biternate (_S. gracilis_, _Acevedo & Badini 1516_). D. Triternate (_S. polyphylla_, _Acevedo & Chinea 2200_).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Leaf types are usually stable in species of Serjania; however, variation exists within species or even within individuals. The variation is usually associated with physiological changes brought about by flowering or with ecological variations (e.g., dry vs. wet habitats or sunny vs. shaded leaves).

Leaf Axes

The petioles and leaf rachis of Serjania are either winged, margined, or naked. They are terete and usually adaxially furrowed. The petiolules, when present, are swollen or may possess a decurrent blade base. Although these characters are usually stable and show little variation within a species, some species show considerable variation of wing width. All species in Serjania section Platycoccus have naked or narrow margined petioles and rachises, and possess petiolules.

Leaflets

Most species of Serjania have elliptic or ovate leaflet blades. However, a smaller number of species have obovate, lanceolate, linear, rhombic, or deltoid leaflets. The size of the leaflet varies from species to species and within individuals, ranging from one to 20 cm in length. The apices are usually acute or obtuse, less frequently acuminate, rounded, or mucronate. The base of the leaflet is usually decurrent or obtuse and leaf texture ranges from membranous to coriaceous. The species of Platycoccus are variable with respect to these characters.

The margins of the leaflets of Serjania display considerable variation, being entire, serrate, dentate, or sinuate. The serrations are either glandular (Fig. 9c) or non-glandular. In young leaves, I have observed ants collecting nectar accumulated at the tip of the glandular serrations. This suggests that nectar production might be part of a reward-protection interaction. Although no data exits to support this suggestion, it seems likely because of the aggressiveness shown by the ants, and the absence of damage in young leaves tissue frequented by ants.

The use of venation patterns in the systematics of the Paullinieae has played a major role only in Paullinia where conspicuous variation is found. Radlkofer (1931), who recognized reticulate, transverse, and clathrate types, incorporated them into his keys and species descriptions of Paullinia. In Serjania, and the other genera of Paullinieae, the use of venation has been neglected, perhaps because of the less conspicuous variation present. The venation patterns of Serjania, Paullinia, and Thinouia, as found in the state of Rio de Janeiro, has been studied by Valente et al. (1984a,b). In their survey, they found Serjania to have brochidodromus, craspedodromus, actinodromus, and craspedobroquidrodomus (mixed) veination patterns. In applying Hickey's (1979) terminology for leaf classification, mixed craspedodromus equals the craspedobroquidodromus of Valente et al. and their designation of S. cuspidata as actinodromus is better referred to as craspedodromus.

The types of venation found in Serjania can be classified into:

1) craspedodromus (Fig. 11b);
2) mixed craspedodromus (Fig. 11d);
3) semicraspedodromus (Fig. 11a);
4) cladodromus (Fig. 11e);
5) brochidodromus (Fig. 11c).

Of these, the first two are by far the most common in Serjania.

Variation of Hickey's types can be found in species which have leaves with both entire and serrate margins. This is the case of S. areolata whose entire leaflets are brochidodromus while the serrate ones are mixed craspedodromus.

Primary veins are usually moderate or stout, or less frequently weak, in thickness. They are unbranched and travel straight into the terminal leaflets whereas they are usually curved in the lateral leaflets. The secondary veins are alternate or opposite, uniformly curved, or straight and form a diverging angle of from 40° to 50° (rarely of 70°) from the primary vein. They also form a marginal loop angle of close to 90° (Fig. 12a). The tertiary vein angles between the secondary abmedial and exmedial are usually not discernible because of reticulation (Fig. 9d). Less often the AR, RR and the AA types of Hickey (1979) are found (Fig. 12c). Tertiary or higher order veins are dark in some species of Serjania (e.g., S. atrolineata, S. marginata, and S. pyramidata) and produce a punctate or punctate-linate design on the abaxial leaflet

Figure 11. Leaflet architecture in *Serjania*. A. Semicraspedodromus (*S*. *dumicola*, *Acevedo & Vargas 1759*). B. Craspedodromus (*S*. *cuspidata*, *Acevedo et al. 1458*). C. Brochidodromus (*S*. *hatschbachii*, *Hatschbach 2957*). D. Mixed craspedodromus (*S*. *communis*, *Acevedo et al. 1456*). E. Cladodromus (*S*. *acutidentata*, *Acevedo et al. 1503*).

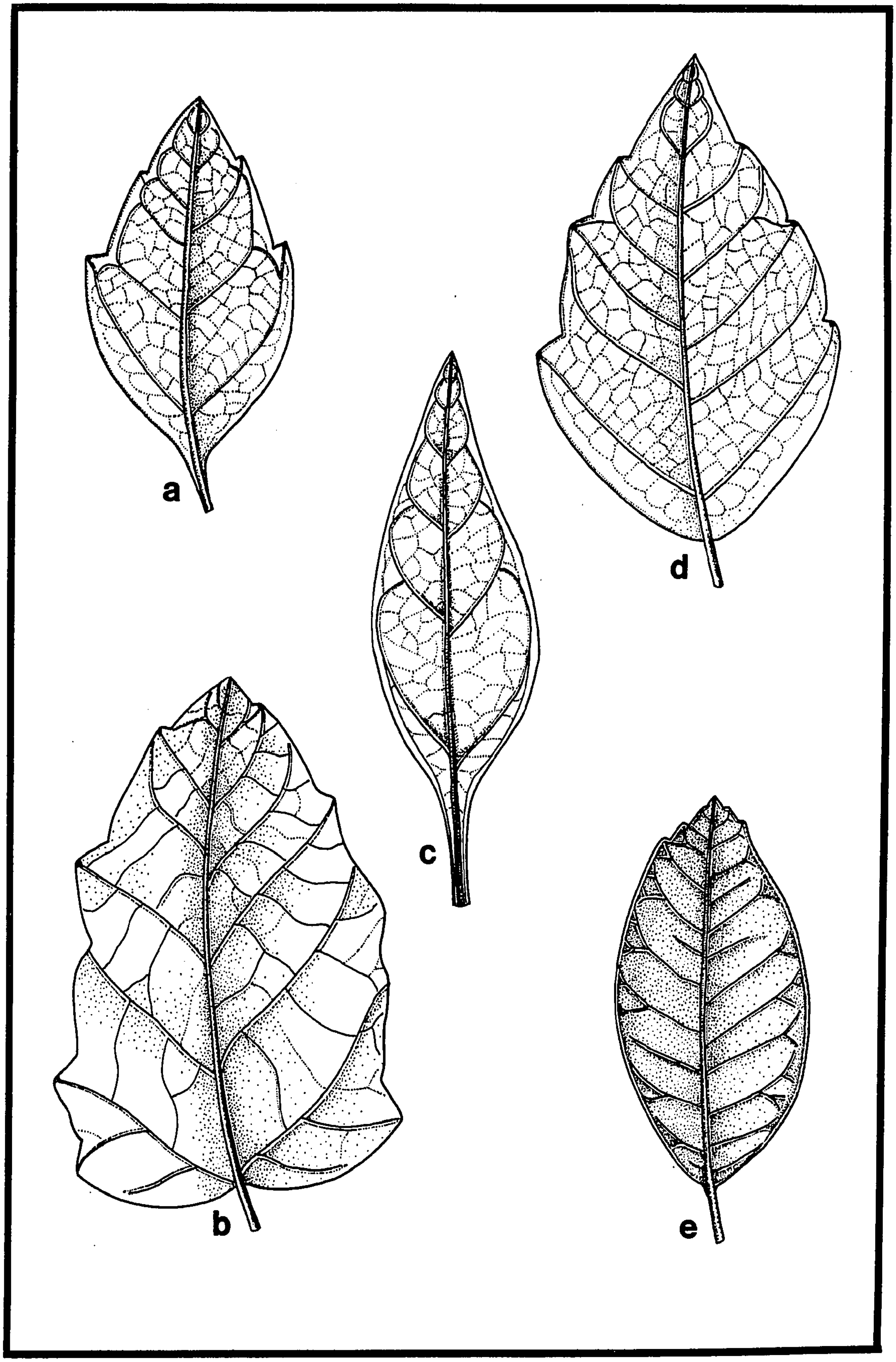
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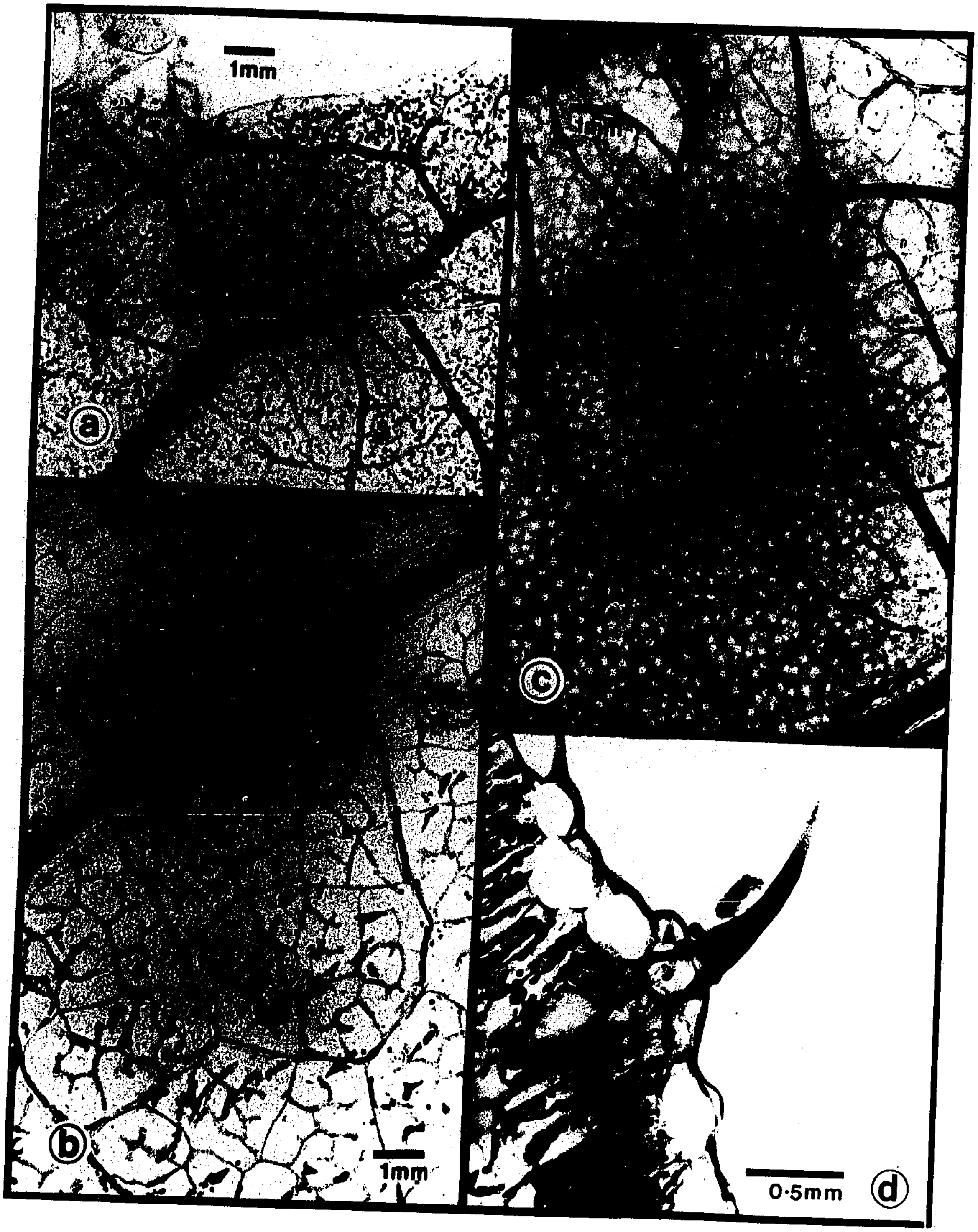
Figure 12. Leaflet features of Serjania. A. Cleared leaflet of S. inscripta showing marginal loop connection of secondary veins (black arrow) at 90° angle (Acevedo et al. 1590). B. Cleared leaflet of S. brachyptera showing small areoles and free veinlets (black arrow) (Lojnant 14995). C. Cleared leaflet of S. dibotrya showing tertiary veins of type AA and oil cells in mesophyll (Acevedo & Vargas 1748). D. Cross section of S. dumicola leaflet showing hair embedded in swollen base (Acevedo & Vargas 1759).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surface. The areoles are formed by quaternary veins, which contain free veinlets divided twice, three, or four times (Figs. 9d, 12b–c).

The stomatal types present in species of Serjania of the state of Rio de Janeiro have been studied by Valente et al. (1984b). They report two types, the anomocytic (Fig. 13b) and the anisocytic, both being equally common. In addition, I have found the encyclocytic type in S. brachyptera (Fig. 13a). Stomata may occur on both surfaces of the blade, although they are more common on the abaxial surface. In S. brachyptera, stomata are found on the upper surface closely dispersed along the veins (Fig. 13c). Epidermal glands have been found in S. confertiflora on the adaxial surface of the leaflet (Fig. 13d).

Hairs found on leaves are non-glandular (Fig. 12d) or glandular (Fig. 14a & b) and are similar to those found on stems. Basal cells of the hairs are sometimes surrounded by swollen epidermal cells (Fig. 12d, 13d). Hair domatia are found at the secondary vein axils of many species.

As viewed in cross section, the cuticle of a Serjania leaflet is thin. The epidermis is not sclerified, and contains elliptic (smaller) and bulliform cells, which sometimes have wavy anticlinal cell walls (Fig. 14d). The bifacial mesophyll has densely packed uniseriate or biseriate (Meijer, 1932) palisade tissue which is sometimes interrupted by isodiametric or bottle-shaped mucilaginous idioblasts (3.5–4.4 um tall) that are also in contact with the

Figure 13. Epidermal features in Serjania. A. Stomata, encyclocytic type (S. brachyptera, Lojnant 14995). B. Stomata, anomocytic type (S. confertiflora, Acevedo & Vargas 1730). C. Stomata distributed along vein on adaxial surface (S. brachyptera, Lojnant 14995). D. Remaining basal cell of severed glandular hair in S. confertiflora (Acevedo et al. 1451).

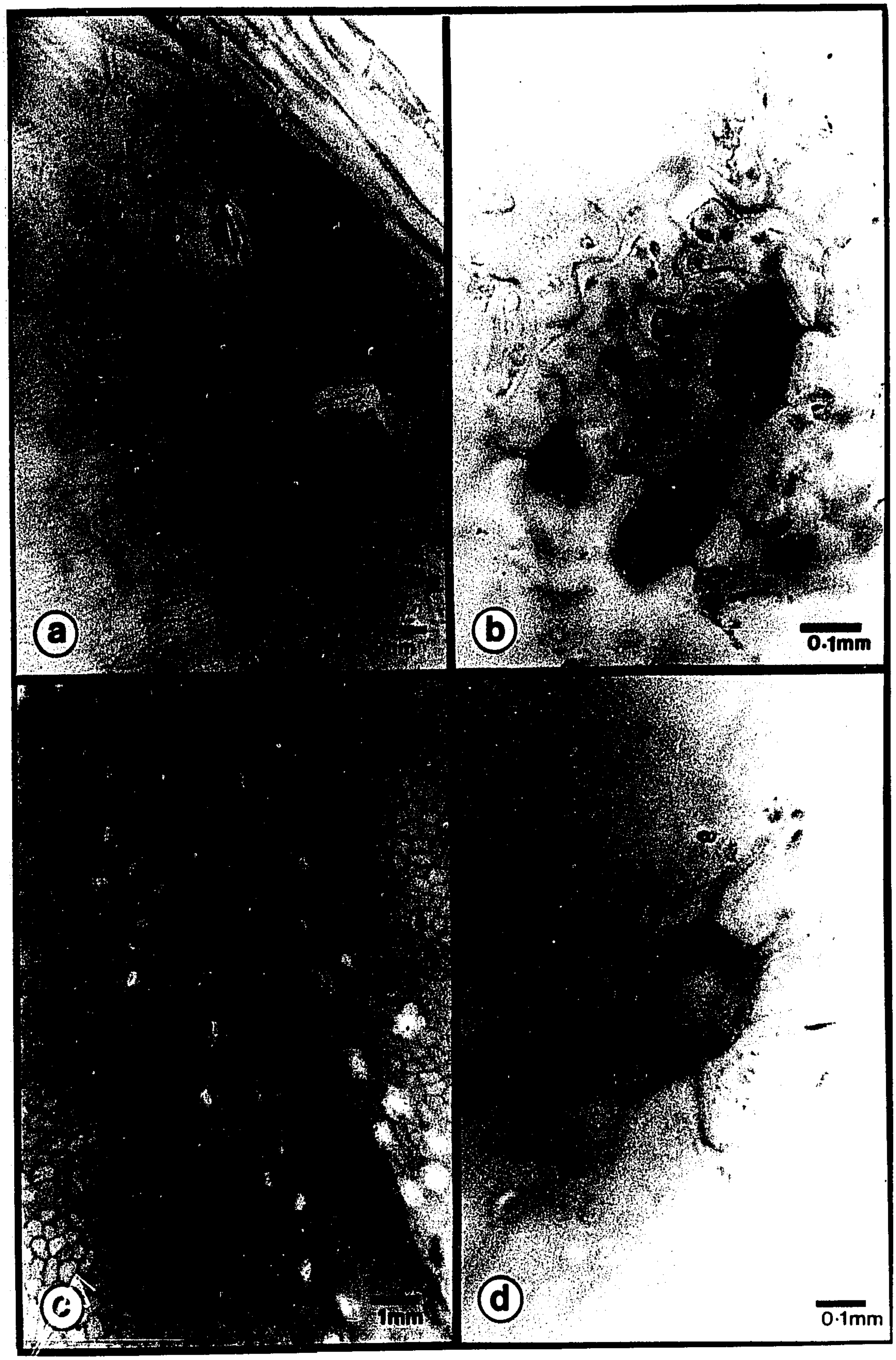
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Figure 14. Leaflet features of Serjania. A. Glandular, spherical hair on leaflet surface of S. confertiflora (Acevedo et al. 1730). B. Glandular, elliptical hair on leaflet surface of S. cuspidata (Acevedo et al. 1458). C. Cleared leaflet of S. dibotrya showing oil cells in mesophyll (Acevedo & Vargas 1748). D. Cross section of S. polyphylla leaflet showing wavy anticlinal walls of epidermis (aw), bulliform cell (bu), and mucilaginous cell (mu) (Acevedo 719).

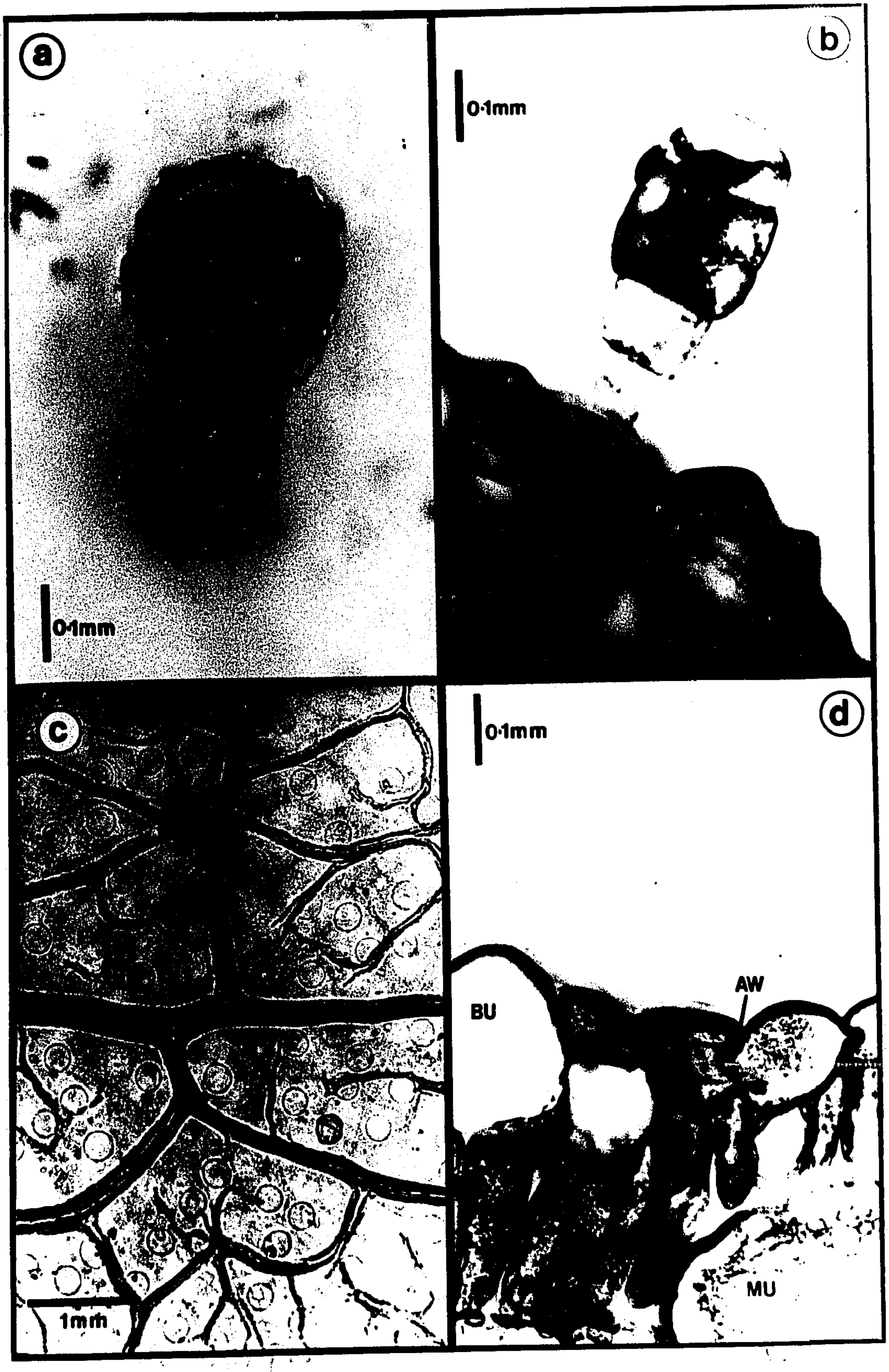
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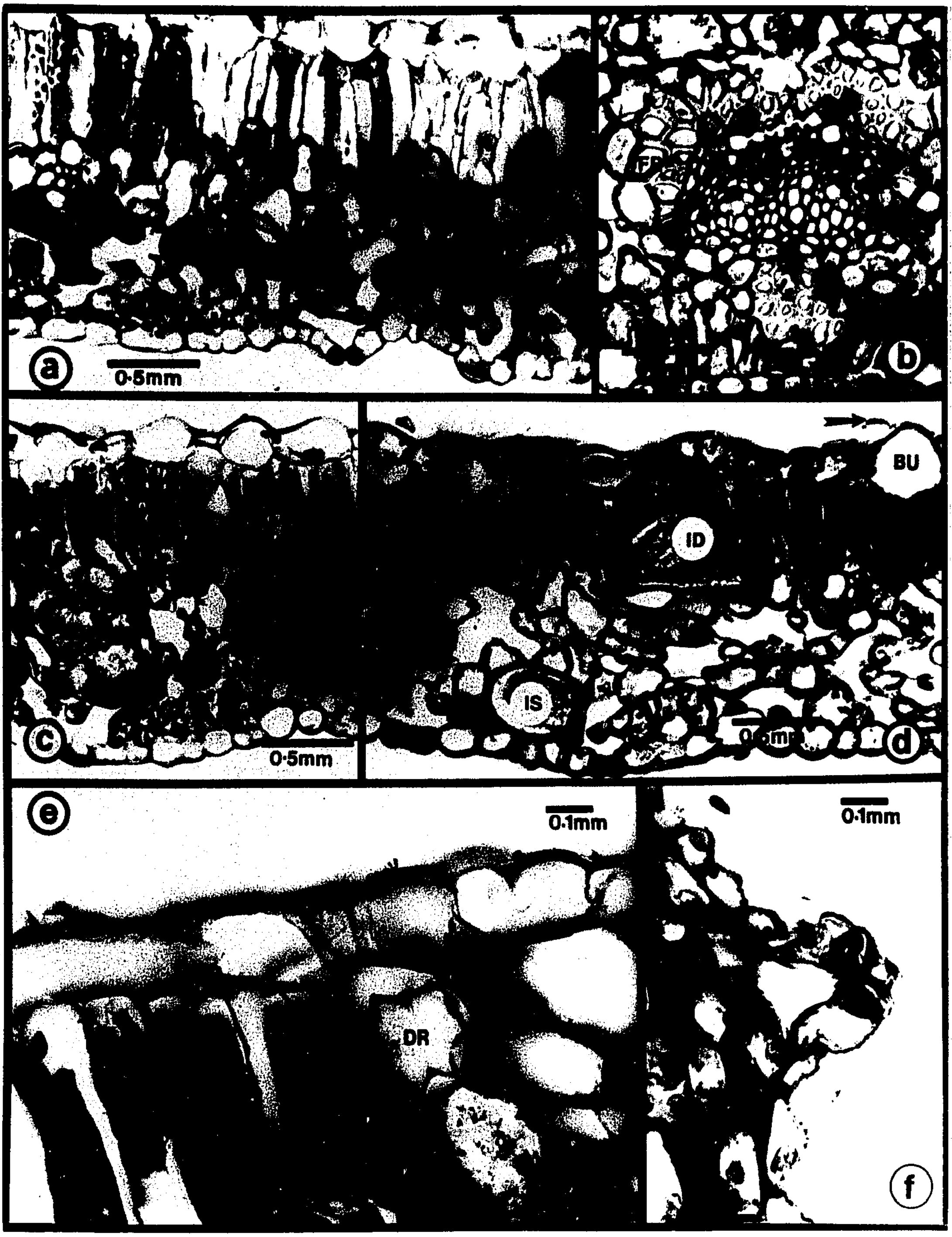
Figure 15. Cross sections of Serjania leaflets (A-E) and stem (F). A. S. dumicola showing laticifers (lt), (Acevedo & Vargas 1759). B. S. polyphylla showing fiber sheath around vascular bundles (fr) (Acevedo 719). C. S. dumicola showing laticifers around vascular bundles (Acevedo & Vargas 1759). D. S. polyphylla showing bottle-shape mucilaginous idioblast in palisade (id), isodiametric mucilaginous idioblast in spongy tissue (is), bulliform epidermal cell (bu), and mucilaginous secretion (arrow). E. S. polyphylla showing druse (dr). F. Cross section of S. communis stem, showing stomata. (Acevedo 1496)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spongy mesophyll (Fig. 15d). Where the mucilaginous cells contact the epidermal cells there is a visible cloudy substance or mucilaginous secretion over the epidermis. The mesophyll parenchyma sometimes contains druses (Fig. 15e). The spongy mesophyll is as thick or twice as thick as the palisade. It is loose or compact andsometimes contains laticifer cells (Fig. 15a), oil cells (Fig. 12c, 14c) and druses (Fig. 15e). The contents of the secretive cells is not known, however, they may contain saponins because these compounds have been reported as abundant in the leaf and stem tissue of species of Serjania (Hegnaver, 1963). The vascular bundles are normally associated with a cluster of fibers on both surfaces (Fig. 15b). Laticifers are associated with the vascular bundles in S. dumicola (Fig. 15c). The lower epidermis is made up of uniseriate, isodiametric parenchyma cells (Fig. 15c-d).

Inflorescences

The terminology developed by Briggs and Jonhson (1979) for the Myrtaceae is used in the following description. The terms blastotelic and anthotelic refer to axes of the inflorescence. A blastotelic inflorescence has indeterminate growth, which either grows seasonally or ends in an aborted meristem. On the other hand, the anthotelic inflorescence has determinate growth with an axis that ends in a flower. The term thyrse refers to a blastotelic inflorescence whose secondary units (branches) are cincinni. A cincinnus is a cymose (anthotelic) inflorescence, whose flowers are produced toward the same side resulting in a scorpioid shape.

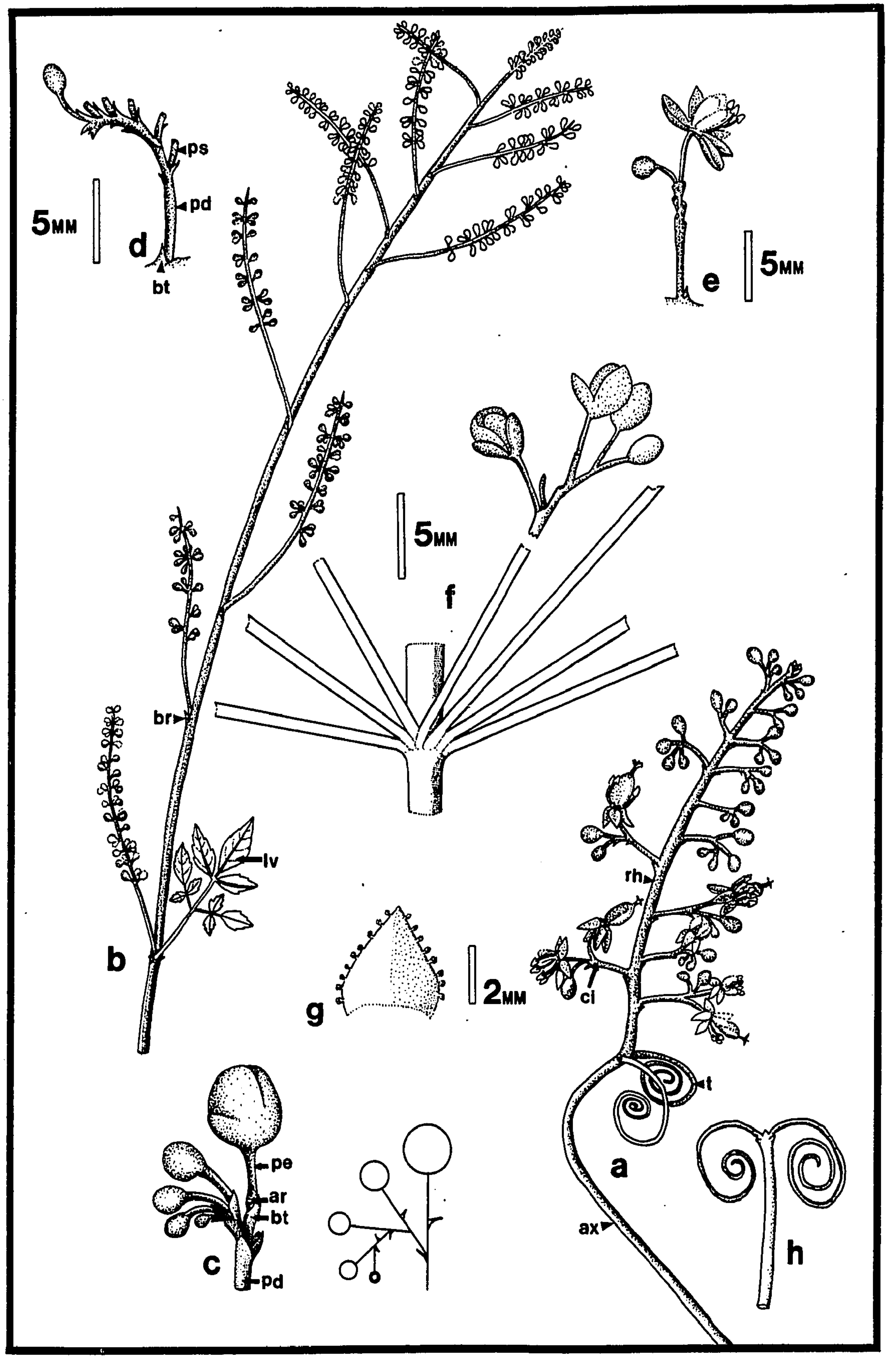
The inflorescences of Serjania are blastotelic, axillary thyrses with the main axis ending in an aborted meristem (Fig. 16a). They are produced sylleptically with the main stem. Cauliflory or ramiflory is not reported for Serjania, which contrasts with Paullinia in which caulifloroous or fasciculate inflorescences occur.

Short internodes are produced at the end of the branches, which results in the aggregation of thyrses to form a thyrsoid inflorescence. This thyrsoid inflorescence ends in a thyrse unit and shows a transition from regular leaves to bracts (Fig. 16b).

Within each thyrse, two oppositely coiled tendrils (homologous to secondary branches) are precociously developed from the prophyll's axillary buds. In young plants or branches, the first inflorescences produced abort the apex after the tendrils are produced. The resulting structure is an axillary short branch with two tendrils at its distal end and an abortive apex (Fig. 16h). In older plants, the main apical meristem of a thyrse is not aborted, instead it develops an axis (beyond the tendrils) which carries secondary anthotelic branches commonly known as cincinni (Fig. 16a, 16c-e). The cincinni may be alternate (Fig. 16a), opposite or whorled (Fig. 16f).

A distinction is made here for the areas of the inflorescence axis below and above the tendrils. The area below is called the inflorescence axis (Fig. 16a) and the area above is called the

Figure 16. Inflorescences of Serjania. A. Thyrse with tendrils (t), lateral cincinni (ci), axis (ax), and rachis (rh) (S. caracasana, Pohl 685). B. Frondobracteate, thyrsoid, terminal inflorescence showing leaf (lv) and bracts (br) (S. clematidea, H.H. Smith 1272). C. Cincinnus with secondary bracteole (bt), pedicel (pe), peduncle (pd), and articulation (ar). D. Cincinnus with remaining long pedicel bases (ps), peduncle (pd), and primary bracteole (bt) (S. equestris, Harris 6039). E. Cincinnus without pedicel bases (S. insignis, Huashikat 1854). F. Rachis with whorled cincinni (S. sufferruginea, Acevedo & Vargas 1726) G. Secondary bracteole with marginal glands (S. didymadenia, Rusby 517). H. Axillary branch carrying only tendrils (aborted inflorescence meristem).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rachis (Fig. 16a). The axis is voluble in most species of Platycoccus. The stipe of the cincinnus is called the peduncle (Fig. 16c & d). Bracts (at the base of thyrses), primary bracteoles (at the base of peduncles), and secondary bracteoles (at the base of pedicels) are usually very similar, having little taxonomic importance. However, in some species they are very distinctive because of their glandular margins (Fig. 16g).

The inflorescences are presented either in upward (Fig. 19b), horizontal (Fig. 19c & d), or pendant (Fig. 19a) positions. Inflorescences in the majority of Platycoccus species are pendant.

Flowers

Radlkofer (1931) considered the flowers of Serjania "hermaphrodites" (structurally perfect) which were either physiologically female or male. Cruz and Melhen (1984) reported the occurrence of hermaphroditic flowers in Serjania inflorescences without discussing their distribution within the species or individuals. After examining numerous herbarium specimens, I conclude that Serjania is **monoecious**, with functionally male and female flowers occurring in the same inflorescence. The female flower resembles a perfect flower with anthers that do not dehisce (Fig. 17a) and the male flower possesses a reduced pistil (Fig. 17b). In S. grandifolia, herbarium specimens of the male and female flowers have slightly different petal coloration. In living material, the anthers of male and female flowers are differently colored.

Serjania flowers are zygomorphic (Fig. 19c & e). The petals have a scale adnate to their adaxial basal surface (Fig. 20.2a-f). The scales are appressed against the anthers in a way that seems to restrict access to the nectary glands (Fig. 20.1c). The flowers of Serjania show some variation in numbers of parts (viz. sepals), as well as in size, indument, structure, and color. They are never larger than 1 cm, and most commonly their size ranges between 4 and 6 mm. Commonly, the petals, scales, and disk glands present considerable variation in shape and size.

The flowers are of limited value in defining the genus, especially from Paullinia whose floral morphology is very similar. However, the flowers of Cardiospermum are easily distinguished from those of Serjania by the presence of reduced outer sepals and by the reduction of the disk glands to two. The flowers of Serjania have been of little use in the infrageneric classification but detailed observations are now providing new insights into their systematic value. Some of the variations include the presence of anther appendages and the presence of basifixed vs. dorsifixed anthers.

Pedicels

The pedicel is the internode(s) between the flower and the node of the axis (Fig. 16c). It is more or less elongated, with a bracteole (Fig. 16c) (homologous to a prophyll) inserted somewhere between the base and its middle. Above the bracteole, there is an articulation whose distance from the bracteole varies from species to species. (Fig. 16c) The segment between the articulation and the bracteole is noticeable in infructescences after the fruits have been dispersed (Fig. 16d).

Sepals

The number of sepals present in the calyx varies from four to five (Fig. 20.1a-b). Species with four sepals have a much wider third sepal (Fig. 20.1b) instead of a third and a fifth sepal (Fig. 20.1a). In other words, the presence of four sepals results from the connation of the third and fifth sepals into a wider one. Some species possess flowers with five sepals, in which the third and the fifth sepals are connate to different degrees. Aestivation of sepals in the flower bud is **quincuncial** (Fig. 20.4a) for those species with five sepals and **imbricate** for those with four sepals. The two outer sepals (Fig. 20.1a-b) are smaller than the inner ones and usually ovate. The inner sepals are ovate or oblong with an obtuse apex (Fig. 20.1a-b). The indument present on the sepals is composed of non-glandular and glandular hairs similar to those occurring on leaves. The number of sepals has been an important character in Radlkofer's classification and was used by him at different taxonomic levels. He used this character to define some species and a subsection of Platycoccus.

Petals

The corolla contains four free petals which are most commonly spathulate, and less frequently obovate or oblanceolate. The vast majority of species have white petals but the petals of S.

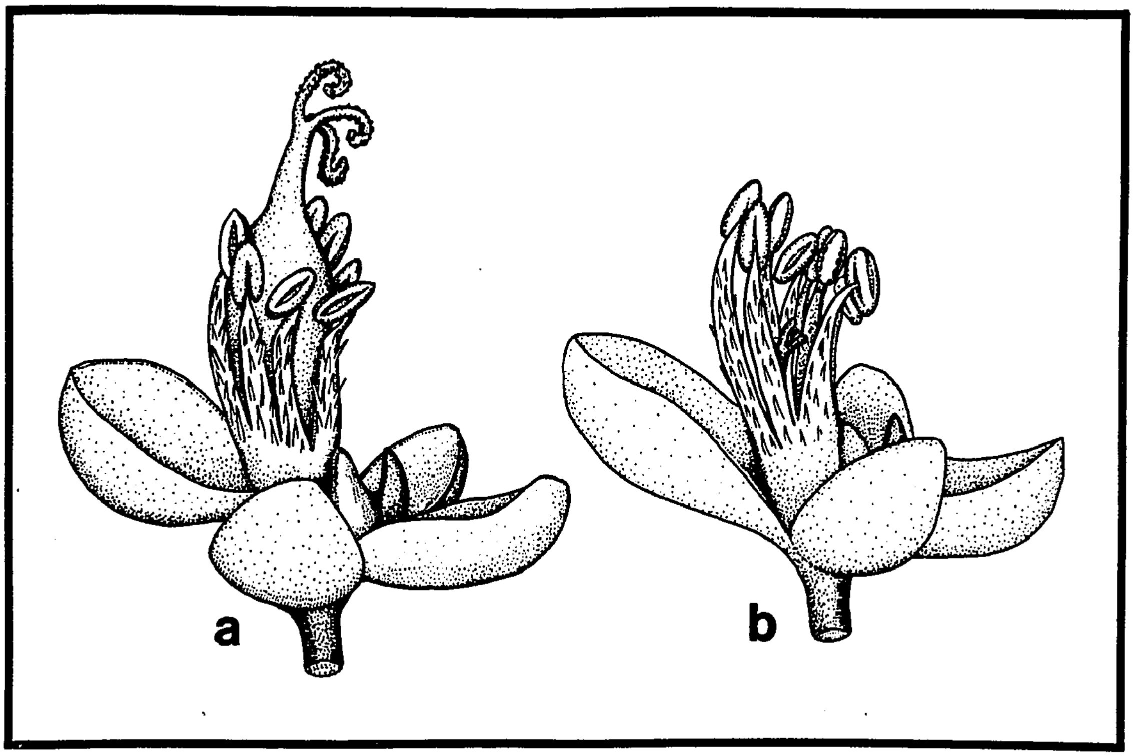
unidentata, S. cardiospermoides, and S. tenuis are light yellow and those of S. velutina are red. Their adaxial surface is sparsely covered with small papillae (Figs. 20.2b, d & e) and has a petaloid scale at its base (Fig. 20.1c, 20.2a-e). The petals are borne at the abaxial base of the disk gland (Fig. 20.1c). The scales are dimorphic, those in the central position (Fig. 20.2a-d) are larger, bilaterally symmetrical, and hood-shaped while those in peripheral (lateral) position are smaller, asymmetric, and semi-hood-shaped (Fig. 20.2e). The hood-shaped area of the scales covers the glands which are situated adaxially to the insertion of the petals (Fig. 20.1c). The scale apex is fleshy (perhaps glandular as suggested by Simpson, 1976) and presents great variation in size and shape (Fig. 20.2a-e). The central scales are very characteristic, usually with a yellow crown-shaped apex which sticks out against the anthers (Figs. 19c & 20.1c). Little importance has been given to the variation present in the petals and scales in the classification of Serjania.

Nectary Disk

There is an unilateral nectary disk with four protruding glands inserted at the base of the androgynoecium. Less commonly, the disk has only two glands or may be semi-annular with four lobes. The glands are variable in size and shape, but they are usually rounded or ovate (Fig. 20.3a-d). Those in the central position are usually larger than those at the periphery which may even be obsolete (Fig. 20.3b). The glands are fleshy and presumably secrete nectar.

Figure 17. Morphology of pistillate and staminate flowers of S. grandifolia (Acevedo & Daly 1619). A. Pistillate flower with indehiscent anthers. B. Staminate flower with reduced gynoecium.

Figure 18. Diagram showing the different dehiscent mechanisms in the Paullinieae. A. Schizocarpic fruit separates in three merocarpic units. The seeds are not exposed (present in Serjania and Houssayanthus). B. Loculicidal fruits open through the locule close to the septae. The seeds are exposed (present in Paullinia, Cardiospermum, and Urvillea).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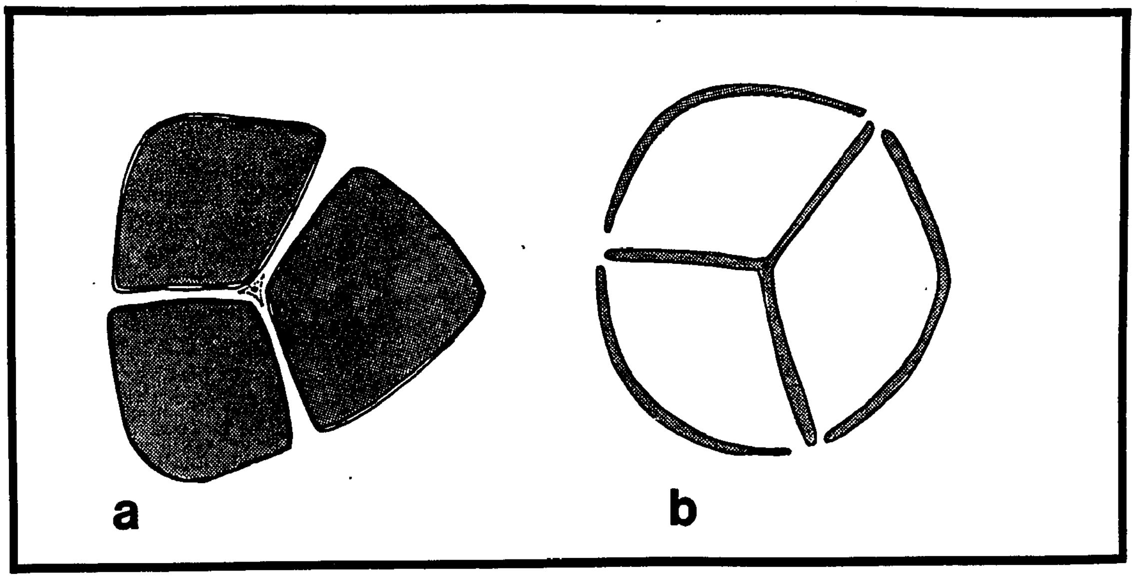
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Figure 19. Presentation of inflorescences in *Serjania*. A. Pendant inflorescence in *S. lethalis* (*Acevedo et al. 1468*). B. Erect inflorescence in *S. caracasana* (*Acevedo et al. 1499*). C. Horizontal inflorescence in *S. polyphylla*. D. Semierect inflorescence in *S. nutans* (*Acevedo & Vargas 1744*). E. Pendant inflorescence in *S. ampelopsis* (*Acevedo & Vargas 1731*).


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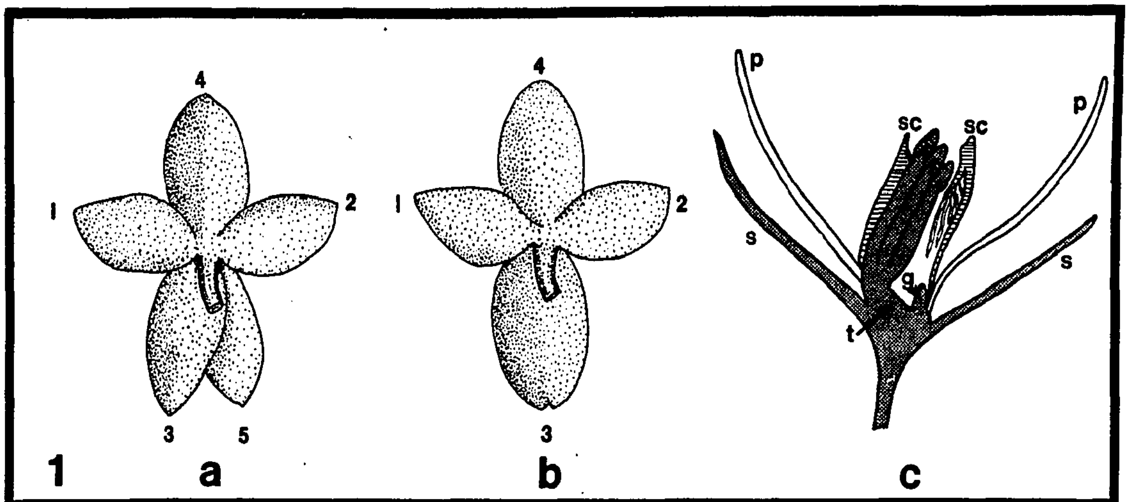
Figure 20. Floral structures of *Serjania*. 1. Calyx: a. with 5 sepals, outer sepals (1 & 2), inner sepals (3, 4 & 5), *S. hebecarpa*, *Acevedo & Vargas 1773*); b. with 4 sepals; c. longitudinal section through a flower (g= gland, p= petal, s= sepal, sc= scale, t= torus).

2. Petals with adnate scales: a-d, central petals; a. *S. subrotundifolia* (*Lechler 2332*); b. *S. paludosa* (*Mori 13281*); c. *S. confertiflora* (*Schunk s.n.*); d. *S. leptocarpa* (*Weir 501*); e. lateral petal, (*S. leptocarpa* (*Weir 501*).

3. Nectary disk with protruding glands: a. deltoid shape with central glands (c) larger than lateral glands (l), *S. pyramidata* (*Acevedo et al. 1495*); b. central glands (c) with deltoid shape, lateral glands (l) adnate to androgynophore (ad), *S. tenuis* (*Schuch s.n.*); c. semiannular disk with reduced glands, *S. longipes* (*Thien 131*); d. round central glands (c), oblong and larger lateral glands (l), *S. unidentata* (*Acevedo et al. 1570*).

4. Floral diagram, anthers and stigma features: a. quincuncial aestivation (numbers represent sepals, b= bracteole), *S. hebecarpa* (*Acevedo & Vargas 1773*); b. basifixed anther, *S. hebecarpa* (*Acevedo & Vargas 1773*); c. dorsifixed anther, *S. dentata* (*Rosa 47*); d. papillose stigmatic surface, *S. hebecarpa* (*Acevedo & Vargas 1773*).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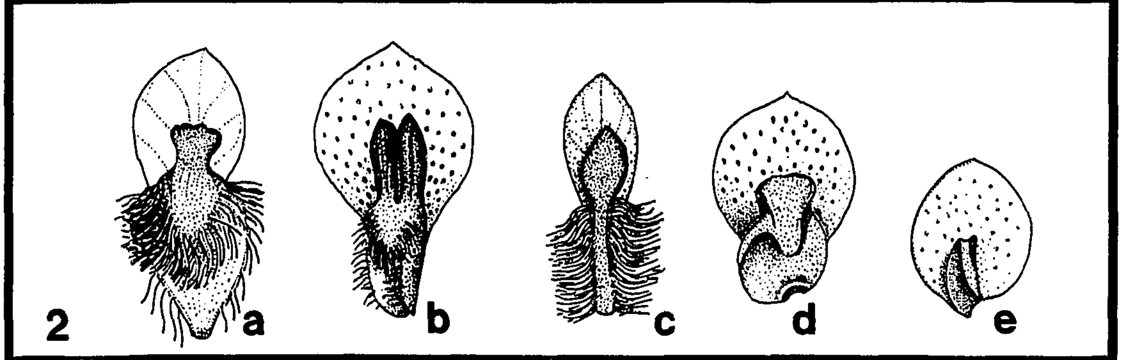
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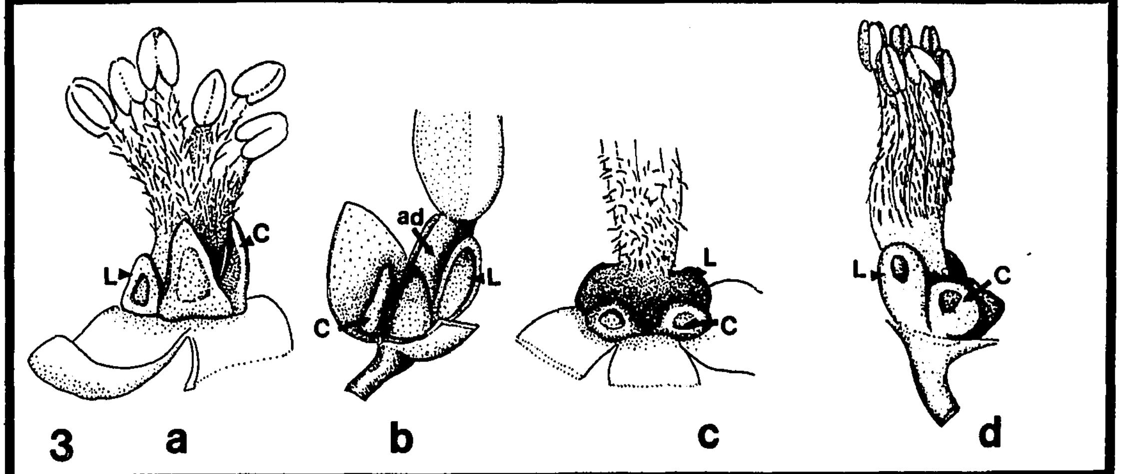
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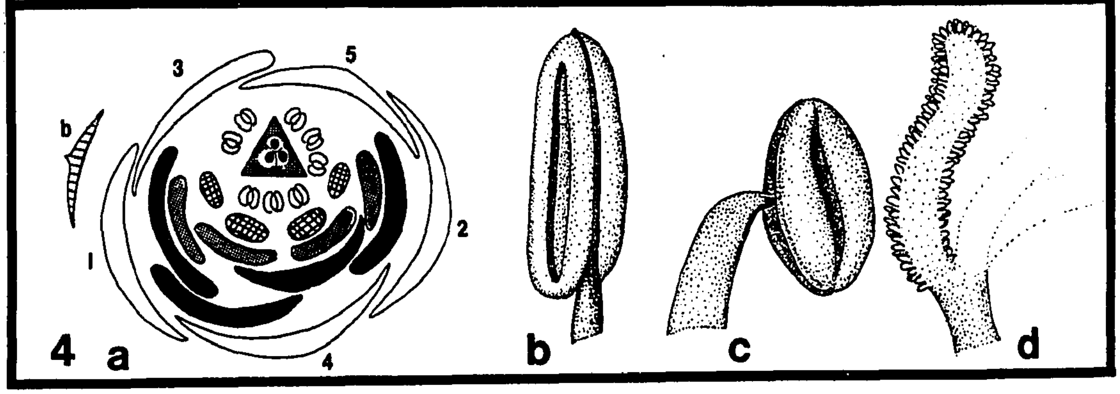
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d

Androecium

In Serjania, as well as in the other members of the Paullinieae, the number of stamens per flower is eight. The filaments are flattened, united at the base, and of unequal length (those toward the central glands shorter). They are usually densely covered with white inflexed hairs (Fig. 20.3 a, c & d). The anthers are small (0.4-0.6 mm), elliptic or oblong, basifixed or dorsifixed, and open by longitudinal slits (Fig. 20.4b-c). In some species, a fleshy appendage is present at the apex of the anthers. Most species have yellow anthers, however, in S. grandifolia, the anthers of the male flowers are light purple while those of the female flowers are whitish. In the field, some individuals of S. membranacea and S. hebecarpa are reported to have lilac and orange anthers, respectively.

The pollen of Sapindaceae has been studied by Muller and Leenhouts (1976) and by Cruz and Melhen (1984). Their studies show that Serjania has **heteropolar, demitricolporate** pollen with a triangular equatorial outline (Figs. 21a-c). One of the poles is convex and the other, where the colpi unite, is flatter (Fig. 21a). Exceptionally, Serjania pollen are isopolar and triporate, e.g., S. caracasana (Cruz and Melhen, 1984) or have a 4-angular equatorial outline (Fig. 21 c) or an oblate equatorial outline e.g., S. ichthyoctona.

Houssayanthus (Fig. 21 d), Cardiospermum, and Urvillea have the same type of pollen grains as Serjania (Muller & Leenhouts, 1976).

However, those of Paullinia differ by being isopolar and triporate. Muller and Leenhouts (1976) considered the triporate pollen to be derived from the hemitricolporate type by the reduction of the colpi, accordingly, the pollen of Lophostigma is further derived, because of its rod-shape outline and biporate condition.

Cruz and Melhen (1984) found the polar diameter of Serjania pollen to vary from 23.6 to 27.8 um and the equatorial diameter to vary from 41.1 to 47.3 um in the nine species they studied. I have found slightly smaller pollen grains in S. ampelopsis and S. communis. In these species the equatorial diameter varies from 30 to 35 um. Cruz and Melhen (1984) also found the size of pollen to vary between male and hermaphrodite flowers in some species of Serjania.

Exine sculpturing is reticulate, foveolate (Fig. 21a-b) or rarely psilate (Fig. 21c). The reticulate loops are larger at the flat pole. The exine consists of a columned sexine which is thicker than the nexine in all species except in S. communis, S. elegans, and S. reticulata in which the nexine is made of two layers (Cruz and Melhen, 1984).

Gynoecium

The syncarpic gynoecium consists of three fused carpels. The ovules are solitary, apotropous, and the placentation is axial. The ovary is glabrous or pubescent and prominently trilobate with an elliptic or oblong outline. The style is usually longer than the

Figure 21. SEM micrographs of _Serjania_ and _Houssayanthus_ pollen. A. _S_. _velutina_,(_Mori et al. 16839_). B. _S_. _hatschbachii_, (_Hatschbach 2957_). C. _S_. _ampelopsis_, (_Acevedo & Vargas 1731_). D. _H_. _incanus_, (_Hassler 7445_).

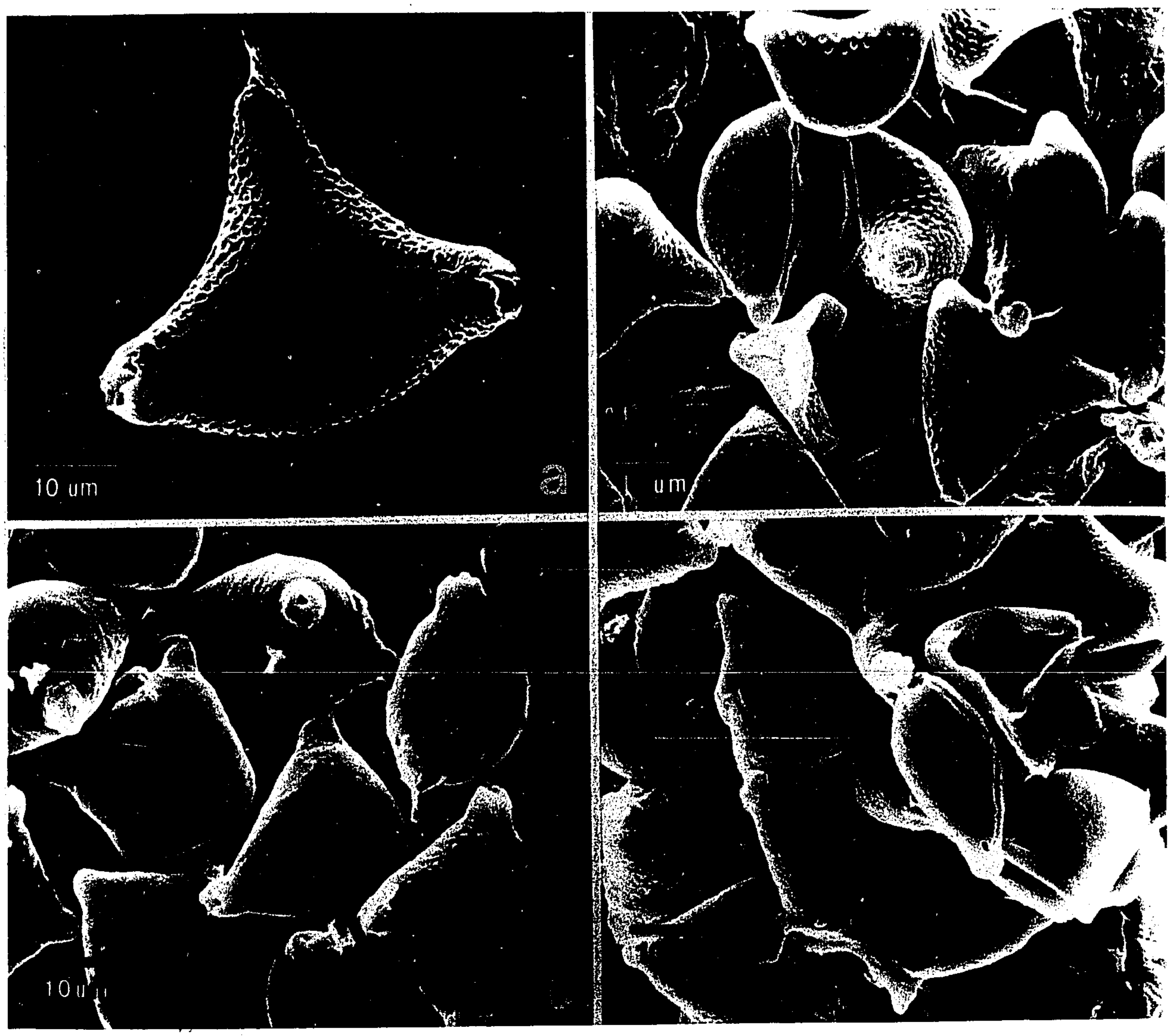

10 um
a
um
10 u

Figure 22. Fruit merocarps in Serjania. A. Merocarp which is still attached to the carpophore, showing different parts. B. Crested merocarp showing angle of spinning in free fall of ca. to 45°. C. Non-crested merocarp showing angle of spinning in free fall of ca. 90°. This type of merocarp is found in all species of section Platycoccus.

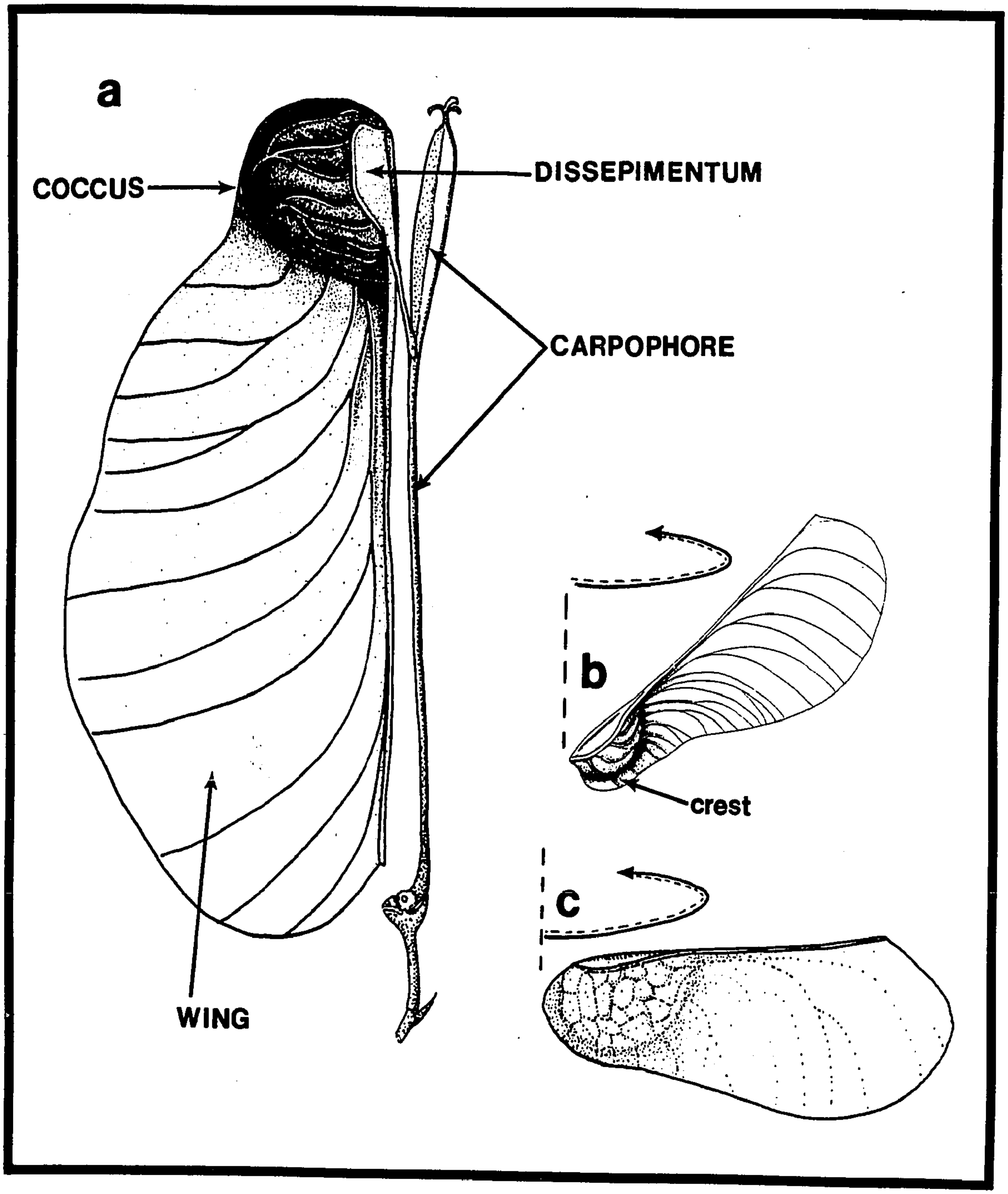
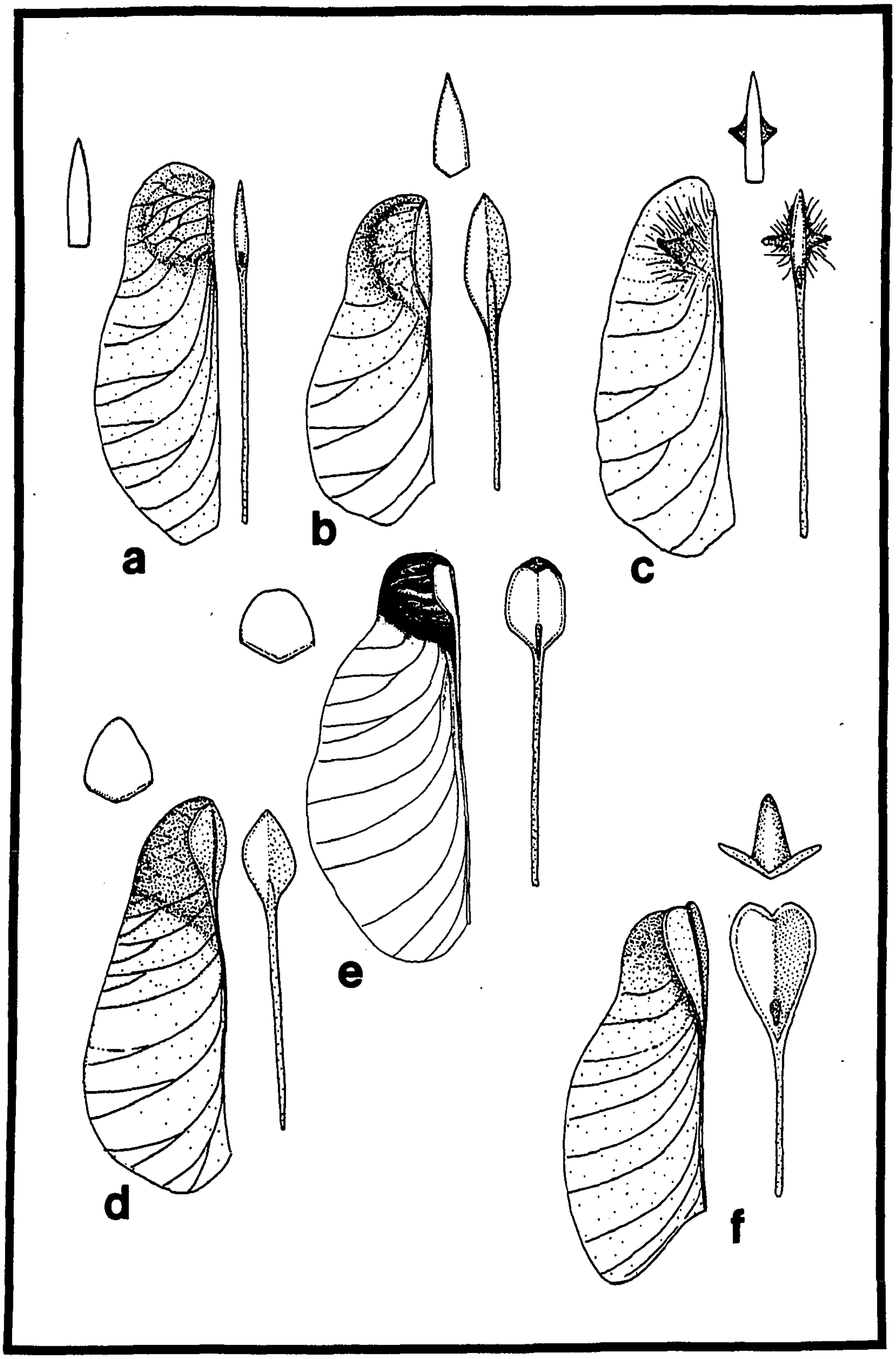

a
COCCUS
DISSEPIMENTUM
CARPOPHORE
WING
b
crest
c

Figure 23. Diagrammatic representation of merocarps found in Serjania which correspond to the six sections of the genus herein recognized. A-F Cross section of coccus at left or at top; lateral view of merocarp; frontal view of dissepimentum on right side. A. Section Platycoccus; coccus flat and membranous, dissepimentum narrow, cross section of coccus on left (S. cuspidata, W. Hoehne s.n. SPF 16098). B. Section Eurycoccus; coccus sub-spheric and woody, dissepimentum wide, cross section of coccus at top (S. salzmanniana, Acevedo et al. 1522). C. Section Ceratococcus; coccus woody with a horn-like projection, dissepimentum narrow, cross section of coccus on top (S. cornigera, Pittier 2568). D. Section Physococcus; coccus membranous and inflated, dissepimentum wide, cross section of coccus on left (S. inflata). E. Section Serjania; coccus woody and globose, dissepimentum wide, cross section of coccus on left (S. fluminensis, Acevedo & Farney 1424). F. Section Confertiflora; coccus woody and flattened, dissepimentum wide, projecting beyond the coccus, cross section of coccus at top (S. inscripta, Acevedo et al. 1590).


a
b
c
d
e
f

stigmas (three in number) which are papillose (Fig. 20.4d).

Fruits

The schizocarpic fruits in Serjania separate into three samaroid merocarps leaving a common thin carpophore (Fig. 22). The size of the merocarps varies from one cm in some species to up to seven cm in other species. Each merocarp is dispersed as a single unit and contains a proximal wing (sometimes very reduced) and a distal coccus where the seed is located (Fig. 22). Young and full grown fruits are often reddish or greenish, the latter turn straw-colored when mature.

Much weight was been given to fruit variation by Radlkofer (1875, 1886, 1931) in his construction of an infrageneric (sectional) classification. Characters such as the width of the partitioning wall (dissepimentum) (Fig. 22), the texture and shape of the coccus (Fig. 23 a-f), and the presence of a crest or wing around the coccus (Fig. 22) were utilized in the delimitation of his sections. Of the twelve sections that he recognized, some are distinctive and easily recognized, but the majority are poorly delimited because of intergradation of characters. I recognize only six sections which are also based on fruit types. One of these sections (section Confertiflora) was not recognized before (Fig. 23a-f, see section on infrageneric classification).

Section Platycoccus is characterized by having fruits with

Figure 24. Anatomical sections of the fruits and seeds of Serjania (all S. communis, Acevedo et al. 1496). A. Cross section of fruit wall with sclereid shield at corner (sh), exocarp not yet suberized (ex) and vascular bundle (vb). B. Detail of cross section of fruit wall showing suberized exocarp (ex) and sclereids in endocarp (sc). C. Seed cross section showing sclereids in seed coat (sc), exotesta (xt), and endotesta (et). D. Cross section of fruit wall showing epidermis (ep), exocarp (ex), mesocarp (me), and endocarp (en) with inner suberized layer (sb). E. Same, in detail showing crystals in mesocarp cells (cr).

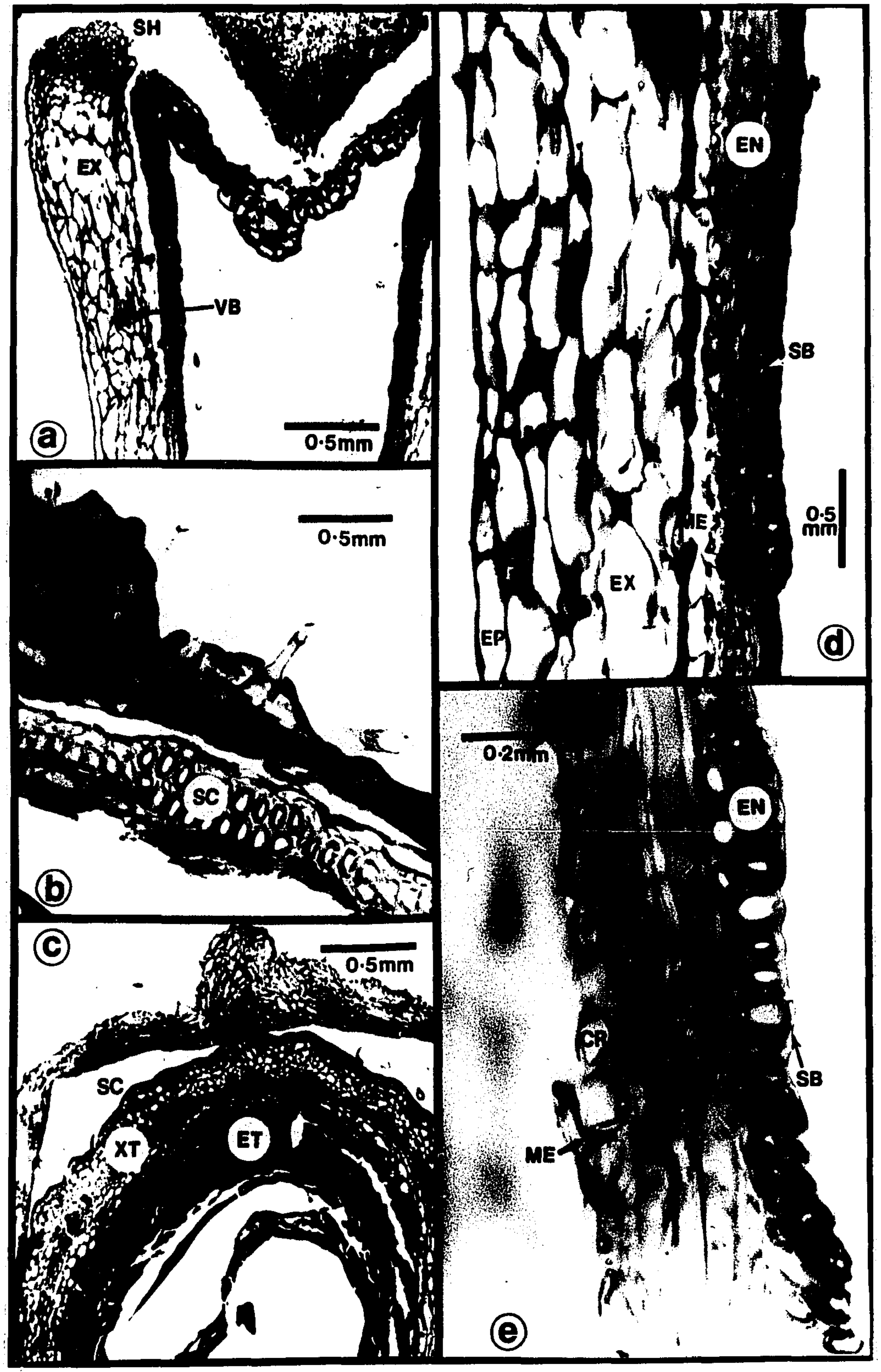
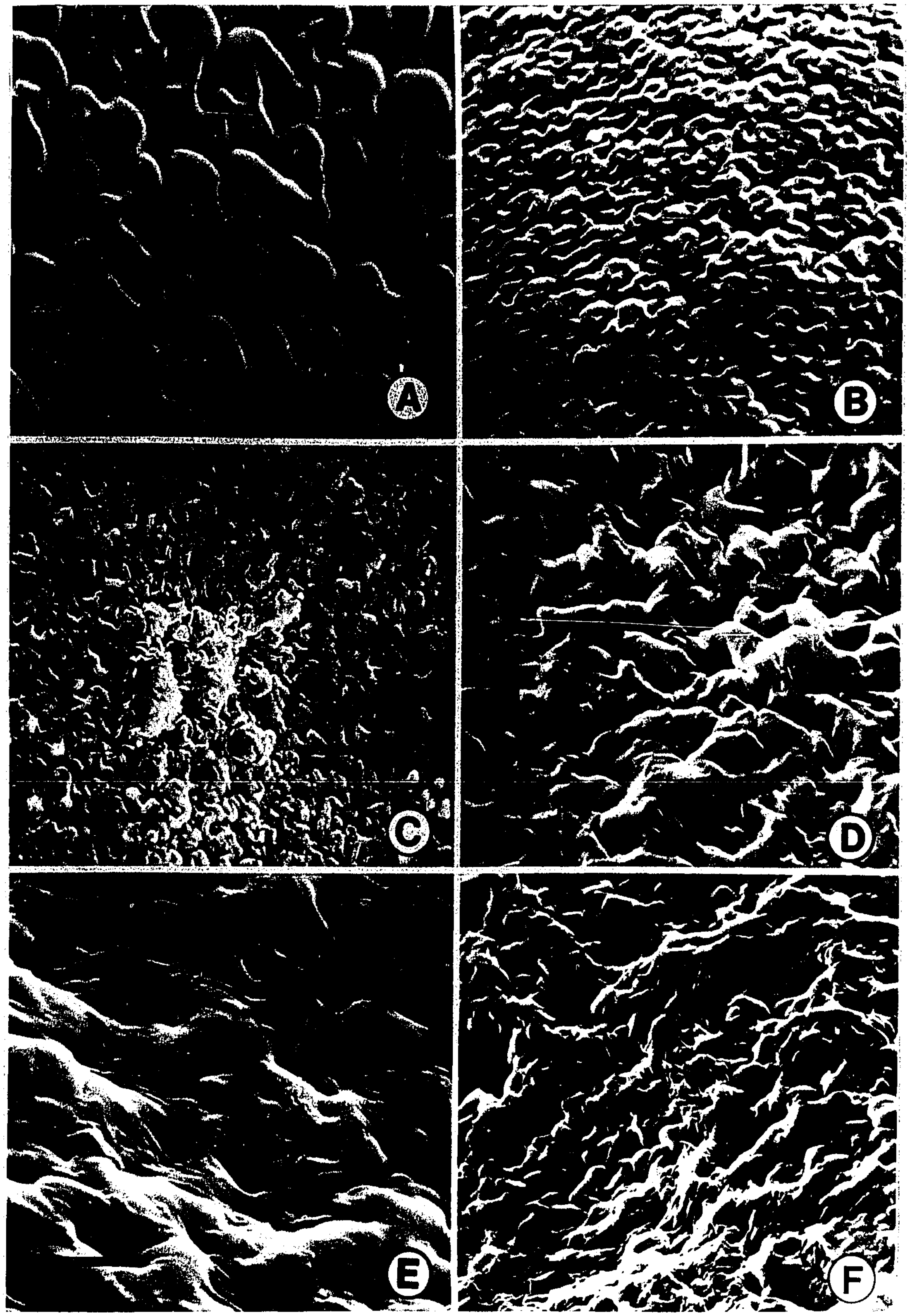

a
SH
EX
VB
0·5mm
b
0·5mm
SC
c
0·5mm
SC
XT
ET
d
EN
SB
0·5 mm
ME
EX
EP
e
0·2mm
EN
CR
SB
ME

Figure 25. Seed coat surfaces in Serjania. A-C. Rugulate pattern, A. S. clematidea, B. S. gracilis, C. S. clematidifolia, D-F. Sub-rugulate pattern, D. S. trichomisca, E. S. confertiflora, F. S. acutidentata.


A
B
C
D
E
F

flat, membranous cocci. These two characters do not occur together in any other species of Serjania.

The fruits of Serjania lack a cuticle. The epidermis is made up of uniform parenchyma cells (1.25 x 2.5-3.7 um) with wavy anticlinal walls (Fig. 24d). The exocarp consists of approximately ten layers of parenchyma with included vascular bundles (Fig. 24a). The corner in contact with the dissepimentum contains a shield of sclereids (Fig. 24a). The exocarp becomes heavily suberized and collapses and sometimes separates from the mesocarp (Fig. 24b). The mesocarp is made up of a middle, uniseriate layer of small, isodiametric parenchyma which contains prismatic crystals and stains heavily with safranin (Fig. 24d-e). The endocarp is a four to eight layered zone of sclereids with overlapping oblique ends. The inner layer of the endocarp is suberized (Fig. 24e). The endocarp is organized into a mesh in which erect and transverse sclereids are found. The partitioning wall consist of short transverse sclereids. The fruit anatomy of Serjania section Platycoccus does not differ from that of other sections of the genus.

Seeds

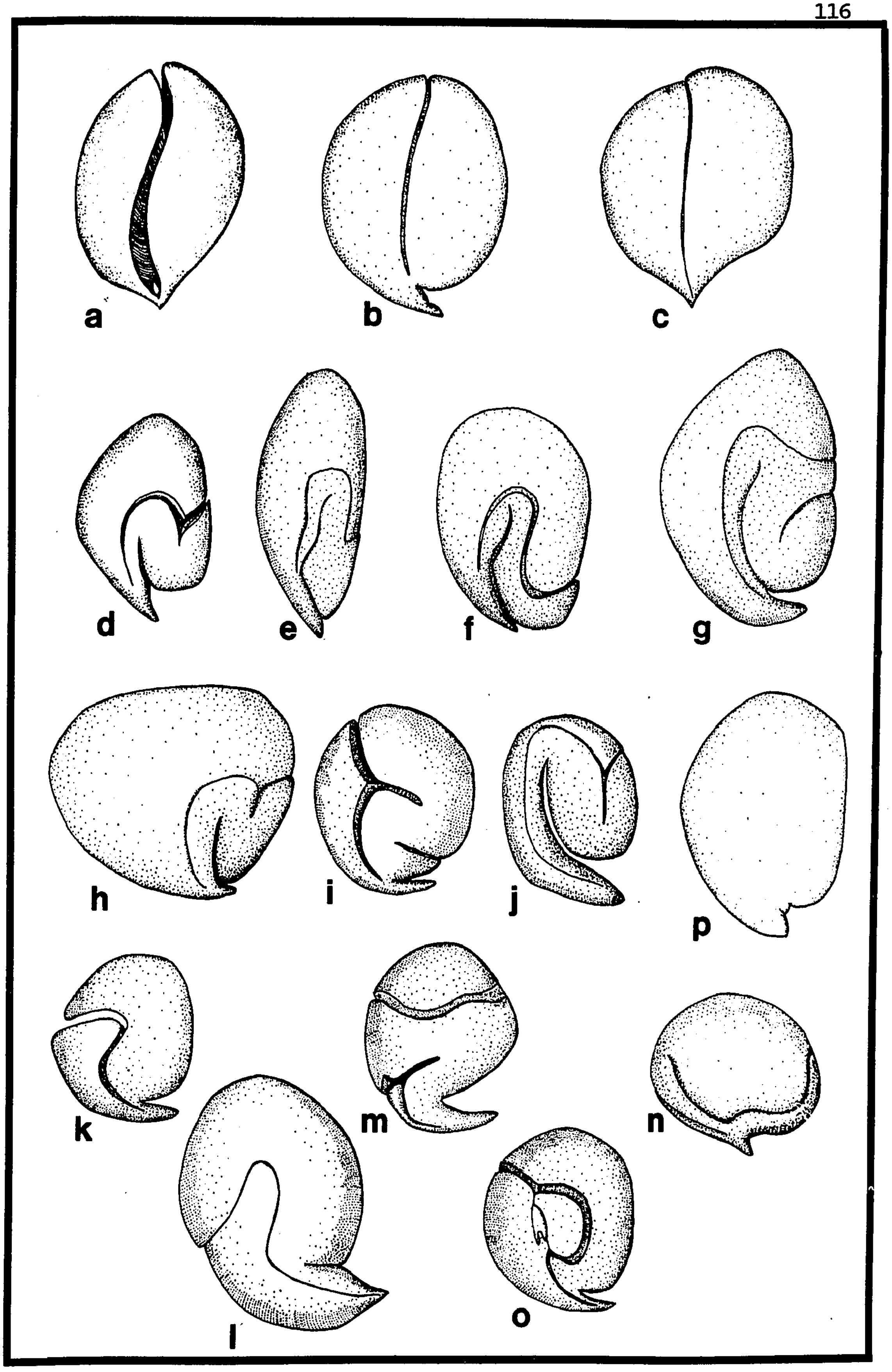
Seeds of Serjania are commonly lenticular, spheric, tear-shaped or rarely oblong with a triangular outline in transverse section. They are usually dark or light brown and the size varies from 3 to 7 mm in length. The seed coat surface is strongly rugulate to weakly rugulate or sub-rugulate (Fig. 25). There is an exotesta below the cuticle which consists of an uniseriate layer of uniform sclereids and a thick tissue of approximately ten cell layers of isodiametric parenchyma cells and vascular bundles (Fig. 24c). The parenchyma in this zone heavily accumulates ergastic substances. The endotesta is a two-celled tissue of larger and darker cells (Fig. 24c). The endosperm is absent in mature seeds.

Different types of cotyledon configurations occur in Serjania. The abaxial cotyledon refers to the cotyledon which is farther away from the fruit axis while the adaxial cotyledon is closest to the axis.

The following four types of cotyledon configuration have been found in the embryos of Serjania: 1) both cotyledons straight and parallel to fruit axis (Fig. 26a-c), 2) the abaxial cotyledon larger and curved over the adaxial which is biplicate (Fig. 26d-h, j), 3) the abaxial cotyledon straight and smaller, and adaxial cotyledon biplicate (Fig. 26i, k-l), 4) both cotyledons straight and perpendicular to fruit axis (Fig. 26p). The third type may be a variation of the second type because some species show both types. Besides these four types, some anomalous embryos (Fig. 26m-o) have been found in species having the second type. The cotyledons are entire and may be either flattened or swollen.

The type of embryo has no systematic value at the tribal

Figure 26. Embryo configuration in Serjania. A-C. Embryo with straight cotyledons, and parallel to fruit axis. D-J. Embryo with curved abaxial cotyledon and biplicate adaxial cotyledon. K-L. Embryo with small straight abaxial cotyledon and large biplicate adaxial cotyledon. M-O. Embryo with abnormal configuration (variable). P. Embryo with straight cotyledons, perpendicular to the fruit axis. A. S. unidentata (Acevedo et al. 1570). B. S. cardiospermoides (Calzada 4247). C. S. cuspidata (SPF 16098). D. S. regnellii (Acevedo & Laca 1512). E. S. confertiflora (Acevedo et al. 1449). F. S. paludosa (Mexia 5682). G. S. paradoxa (Acevedo et al. 1502). H. S. nutans (Killip 27573). I. S. lethalis (Eiten 5524). J. S. fluminensis (Acevedo & Farney 1424). K. S. marginata (Kunth 92). L. S. gracilis (Acevedo et al. 1514). M. S. sinuata (Leonard 8014). N. S. paniculata (Camp 545). O. S. dibotrya (Acevedo & Vargas 1748). P. S. brachyptera (Macbride 2291)


a
b
c
d
e
f
g
h
i
j
p
k
m
n
l
o

level because they have been independently developed in different species of different tribes. However, this character provides systematic information at the species level.

The seeds of Serjania section Platycoccus are lenticular and their seed coat surface varies from rugulate to weak rugulate. The embryos are either type 1, 2, or 4.

CYTOLOGY

Although I collected material for cytological study of Serjania no chromosome counts were obtained. None of the buds collected were fixed at the proper stage of meiosis.

Reports on chromosome numbers have been published for 13 species of Serjania. All reported numbers are N= 12 (Table VIII). Chromosome numbers in the woody Paullinia and Houssayanthus are n=12 while the herbaceous Cardiospermum and Urvillea are n=11 (10) (Ferrucci, 1981b). The herbaceous members of the Paullinieae seem to be more derived, a suggestion which is supported by their shorter life cycles and reduced chromosome numbers. A similar trend has been observed in other groups in which a reduction of nuclear DNA correlates with shorter life cycles and adaptation to disturbed or rapidly changing environments (Bennett, 1972). It is expected that a similar trend may occur in species of Serjania section Platycoccus which has many herbaceous members. However, confirmation of this hypothesis awaits chromosome counts for the herbaceous species of the section.

TABLE VIII

Chromosome counts in Serjania.

Species	number	reference
caracasana	n= 12	Ferrucci, 1981b
cissoides	n= 12	Ferrucci, 1981b
confertiflora	n= 12	Fernández Casas, et al. 1982
erecta	n= 12	Ferrucci, 1981b
exarata	n= 12	Guervin, 1961
glabrata	n= 12	Ferrucci, 1985b
glabrata f. mollior	n= 12	Ferrucci, 1981b
hebecarpa	n= 12	Ferrucci, 1981b
lucida	n= 12	Guervin, 1961
mansiana	n= 12	Ferrucci, 1985b
marginata	n= 12	Ferrucci, 1985b
meridionalis	n= 12	Ferrucci, 1981b
perulacea	n= 12	Ferrucci, 1981b
tripleura	2n= 24	Ferrucci, 1985b

DISTRIBUTION and ECOLOGY

Serjania is a New World genus with approximately 226 species, distributed from southwestern USA to northern Argentina, including the West Indies (Fig. 27). A few species are grown as ornamentalsin the Old World and in the Pacific. At the present stage of knowledge of Serjania, it seems that the majority (60 %) of species occupy a medium geographical range (i.e., a quarter to a third of the area of the continent), followed by species (35 %) which occupy a restricted range (endemic, usually known from a few collections) and by species (5%) with a wide geographical range (i.e., throughout the continent). This pattern agrees with that found by Gates (1982) for Banisteriopsis (Malpighiaceae) which has winged diaspores similar to Serjania. However, it clearly differs from that found by Gentry (1979) for most of the wind dispersed Bignoniaceous lianas which occupy wide geographical ranges.

There are two major centers of distribution for Serjania-- one in Mexico and another in the central Brazilian cerrado. Both regions have about 48 species. A minor center, containing 24 species, is found along both sides of the Andes at middle elevations.

The great majority of Serjania species occur in thickets or in open and relatively dry vegetations (50%) such as cerrado, campo rupestre (Fig. 28a), and restinga (Fig. 28b). A vast number of species (35%) occur along margins of gallery forests, and a small percent (8%) are found usually associated with disturbed areas or

Figure 27. Distribution of Serjania per countries in the Americas. Number above line equals total number of species while number below line equals number of endemic species in a given country.

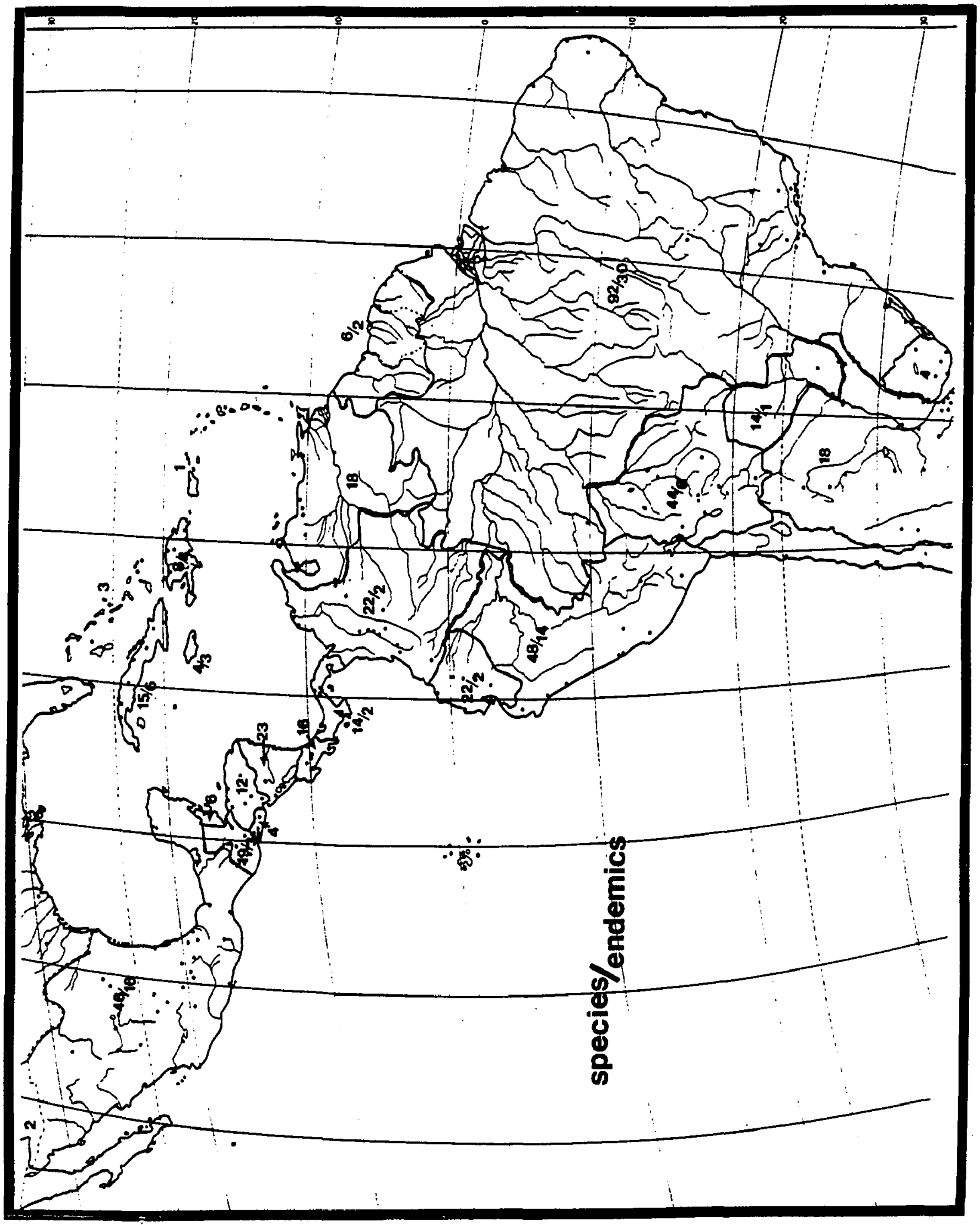
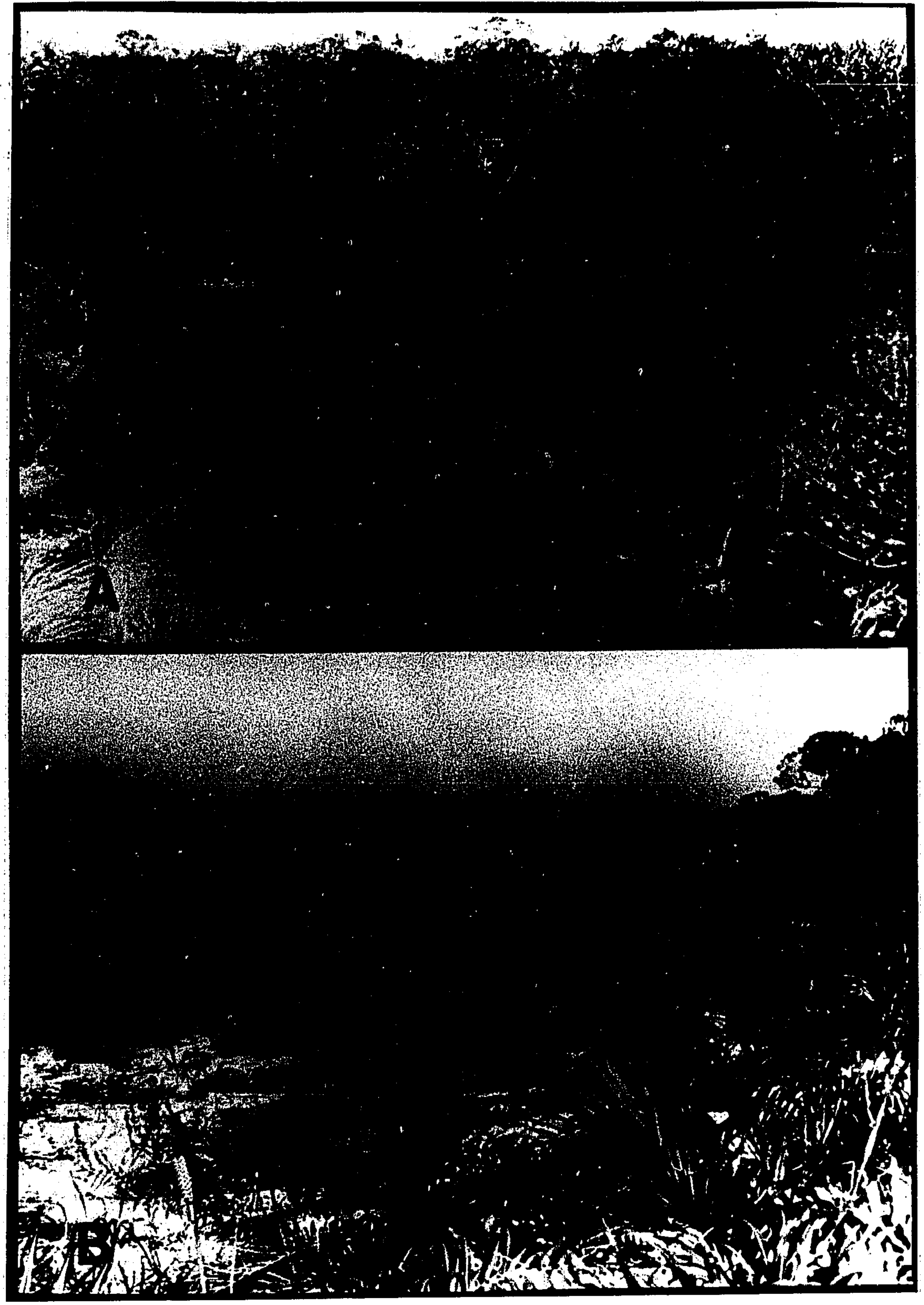

92/30
6/2
14/1
18
18
44/6
22/2
48/14
22/2
14/2
1
3
8/4
4/3
15/6
18
23
12
6
4
49/4
46/16
2
species/endemics

Figure 28. Typical habitats of Serjania. A. Campo rupestre (Serra do Cipó, Minas Gerais, Brazil). B. Restinga de Massambaba (Rio de Janeiro, Brazil).


A
B

gaps in dense tall humid forests (Table IX). Few species occur in areas above 1500 m elevation, and no species have been collected above 3000 m. The importance of Serjania seems to decrease from wetter to drier vegetation types. Goodland (1969) showed how the abundance of S. grandiflora and S. erecta decreases along vegetation with increasing drier regimes and fewer arboreal elements, i.e., there are fewer species of Serjania in the continuum from cerradao-cerrado-campo cerrado to campo sujo.

It is possible that Serjania, in spite of being very diverse in the cerrado, does not constitute a very important ecological element for the flora of the area. This conclusion has been reached through different studies of cerrado vegetation. Goodland (1970), in his ecological studies of the Triângulo Mineiro did not mention Sapindaceae, and Rizzini (1971) only cited three species of Serjania in his survey on woody cerrado plants. It seems that many herbarium collections of Serjania marked as from "cerrado", actually come from the gallery forests which dissect most of the cerrado region.

The distribution of Serjania contrasts with that of the closely related Paullinia because of its preference for drier and more open environments. Although there is some overlap in the distribution of the two genera, the vast majority of species of Paullinia occupy humid dense forests, especially in the Amazon area. This pattern is understandable in light of the fact that the major mode of dispersal in Paullinia is zoochory.

All species of Serjania section Platycoccus occur in South

TABLE IX

Occurrence of *Serjania* in major vegetation types

as determined from exsiccatae.

Abbreviations in parenthesis stand for the Brazilian states.

Caatinga (Brazil)

bahiana	(BA)	*glabrata*	(BA)
clematidifolia	(BA)	*pernambucensis*	(BA)
faveolata	(BA)	*pinnatifolia*	(BA)
fuscifolia	(BA)		

Campo Rupestre (Brazil)

acoma	(GO, MG)	*hebecarpa*	(MT)
acutidentata	(MG)	*lethalis*	(MG)
caracasana	(MG)	*meridionalis*	(GO)
clematidifolia	(RJ)	*multiflora*	(MG)
elegans	(MG, BA)	*noxia*	(MG)
erecta	(GO, MG)	*paradoxa*	(MG)
glutinosa	(MT)	*regnellii*	(MG)
gracilis	(BA)	*reticulata*	(MG, GO)

TABLE IX (cont.)

Cerrado (Brazil)

acoma	(GO, MG, MT, PR, SP)	mansiana	(MG)
acutidentata	(BA, MG)	marginata	(BA, GO)
bahiana	(BA)	membranacea	(PA)
caracasana	(GO, SP)	meridionalis	(GO)
cissoides	(MG)	multiflora	(GO)
comata	(GO, MT, PR)	obtusidentata	(DF, MG, MT)
corrugata	(BA, MG)	ovalifolia	(DF, GO, MG, MT)
crassifolia	(MT)	paradoxa	(BA, DF, MG)
elegans	(MG)	perulacea	(GO)
erecta	(BA, GO, MG, MT, PR, SP)	pinnatifolia	(MG)
fuscifolia	(MG)	piscatoria	(GO)
glutinosa	(GO, MT)	pyramidata	(MG)
hebecarpa	(MT, DF)	reticulata	(GO, MG, MT, PR, SP)
lethalis	(DF, GO, MG, MT, SP)	velutina	(GO)

TABLE IX (cont.)

Gallery Forest (in many countries)

acoma
altissima
ampelopsis
atrolineata
caracasana
cardiospermoides
clematidea
clematidifolia
comata
communis
crassifolia
crassinervis
dibotrya
diffusa
diversifolia
elongata
erecta
eucardia
exarata
foveata
fuscifolia
grammatophora
grandifolia
grandis
grosii
herteri
inflata
lamprophylla
laruotteana
laxiflora
leptocarpa
lethalis
macrocarpa
mansiana
marginata
membranacea
meridionalis
mexicana
multiflora
nigricans
noxia
nutans
paniculata
paradoxa
paucidentata
pedicellaris
peruviana
pinnatifolia
piscatoria
platycarpa
plicata
polyphylla
punctata
purpurascens
pyramidata
racemosa
rachyptera
reticulata
rhombea
rubicaulis
squarrosa
tenuifolia
triquetra

TABLE IX (cont.)

Gallery Forest

glabrata
glutinosa
gracilis
hebecarpa
obtusidentata
ovalifolia
pernambucensis
perulacea
trirostris
velutina

Restingas (southeastern Brazil)

caracasana	(RJ)	dura	(SP)
ichthyoctona	(BA, RJ)	clematidifolia	(BA, RJ)
elegans	(RJ)	salzmanniana	(RJ, BA)
cuspidata	(RJ)	eucardia	(RJ)
scopulifera	(BA)	dentata	(BA, RJ)
fluminensis	(RJ)	tenuis	(RJ*)
		truncata	(RJ)

* Reported by Araújo de D.S.D. & R.P.B. Henriques, 1984.

TABLE IX (cont.)

Savannas

acoma	Brazil (DF)	*mexicana*	Venezuela
atrolineata	Venezuela, Mexico	*orbicularis*	Brazil(PA)
caracasana	Paraguay	*ovalifolia*	Brazil(MA)
communis	Venezuela	*paucidentata*	Venezuela
inflata	Peru	*reticulata*	Bolivia

Terra Firme Forest (Amazon basin)

- *caracasana*
- *circumvallata*
- *clematidifolia*
- *elongata*
- *glutinosa*
- *grandifolia*
- *lethalis*
- *membranacea*
- *noxia*
- *paucidentata*
- *pyramidata*
- *salzmanniana*
- *tenuifolia*

Várzea Forest (Amazon basin)

- *dibotrya*
- *exarata*
- *inscripta*
- *leptocarpa*
- *membranacea*
- *paucidentata*
- *purpurascens*
- *pyramidata*

TABLE IX (cont.)

Disturbed Vegetation (in many countries)

acoma
acutidentata
adiantoides
altissima
aluligera
ampelopsis
atrolineata
brevipes
calligera
caracasana
cardiospermoides
chaetocarpa
circumvallata
clematidea
clematidifolia
columbiana
comata
communis
corrugata
crassifolia
crassinervis
cuspidata
dentata
dibotrya
didymadenia
diffusa
diversifolia
dumicola
dura
elongata
erecta
eucardia
exarata
foveata
fuscifolia
fuscostriata
glabrata
glutinosa
goniocarpa
gracilis
grandifolia
grandis
grosii
hebecarpa
inflata
inscripta
insignis
laevigata
laruotteana
lateritia
leptocarpa
lethalis
lobulata
longipes
lundellii
mansiana
membranacea
meridionalis
mexicana
mucronulata
multiflora
nigricans
noxia
nutans
oblongifolia
obtusidentata
paniculata
paradoxa
paucidentata
perulacea
peruviana
pinnatifolia
plicata
polyphylla
punctata
punctulata
purpurascens
pyramidata
racemosa
regnellii
rekoi
reticulata
rhombea
rufa
salzmanniana
setigera
sphaerococca
squarrosa

TABLE IX (cont.)

Disturbed Vegetations			
dasyclados	*hispida*	*ovalifolia*	*sufferruginea*
deflexa	*ichthyoctona*	*orbicularis*	*tenuifolia*
deltoidea	*impressa*	*oxyphylla*	*tenuis*
trifoliolata	*triquetra*	*trirostris*	*velutina*

America except for *S. cardiospermoides*, which has a middle to northern Central America distribution. Most of the species have a rather restricted distribution. However, *S. communis* is widely distributed and three other species (*S. ampelopsis*, *S. leptocarpa*, and *S. squarrosa*) have moderately wide distributions. Two species, *S. cuspidata* and *S. tenuis*, occur along the coastal scrubby vegetation (restinga) of southeastern Brazil. *Serjania cuspidata* ranges from Bahia to Sao Paulo and is sympatric with *S. tenuis* in Rio de Janeiro where the latter occurs. Other endemics are found in Brazil— *S. regnellii* in the central planalto in Minas Gerais, *S. morii* in the Atlantic forest in Bahia, and *S. hatschbachii* in the Atlantic forest in Sao Paulo. *Serjania schunkei* is another endemic species, restricted to the tall forest of Tocache Nuevo in the Peruvian Amazon. The rest of the species are distributed along middle elevations in the Andes. *Serjania ampelopsis* ranges from Colombia to Bolivia, *S. leptocarpa* is found from Venezuela to Bolivia, *S. squarrosa* is endemic to central Peru, and *S. dumicola* is endemic to central Bolivia.

REPRODUCTIVE BIOLOGY

In spite of the interesting floral morphology, which has drawn the attention of many taxonomists, no studies have been published on the pollination biology of *Serjania*. The only mention of reproductive biology in *Serjania* is that of Müller (1873), in which the flowers of *S. cuspidata* are said to be protandrous.

There are only a few publications which treat the pollination biology of other genera of Paullinieae. Simpson (1976) suggested that the petal scales of Paullinia accumulate nectar in their hoods. He also speculated that insects would necessarily approach the flowers from above and that pollination is nototribic. My observations, however, indicate that pollination of Serjania is sternotribic.

The flowers of Serjania, in spite of being apopetalous, restrict entrance to the nectary disk because the petal scales are close together and pressed against the anthers. Therefore, insects must approach the flowers from above in order to enter the tube-like arrangement of petal scales and stamens (Figs. 19c & 20.1c). The flowers of Serjania are upwardly to laterally oriented in the inflorescence, and produce a strong sweet smell which attracts many different kinds of insects (Table X).

Among the most prominent visitors are small to medium-sized bees. Equal numbers of wasps and flies, as well as a small number of moths, have also been collected visiting the flowers. Bees are the most likely pollinators of Serjania because, when examined, they had pollen grains all over their ventral surface. Most of them also had massive amounts of pollen accumulated in their rear leg corbiculae. The pollen from the corbiculae turned out to be almost exclusively from the species of Serjania upon which the bee was collected. This shows the high fidelity of these insects toward the same source species, at least on a given foraging flight. One of

TABLE X

List of insects collected during field work,
while visiting Serjania flowers.

Serjania ampelopsis. Bee (Apis mellifera L.) carrying no pollen, except for a few grains on corbiculae. Fly (Copestylum sp.) carrying no pollen.

Serjania confertiflora. Bees (Trigona bipunctata Lep.) abundant Serjania pollen on leg corbiculae, (Trigona dorsalis Sm.) no pollen seen, (Trigona jaty Sm.) Serjania pollen on middle legs.

Serjania crassifolia. Bees (Apis mellifera L.) carrying Serjania and other type of pollen, (Melipona interrupta Latr.) carrying few Serjania pollen on mouth parts, (Melipona interrupta Latr.) carrying few Serjania pollen on leg corbiculae, (Trigona testaceicornis var. punctata Sm.) carrying Serjania pollen on abdomen and rear legs. Wasp (Brachygastra augusti Saussure) carrying no pollen.

Serjania deltoidea. Bee (Neocorynura sp.) carrying no pollen. Flies (Xanthoepalpus sp.), carrying Serjania pollen on mouth parts, (Trichopoda sp.) carrying Serjania-type pollen on lower abdomen, head and mouth parts, (Ornidia obesa) carrying Serjania-type pollen on lower part of body and mouth parts, (Tachinidae) carrying no pollen. Moth (unidentifiable) carrying no pollen. Wasps (Polybia dimidiata Oliver) carrying no pollen,

TABLE X (cont.)

(*Polybia occidentalis* Oliver) carrying *Serjania* pollen on mouth parts.

Serjania dumicola. Bees (*Augochlora sp.*) and (*Colletes sp.*) carrying no pollen. Wasp (*Polistes sp.*) carrying no pollen.

Serjania grandifolia. Bees (*Trigona hypogea* Silvestri) pollen grains all over abdomen, those on leg corbiculae exclusively *Serjania* type, (*Colletes sp.*) carrying non-*Serjania* pollen type. Various butterflies in the Hesperidae, carrying no pollen. Wasps (*Camsomeris servillii* Guerin), carrying no pollen, (*Mischocyttarus sp.*) carrying no pollen, (*Montezumia dimidiata* Saussure) carrying *Serjania* pollen on mouth parts, (*Pepsis sp.*) carrying *Serjania* pollen on mouth parts, (*Synoecoides sp.*) carrying *Serjania* pollen on neck.

Serjania cf. *leucosepala*. Bee (*Neocorynura sp.*) carrying no pollen.

Serjania sphaerococca. Bee (*Paratetrapedia sp.*) carrying very few *Serjania* pollen over lower part of abdomen.

Serjania sufferruginea. Bees (*Apis mellifera* L.) carrying *Serjania* pollen on leg corbiculae. Fly (*Allograpa exotica*), carrying no pollen.

Serjania tenuifolia. Bees (*Apis mellifera* L.) carrying no pollen, (*Trigona bipunctata* Lep.) carrying no pollen, (*Trigona fulvohirta* Fr.) carrying no pollen, (*Trigona postica* Latr.) carrying

TABLE X (cont.)

mostly Serjania pollen on posterior part of abdomen, on legs and rear leg corbiculae, (Trigona tataira var. mellicolor Pack.) carrying few Serjania pollen over lower part of body.

Serjania sp. Bees (Trigona compresa Latr.) and (Neocorynura sp.) carrying no pollen. Beetle (Polymerus sp.), carrying no pollen.

the bees collected had three other kinds of grains, but _Serjania_ pollen was by far the most abundant. Flies are also potential pollinators because they had pollen grains dusted over their ventral surfaces. Flies also had abundant grains on their mouth parts which indicates that they utilize _Serjania_ pollen as a food source. Different species of medium-to large-sized wasps were also collected visiting the flowers of _Serjania_. They contained large amounts of _Serjania_ pollen on their mouth parts, which suggests that also they consume _Serjania_ pollen. No pollen grains were observed elsewhere on their bodies, except for one large wasp, which was carrying _Serjania_ pollen on its neck. It is possible that this wasp is also an effective pollinator. The moths collected did not carry pollen on their bodies.

At this moment, it is not clear whether pollen or nectar is the major reward for pollinators of _Serjania_. The presence of sterile stamens with aborted pollen in pistillate flowers might constitute an attractive feature for pollen foragers. The studies of Bawa (1976) and Subba Reddi et al. (1983), in other members of Sapindaceae (_Cupania_ _guatemalensis_ Radlk. and _Sapindus_ _emarginatus_ Vahl.), which have floral biology similar to _Serjania_, showed that pollen is the major reward for their pollinators.

My observations indicate that more insects visit plants of _Serjania_ during the early morning and late afternoon than at mid-day and evening.

The fruits of _Serjania_, as already mentioned (Fig. 18, 22), split into three merocarpic units which are either dispersed by wind or water currents. In dry, open areas, wind is the predominant dispersal vector whereas in gallery or seasonally flooded forests water currents are the principal mode of dispersal.

Once the fruits reach maturity, the merocarps are aided in abscission by the wind. The wind speed required for fruit abscission may vary from species to species, depending on weight, shape, and size of the merocarps. These three factors may have an effect on the dispersal potential of merocarps as well. Smaller or lighter merocarps are expected to travel longer distances than larger or heavier ones under the same wind conditions.

After abscission, the merocarps spin in the air around the seed-bearing portion (coccus) with the wing oriented at ca. 45° (Fig. 22b) from the axis of spin. A slight variation is found in the species of section <u>Platycoccus</u> in which the angle of wing orientation is ca. 90° (Fig. 22c). Consequently, the merocarps in this section tend to glide rather than spin. According to Augspurger (1986), gliding diaspores of tropical trees have a smaller dispersal potential than autogyros diaspores (spinners) under the same wind conditions. This difference in dispersal behavior might account for the more restricted distribution of species of section <u>Platycoccus</u>, in comparison to species of other sections of <u>Serjania</u>. It seems that subsequent dispersal of merocarps by water is also common in <u>Serjania</u> because many of the species occur along rivers and streams.

ECONOMIC BOTANY

Serjania is well known for its ichthyotoxic activity. In a worldwide survey of ichthyotoxic plants, *Serjania* has the greatest number of species utilized for this purpose (Acevedo-Rodríguez, 1989). A total of 57 species ranging from Central to South America and into the West Indies, have been reported to be used as fish poisons. The main compounds responsible for the ichthyotoxism seem to be saponins. Fish in contact with saponins die from asphyxiation because the saponins reduce the surface tension of water and thereby block respiration at the gills. The fish are easily caught because they float near the surface of the water.

The stems of various species of *Serjania* (*S*. *polyphylla*, *S*. *mexicana*, and *S*. *subdentata*) are utilized in the manufacture of baskets and as binding material in the construction of small houses or huts in Cuba and Puerto Rico (Vélez, 1950; Morton, 1981). In the Dominican Republic, the bark of various species of *Serjania* is used for making ropes (Zanoni, pers. comm.)

Various other species have been utilized in folk medicine for the treatment of toothache, rheumatism, and venereal diseases (Morton, 1981).

In Minas Gerais (Brazil), thin cross sections of various species of *Serjania* (along with other species of lianas) are used to decorate small souvenir boxes.

PHYLOGENY

It is apparent that *Serjania* evolved in the Americas because of its absence from other continents, both as living plants and fossils. The oldest known fossil for Serjania and the closely related genera, Paullinia and Cardiospermum, are from the Gatuncillo formation of Panama, which dates from the middle to the upper Eocene(Graham, 1985). The pollen fossil flora of the Gatuncillo formation suggests the prevalence of a tropical climate during the Eocene because it is composed of elements believed to be closely related to modern tropical taxa. If this assumption is correct, then the Paullinieae have had a long evolutionary history under tropical regimes.

If the evolution of Serjania has occurred primarily in the tropics, its most likely center of origin is South America. This hypothesis is supported by the fact that the Eocene floras of southern North America are regarded as subtemperate (Dilcher, 1973), while those of northern South America contain many tropical elements (González Guzmán, 1967). The greater diversity of Serjania in South America might be indicative of a more ancient history for the genus in that region. It is quite possible that Serjania has been present in South America since the Eocene. Cerrado vegetation, where a great number of species of Serjania are found, is also known to date from the Eocene (Eiten, 1972).

However, Mexico is another major center of diversity of Serjania and has a high percentage of endemics. Moreover, there are no fossil records for the group in South America (perhaps because of inadequate preservation), whereas both Serjania and Paullinia are known from as early as the Miocene in Mexico (Graham, 1979). In any case, the existing high diversity of Serjania in both Mexico and South America (particularly Central Brazil) might have to be explained by dispersal from one region to the other through the putative volcanic island arc formed in the late Cretaceous (Raven & Axelrod, 1981). There are two fossil records assignedto the closely related genera Thouinia and Cardiospermum from the Eocene in the U.S.A., which might indicate an ancient history of the group in North America. However, both records lack documentation, and are therefore not reliable (Muller, 1981).

If the conclusions of the cladistic analysis are correct, Serjania is more closely related to the ancestral group from which Paullinia is derived. It is possible that Paullinia and Serjania radiated into different environments at different periods of time. Paullinia might have evolved under the pressures caused by expanding humid forests, while Serjania developed under the pressures of expanding drier vegetation types.

Fossil records for Serjania are known only for a few species. Unfortunately there are no fossil records for species of section Platycoccus. However, judging from its present distribution, it seems most likely that section Platycoccus had its origin in South America.

The phylogeny of the species of Platycoccus are at this moment unresolved. A cladistic analysis of its species (with PAUP) utilizing 15 characters produced 123 equally parsimonious trees at 39 steps. These trees suggest completely different relationships which range from highly unlikely to plausible. A consensus tree produced with the output data of the analysis revealed, as in most of the trees, that *S. squarrosa* is at the very base of section *Platycoccus* and therefore may not even belong in the section. This tree also showed that *S. schunkei* and *S. ampelopsis* share some apomorphic characters and therefore comprise a clade. However, all other species come from the same branching point as the *S. schunkei*-*S. ampelopsis* clade does. The unresolved nature of this cladogram might be due to difficulties in polarizing the characters utilized, as well as to the lack of knowledge of characters in some of the taxa. At this moment, a cladistic analysis is not particularly useful in resolving the phylogeny of section *Platycoccus* and it seems preferable to group the species based on overall similarity.

Serjania communis might represent the ancestral species because it has the widest distribution as well as marked subspecific differentiation. In addition, *S. communis* is marginal to the section because of its fruits which resemble somewhat those of other sections (e.g., section *Eurycoccus*). *Serjania leptocarpa* and *S. dumicola* are very similar to *S. communis*, especially when vegetative characters are considered. Judging from overall similarity and by the distributional ranges of the species, it seems that *S. leptocarpa* and *S. dumicola* (both with a distribution restricted to the Andes) constitute two vicariant species that might have arisen from isolated populations of *S. communis* caused by uplift of the Andes.

Serjania cardiospermoides, *S. cuspidata*, *S. morii*, *and S.*

regnellii are phenetically very similar which suggests a close relationship. The distribution of *S. cardiospermoides* is disjunct from the other three species

Serjania cuspidata resembles *S. communis* var. *communis*, indicating the possible relationship of the two taxa. *Serjania cuspidata* is endemic to the restinga vegetation in southeastern Brazil where *S. communis* constitutes a rare element. It is possible that *S. cuspidata* evolved from peripheral populations of *S. communis* and became adapted to the drier regimes present in the restingas. Gene flow might have been prevented by the depressed fitness of intermediate populations.

Serjania tenuis, restricted to the restingas of southeastern Brazil, seems to be closer to *S. communis*, at least phenetically. The younger substrate where *S. tenuis* occurs, along with its restricted distribution, might indicate that *S. tenuis* is in fact a more recent species, perhaps derived from *S. communis* or from a common ancestor.

Infrageneric Classification

Serjania as treated by Radlkofer (1875), consisted of 12 sections based on fruit morphology (Table XI). The most important characters used were shape and texture of the coccus, width of the partitioning wall, and the presence of a crest or wing around the coccus. His system is difficult to use because there are no qualitative characters defining some of the sections. This results in some intergradation. Moreover, the position of some species treated by Radlkofer was provisional because no fruiting material was known for them.

The suggested interspecific relationship in Radlkofer's classification of Serjania does not stand when modern collections are taken into consideration. As a result, it is necessary to redefine the original sectional concepts in order to account for the variation present in Serjania. Consequently, fewer sections are recognized by me as discrete units within Serjania.

I have combined eight of Radlkofer's sections into one and have created a new section (Table XI). In figure 23, I have illustrated the fruit features defining my concept of the sections of Serjania.

TAXONOMIC TREATMENT

SAPINDACEAE Jussieu, Gen. pl. 246. 1789.

Type genus: Sapindus L.

Tribe **Paullinieae** Kunth, in H.B.K., Nov. gen. sp. V: 77. 1821.

Type Genus. Paullinia L.

Subtribe Paullininae. Type Genus Paullinia L.

Subtribe Eupaullinineae Radlkofer in A. Engler, Pflanzenr. IV: 165 (Heft 98a): 19. 1931.

TABLE XI

Comparison of the proposed classification of Serjania with that of Radlkofer.

Radlkofer's classification (1875)	New classification, proposed here
Section Platycoccus	Section Platycoccus Section Confertiflora
Section Ceratococcus	Section Ceratococcus
Section Eurycoccus	Section Eurycoccus
Section Eucoccus Section Pachycoccus Section Holcoccus Section Dictyococcus Section Simococcus Section Oococcus Section Phacococcus Section Syncoccus	Section Serjania
Section Physococcus	Section Physococcus

Woody climbers. Leaves ternately, biternately, or pinnately compound (less often further divided) with a terminal leaflet; stipules present, although in many species early deciduous. Inflorescences thyrses, the axillary ones bearing a pair of opposite tendrils at lower node, the terminals without tendrils. Flowers zygomorphic; calyx 4-5-merous; corolla of 4 distinct petals, with adnate hood-shape appendage at adaxial surface; nectary disk unilateral, modified into (2) 4 protruding glands; stamens 8, unequal, the anthers dorsifixed or less frequently basifixed, introrse; pollen grains triangular (demitricolporate, triporate) or rod-shape (biporate); ovary tricarpelar, each carpel with a single ovule.

Synoptic Key to Genera of Paullinieae

1. Stigma unbranched, capitate, plumose; pollen grains rod-shaped (biporate)....... <u>Lophostigma</u> Radlk. (monotypic, from Bolivia.)

1. Stigma three-branched not capitate, papillose; pollen grains triangular (demitricolporate or triporate).
   2. Fruits schizocarpic, separating into merocarps; seeds not exposed.
      3. Merocarps samaroid, with proximal wing................. <u>Serjania</u> Miller (about 230 species, from tropical and subtropical America).

3. Merocarps not samaroid, with short wing all around coccus..

   Houssayanthus Hunziker (three species from tropical America).

2. Fruits loculicidal capsules, not separating into merocarps; seeds exposed.

4. Fruits papery and inflated; seeds with white reniform or cordiform hilum; plants herbaceous.

5. Fruits not completely inflated, with marginal wing; anthers with apical appendage; disk glands four; plants producing milky sap........................

   Urvillea Kunth (about 15 species from tropical and subtropical America).

5. Fruits completely inflated, without marginal wing; anthers without apical appendage; disk glands two; plants not producing milky sap....................

   Cardiospermum Linnaeus (about 14 species from tropical and subtropical America).

4. Fruits woody; seeds usually with sarcotesta, but without white hilum; plants woody.....................

   Paullinia Linnaeus (about 150 species from tropical and subtropical America).

SERJANIA Plumier ex Miller, Garden Dict. abr. ed. 4. 1754. Type Species. _Serjania_ _sinuata_ Schumacher (lectotype designated by Croat, 1976) .

Woody climbers. Monoecious with functionally male and female flowers in same inflorescence. Plants usually secreting white resin. Cross section of stems usually with multiple cylinders, or frequently simple. Leaves usually ternately, biternately or pinnately compound; stipules small (except in a few species) and deciduous. Inflorescence axillary or terminal thyrses, never cauliflorous. Fruits schizocarpic, separating into three samaroid merocarps, the wing proximal.

SYNOPTIC KEY TO SECTIONS OF SERJANIA

1. Fruit wing not or hardly distinct from coccus (not or slightly constricted below coccus, coccus flattened, elliptic in cross section.
  2. Seeds spherical or nearly so...... section _Eurycoccus_.
  2. Seeds flattened, lenticular.
    3. Coccus woody with a horn-like projection on lateral wall........................ section _Ceratococcus_.
    3. Coccus membranous or chartaceous, without a horn-like projection......... section _Platycoccus_.

1. Fruit wing strongly differentiated from coccus (strongly constricted below coccus); coccus globose, triangular, or inflated in cross section.
   4. Coccus inflated and membranous... section Physococcus.
   4. Coccus not inflated, woody.
      5. Partitioning wall with a rib (all around) projecting beyond the cocci wall; coccus triangular in cross section.................... section Confertiflora.
      5. Partitioning wall not projecting beyond cocci wall; coccus spherical or triangular in cross section. .... section Serjania.

Section Confertiflora Acevedo-Rodgz. sect. nov.

Cocci transsecti triangulares; dissepimenta ultra coccos excurrentia; cincinni verticillati.

Fruit coccus triangular in cross section; dissepiment projecting beyond coccus, forming a rib-like structure. Inflorescence with whorled, long-peduncled cincinni.

Type species. Serjania confertiflora Radlkofer.

Section Platycoccus Radlkofer, Consp. sect. sp. Serjan. 3, 1874.

Type species. Serjania cuspidata Cambessèdes, (lectotype here designated.

Subsection 1. Radlkofer, l.c.

Subsection 2. Radlkofer, l.c.

Woody to herbaceous climbers. Plants not producing milky (resin) secretion. Stems obtusely 3-5-angular or terete; cross section of stem with multiple steles usually a central and three peripheral ones, (S. hatschbachii has 5 to 7 peripherals) or simple. Leaves ternately or biternately (furtherly compound in S. squarrosa); stipules minute and deciduous. Inflorescence usually long and pendant, with voluble axis. Nectary disk often reduced to two glands, the torus enlarged. Samaras with flat coccus not differentiated from wing, coccus not crested or winged, wing not or slightly constricted below coccus, the partitioning wall oblong or narrow elliptic. Seeds lenticular, flattened.

Distribution. Most of the species in section Platycoccus have restricted distributions. Of the 12 species here recognized, eight are endemic to small areas (Figs. 36, 41), one (Serjania communis) has a very wide distribution (Fig. 29), and three have relatively wide distributions (Figs. 32, 39). As pointed out before, it seems that the restricted distribution of the species of section Platycoccus is related to the dispersal capability of their fruits.

Within section Platycoccus, Radlkofer recognized two subsections and 24 species. In this revision, no subsections are recognized and only nine species are recognized (Table XII). Of the species Radlkofer recognized, nine (known by him from inadecuate fruiting material) belong to other sections of <u>Serjania</u> and another five are here treated as synonyms of species within section <u>Platycoccus</u> (Table XII). Three recently described species belong to <u>Platycoccus</u>, thereby bringing the total number of species I recognize in the section to twelve.

Key to the species of <u>Platycoccus</u>

1. Cross section of stem with single stele.
    2. Leaves biternate, chartaceous; fruit oblong. .... 10. S. ampelopsis.
    2. Leaves ternate, coriaceous; fruit pyriform. .... 11. S. schunkei.
1. Cross section of stem with multiple steles.
    3. Leaves decompound (3-to 5-jugate, lower jugae further divided). ....12. S. squarrosa.
    3. Leaves ternate or biternate.
        4. Cross section of stem with (3) 4 to 5 peripheral steles; fruit wing reduced. .... 9. S. hatschbachii.
        4. Cross section of stem with 3 peripheral steles; fruit wing developed.
            5. Leaves ternate.
                6. Stems sharply triangular (sometimes obtuse in <u>S. regnellii</u>).
                    7. Stem with long (1.5-3 mm), hispid, ferruginous hairs only along ridges.

8. Leaflets ovate sometimes with 3-5-lobate margins, densely hirsute on lower surface. ....4. S. cuspidata.

8. Leaflets oval shape, unlobed, essentially glabrous on both surfaces. .... 5. S. morii.

7. Stems sparsely covered with short, (0.5-0.8 mm long), yellowish hairs. .... 6. S. regnellii.

6. Stems obtusely 3-5 angular

9. Terminal leaflets ovate, widely ovate, sometimes with trilobate margin, lower surface densely to sparsely covered with yellowish, prostrate hairs. .... 7. S. cardiospermoides.

9. Terminal leaflets ovate, elliptic, oblong, or lanceolate, unlobed, with lower surface glabrous. .... 8. S. tenuis.

5. Leaves biternate.

10. Calyx with third and fifth sepals connate 3/4 to entire length; mature stems obtusely to sharply angular, ferruginous-tomentose or glabrescent. .... 1. S. communis.

10. Calyx with third and fifth sepals distinct; mature stems usually obtusely angled, glabrescent.
    11. Petals 3-4 mm long; fruit oblong in outline, 2.2-2.7 cm long.
    .... 3. S. dumicola.
    11. Petals 5-7 mm long; fruit pyriform in outline, 5-6 cm long.
    .... 2. S. leptocarpa.

1. Serjania communis Cambessèdes, in St. Hilaire, Fl. Bras. Mer. 362. 1828. Type. Brazil. Rio de Janeiro; s.d. (fl, fr), St. Hilaire s.n. (lectotype, P, here designated; isolectotype, MPU, n.v.; photo NY of MPU).

Figs. 11d; 15f; 24; 29.

Semi-woody climber to 15 m long. Stems slender (less than 1 cm in diam.), obtusely or sharply 3 or 5-angular, with three major ribs, stems ferruginous-tomentose, especially on main ribs, or glabrescent, the cross section with large, central, subterete or obtusely 5-angled vascular cylinder and three smaller, subterete, elliptic or laterally compressed, peripheral vascular cylinders, these slightly included in central cylinder. Stipules deltoid or subulate, 0.5-1.5 mm long, with same indument as stem. Leaves

TABLE XII

Comparison of the species placed by Radlkofer in Section Platycoccus with the classification proposed here

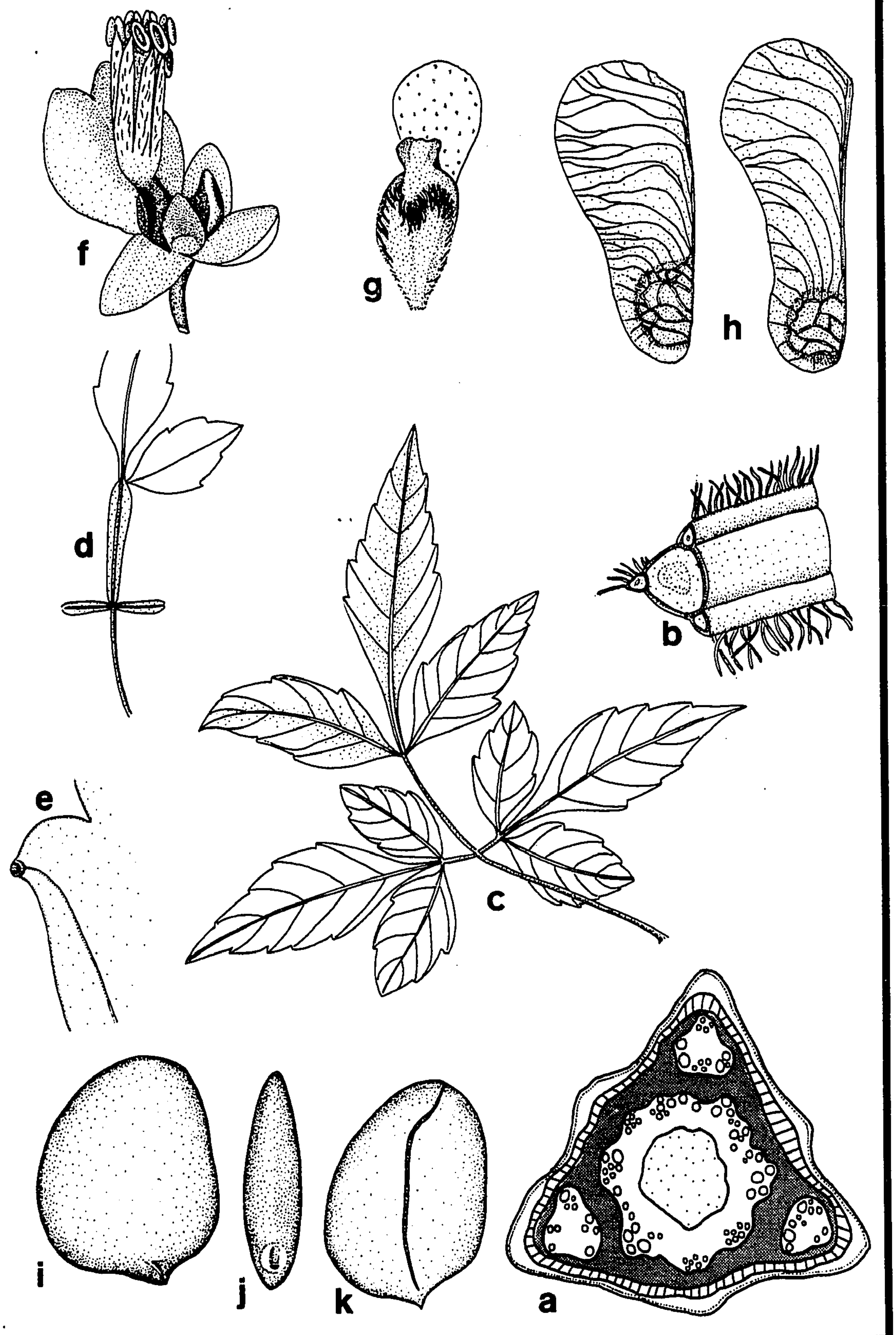
Radlkofer's classification (1931)	classification, here proposed
PLATYCOCCUS	PLATYCOCCUS
1. S. communis	1. S. communis
2. S. hirsuta	S. hirsuta
3. S. stenopterygia	S. stenopterygia
4. S. leptocarpa	2. S. leptocarpa
5. S. viridissima	S. viridissima
6. S. dumicola	3. S. dumicola
7. S. cuspidata	4. S. cuspidata
	5. S. morii
8. S. regnellii	6. S. regnellii
9. S. cardiospermoides	7. S. cardiospermoides
	S. phaseoloides
10. S. tenuis	8. S. tenuis
	9. S. hatschbachii
11. S. ampelopsis	10 S. ampelopsis
12. S. areolata	S. areolata
	11. S. schunkei
13. S. squarrosa	12. S. squarrosa
14. S. platypetala	S. platypetala

TABLE XII (cont.)

Radlkofer's Classification	Classification here proposed
PLATYCOCCUS	CONFERTIFLORA
15. S. grandidens	S. grandidens
16. S. paludosa	S. paludosa
17. S. chartacea	S. chartacea
18. S. confertiflora	S. confertiflora
19. S. inscripta	S. inscripta
20. S. minutiflora	S. minutiflora
21. S. decemstriata	S. decemstriata
	EURYCOCCUS
22. S. trichomisca	S. trichomisca
	PHYSOCOCCUS
23. S. brachyptera	S. brachyptera
	SERJANIA
24. S. foveata	S. foveata

biternate; petioles not winged, sub-terete or angular, adaxially furrowed, 1.7-4.5 cm long, densely to sparsely tomentose, the main rachis sub-terete, margined or narrowly winged, adaxially furrowed, 1-4 cm long, with same indument as petioles, the secondary rachises sub-terete, adaxially furrowed, 1-3.3 cm long, with same indument as petioles; leaflets chartaceous, acute or long acuminate (less often obtuse) and mucronate at apex, the terminal leaflet larger, 3-7.5 (11) x 1.7-3 (5) cm, elliptic, narrow elliptic, ovate, lanceolate, rhombic or less often trilobate, with attenuate or cuneate base, sometimes tapering into more or less prolonged petiolule, the lateral leaflets 2-5 x (0.5) 1.4-2.7 cm, oblong, elliptic, or lanceolate, with obtuse (or rarely obcordate) and oblique base, sessile or petiolulate, the upper surface glabrous or sparsely covered with 0.7-1.5 mm long, yellowish, inflexed or erect hairs with swollen bases and glandular hairs, especially on veins, the lower surface lighter, sparsely covered with same indument as upper surface especially on veins, or glabrescent, the margins ciliate, acutely or obtusely serrate, the teeth clear glandular, the veins mixed craspedodromus, the primary vein slightly prominent on abaxial surface. Inflorescence longer than subtending leaf, the axis 4-angular, 3-6.4 (12.5) cm long, densely covered with same indument as stem, especially on angles, or glabrous, the rachis 4.5-9.3 (12.5) cm long, subterete or angular, furrowed, densely covered with same indument as stem; bracts and bracteoles subulate, 1.2-1.5 mm long, with same indument as rachis, with glandular hairs on margins; cincinni alternate, opposite, or whorled, the peduncle 0.5-1 cm long, with same indument as rachis, 4-5-flowered, the pedicels 1.7-3 (4) cm long, slightly flattened, with same indument as peduncle, articulate at 1 mm or less from base, with tertiary bracteoles at base. **Flowers:** sepals obtuse at apex, minutely ciliate at margins, abaxially covered with whitish, woolly hairs, the outer sepals ovate, (1.5) 2-3 (3.5) mm long, the inner sepals 3-5 mm long, elliptic or ovate, the third and fifth 3/4 to completely connate; petals white or light yellow, spathulate or obovate, clawed, rounded at apex, (4) 4.5-6 (6.5) mm long, densely to sparsely papillate on adaxial surface, the scales ca 3.5-5 mm long, with densely hairy margins, the central ones hood-shaped with fleshy, crown-shaped apex, the lateral ones not fleshy, asymmetric, with outer side bent over disk glands; disk with two central glands, ovate or sub-rounded in outline, periclinally flattened, ca 0.5-1 mm long, the laterals glands obsolete, the torus enlarged; stamens with filaments flattened, densely covered with inflexed, white, 0.2 mm long hairs, the anthers dorsifixed near base, 0.5-0.6 mm long; ovary obovate in outline, densely covered with whitish, inflexed hairs 0.2 mm long, the style with same indument as ovary, the stigmae papillose. **Fruits** widest at base, notched at apex, subcordate or truncate at base, the coccus slightly prominent, not crested, with slightly prominent, reticulate vein network, wing glabrous or with short, yellowish hairs with swollen bases, outline not constricted below

Figure 29. Serjania communis. A. Cross section of stem of S. communis var. communis showing a central and three peripheral steles (Acevedo 1431). B. Cross section of stem of S. communis var. glabra showing indument (Jouvin 465). C. Biternate leaf of S. communis var. communis (Krapovickas 37000). D. Winged rachis, S. communis var. communis (Fdz. Casas 6083). E. Recurved lower glandular tooth on leaflet margin, S. communis var. alsmithii (Klug 2557). F. Staminate flower with petals removed, S. communis var. communis (Heiner 482). G. Central petal with adnate scale, adaxial surface sparsely papillose, S. communis var. communis (Heiner 482). H. Fruits merocarps; right side Krapovickas 37000, left side Belem 1598. I. Seed, lateral side, S. communis var. alsmithii (Killip 28301). J. Seed, ventral side (same as I). K. Embryo with straight cotyledons (same as I).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coccus, the partitioning walls to 2 mm wide. Seeds lenticular, light brown, ca 5 mm long, the embryo with straight cotyledons.

Distribution. *Serjania communis* is the most polymorphic and widely distributed of the species of section *Platycoccus*. It occurs in Colombia, Venezuela, Ecuador, Peru, Brazil, Bolivia, and Paraguay and has been collected in savannas, restingas, dense humid forests, dry scrublands, gallery forests, and in open areas such as forest margins, road margins, and from secondary vegetation. It is found from sea level to 1500 m elevation. It flowers and fruits year-round.

Local Name. Brazil, Sao Paulo: Timbó miúdo.

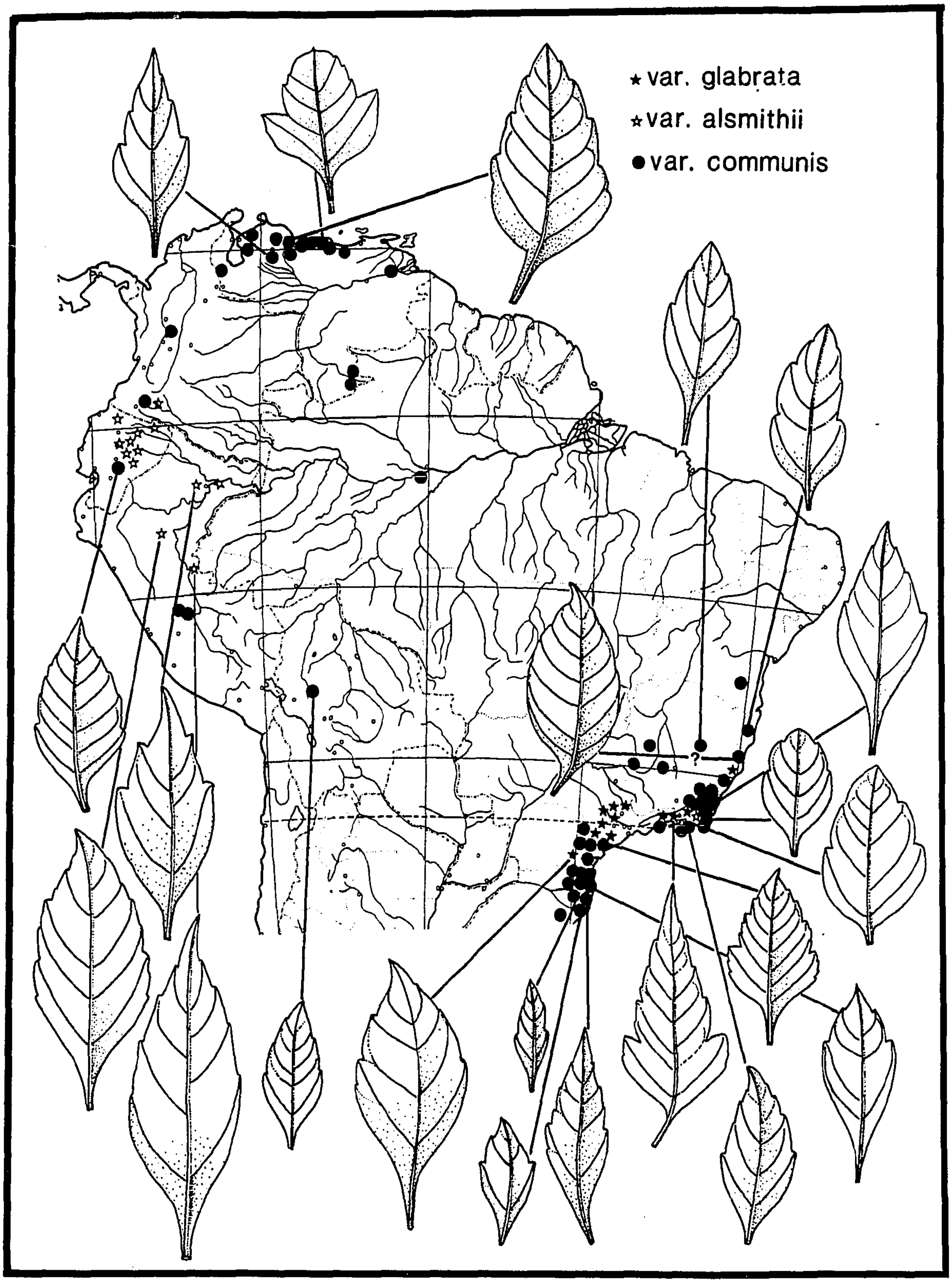
Field observations. The stems of *S. communis* produce a watery sap (not milky) when cut and the inflorescences are pendulous.

The name *communis* refers to the common occurrence or wide distribution of this species.

Key to varieties of *S. communis*.

1. Teeth of leaf margin straight; inflorescence up to two times longer than subtending leaf.
    2. Upper leaf surface smooth; stems obtusely three to five angular, ferruginous tomentose or glabrescent. .... *S. communis* var. *communis*.
    2. Upper leaf surface foveolate; stems sharply triangular, commonly tomentose at angles...... *S. communis* var. *glabra*.
1. Leaf margin teeth recurved; inflorescence ca three times longer than subtending leaf............... *S. communis* var. *alsmithii*.

Figure 30. Distribution and leaf variation of the varieties of *S. communis*.


★var. glabrata
☆var. alsmithii
●var. communis
?

1a. Serjania communis Cambessèdes var. communis.

Type. Brazil. Rio de Janeiro; s.d. (fl, fr), St. Hilaire s.n. (lectotype, P, isolectotype, MPU, n.v.; photo NY of MPU).

Serjania hirsuta Cambessèdes, in St. Hilaire, Fl. Bras Mer. 1: 367. 1828. Type. Brazil. Minas Gerais: Onça, in pasture, s.d. (fl), Laruotte s.n. (lectotype, P, here designated; isolectotype, MPU, n.v., photo NY of MPU).

Serjania communis Cambessèdes var. mollis Radlkofer, Monogr. Serjania 110, 1875. Type. Brazil. Minas Gerais: Caldas, 24 May 1868 (fl), Regnell I 38* (lectotype, MO, here designated).

Serjania communis Cambessèdes var. pilosula Radlkofer, Monogr. Serjania 110, 1875. Type. Brazil. Rio de Janeiro: s.d. (fl), St. Hilaire s.n. (lectotype, P, here designated).

Serjania stenopterygia Radlkofer, Monogr. Serjania, 110. 1875. Type. Brazil. Bahia: s.d. (fl), Blanchet 3747 (lectotype, F, here designated; isolectotypes, F, GH, NY).

Stems 3-5-angular, with 3-5 major ribs. Plant densely pubescent to glabrescent, hairs minute and glandular or not-glandular, yellowish or whitish, erect or prostrate, with swollen base.

Leaflets lanceolate, elliptic, narrowly elliptic, rhombic, or trilobate, the margins acutely or obtusely serrate.

Distribution. *Serjania communis* var. *communis* has the widest distribution of the varieties of *S. communis* (Fig. 30). It has been collected in Venezuela, Colombia, Ecuador, Peru, Brazil, Bolivia and Paraguay from a wide array of ecosystems such as humid forest, gallery forest, open disturbed areas, scrublands, savannas, and the sandy restingas of southeastern Brazil. It ranges from sea level to 1500 m elevation.

The recognition of vars. *mollior* and *pilosula* is not warranted because these taxa are based on insignificant differences. Moreover, Radlkofer cited the same collection under different varietal names. The recognition of *S. hispida* is not accepted here because it represents an extreme in variation in indument character. Likewise, *S. stenopterygia*, differs from the remaining specimens of *S. communis* var. *communis*, only in its winged rachis.

Specimens examined. **VENEZUELA.** Without specific locality; s.d. (fl, fr), *Landsbergen 196* (L). Amazonas: Raudal de los Guaharibos, 2°16'N, 64°38'W, at water's edge, 24 Jul 1951 (fl), *Croizat 294* (NY); Raudal Monserrat, by riverside, 19 Sep 1951 (fl), *Croizat 658* (NY). Anzoátegui: Freites, trail between San Durrial and Los Pajaritos, 64°06'W, 10°03'N, 1200-1400 m, mountain savanna, along creek, 1 Dec 1981 (fl), *Davidse & González 19783* (NY, MO). Aragua:

Colonia Tovar, 10°25'N, 67°17'W, 1854-55 (fl), Fendler 203 (GH, K, US); Turiamo, 500 m, s.d.(fl), Williams 10420 (F-2 sheets, US). Distrito Federal: Caracas, Oct 1846 (fl), Landsberge 166 (S); lower Cotiza, ca Caracas, in savanna, 1200m, 23 Sep 1917 (fl), Pittier 7420, pro parte (US); lower Cotiza, in savanna, 800-1200 m, 14 Oct 1917 (fl), Pittier 7484 (US); Middle Cotiza, ca. Caracas, in savanna, 1100 m, 18 Sep 1921 (fl), Pittier 9840 (GH, NY, US); Catia, Caracas, 950 m, 24 Nov 1938 (fl), Williams & Alston 10674 (F-2 sheets, US, WIS). Miranda: Los Teques, Parque de los Bárbaros, 1100-1500 m, 21 Dec 1917 (fl, fr), Pittier 7610 (G, US). Táchira: Lobatera, La Cazadora, 7°55'N, 72°18'W, dry disturbed evergreen scrub, 21 Jul 1983 (fl), Werff & Ortiz 5405 (MO). Zulia: Bolívar, El Pensando-Las Tres Marias, 10°25'N, 70°55'W, evergreen forest, 7 Feb 1980 (fl), Bunting 8724 (NY).

COLOMBIA. Tolima: La Trinidad, along ravine, 1100-1300 m, 21-25 Dec 1917 (fl), Pennell 3313 (GH, MO, US).

ECUADOR. Santiago-Morona: El Partidero, ridge between rivers Paute and Negro, 730-1180 m, 14 Dec 1944 (fl), Camp 1521 (NY).

PERU. Huancavelica: Tayacaja, above Virgen-Pampa, SE of Tintay, low, evergreen forest, 1000 m, 11 Apr 1964 (fl), Tovar 4602 (US). Junín: La Merced, dense forest, 700 m, 29 May-4 Jun 1929 (fl), Killip & Smith 25408 (F, NY, US).

BRAZIL. Bahia: Prado, 6 km S of Prado, near sea level, 4 Sep 1986 (fr), Acevedo et al. 1542 (CEPEC, MO, NY). Distrito Federal: Without specific locality, 14 Apr 1959 (fl), Pereira 4563 (US).

Espírito Santo: Aracruz, Estaçao de Biologia Marinha Mello Leitao, 9 Jan 1986 (fr), Araujo & Peixoto 296 (NY); Itaguassú, Alto Limoeiro, 22 May 1946 (fr), Brade et al. 18348 (RB-3 sheets). Minas Gerais: Teófilo Otoni, roadside, 14 Aug 1965 (fr), Belém 1598 (CEPEC, NY); Viçosa, road to Sao Miguel, córrego Sujo, 600 m, 28 Jul 1930 (fl, fr), Mexia 4909 (F, GB, MO, NY, US). Paraná: Morretes, Graciosa-Serra Paranapiacaba, 23 Jan 1953 (fl), Stellfeld s.n. (US); Ypiranga, forest margin, 4 Jan 1909 (fl), Dusén 7490 (GH, US). Rio de Janeiro: Alto de Teresópolis, 850 m, s.d. (st), RB 69656 (RB-2sheets); Casimiro de Abreu, roadside, 13 Aug 1986 (fl, fr), Acevedo et al. 1439 (MO, NY, RB); Mangaratiba, Ilha de Marambaia, 14 Jul 1983 (fl), Pace & Ribeiro 14 (NY); Majé, Mar-Apr 1823 (fr), Riedel s.n. (NY); Maricá, secondary forest, low elevation, 15 Aug 1986 (fl, fr), Acevedo et al. 1455, 1456 (MO, NY, RB); Parati-Mirim, 29 Jun 1977 (fl), Almeida et al. 255 (RB-2 sheets); Petrópolis, montane forest, 700- 1044 m, 10-16 Jul 1882 (fl), Ball s.n. (NY); Petrópolis, Jul 1944 (fl), Joes 625 (RB); Piraí, Ribeirao das Lajes, 5 Jul 1983 (fl), Peixoto & Peixoto 1874 (NY); Rio Bonito, Brasilia, Faz. Cachoeiras, secondary vegetation, 13 Aug 1986 (fl, fr), Acevedo et al. 1431 (MO, NY, RB); Rio de Janeiro, Barra da Tijuca, restinga, 11 Jul 1964 (fr), W. Hoehne 5738 (RB), Jardim Botânico, 19 Aug 1945 (fr), Kulmann 6262 (NY, RB-7 sheets), Tijuca, 22 May 1963 (fl), Martins 315 (MO), s.d. (fl), Vauthier 16 (K), Vista Chinesa, roadside, s.d. (fl) Almeida 1609 (NY), Aug 1877 (fl), Glaziou 8592, 8593, 8598, (all K) s.d. (fl), 8963 (K), s.d. (fl), Graham s.n. (K), 1839 (fl), Guillemin 782

(F-2 sheets), s.d. (fr), Riedel 130 (GH), Oct 1828 (fr), Gay s.n. (NY). Rio Grande do Sul: Vic. Sao Leopoldo, Oct 1941 (fl), Leite 570 (NY). Santa Catarina: Without specific locality, s.d. (fl, fr), Mueller 194 (K), s.d. (fl), Schott 5588 (F, NY); Alto Matador, Rio do Sul, forest, 700 m, 17 Oct 1958 (fl), Reitz & Klein 7320 (NY, US); Brusque, secondary vegetation, 10 Oct 1949 (fl), Reitz 3088 (F, US), Azambuja, secondary vegetation, 50 m, 18 Nov 1953 (fr), Klein 742 (US); Ibirama, riverside, 100 m, 20 Sep 1956 (fl), Reitz & Klein 3710 (NY, US); Ilhota, secondary vegetation, 100 m, 21 Oct 1960 (fr), Reitz & Klein 10256 (NY, US); Itajai, Morro da Ressacada, secondary vegetation, 50 m, 14 Oct 1955 (fl), Klein 1706 (NY, US); Sanga da Areia, roadside, 27 Nov 1980 (fr), Krapovickas & Vanni 37000 (CTES). Sao Paulo: Campinas, Chacra Procuça, 24 May 1905 (fl), Heiner 452 (MO).

BOLIVIA. La Paz; NorYungas, ca. Coroico on road from Caranavi to Yolosa, 1000 m, 31 May 1987 (fl), Acevedo & Vargas 1742.(LPB, MO, NY).

PARAGUAY. Amambay: Parque Nacional Cerro Corá, 8 Feb 1982 (fl), Fernández Casas 6083 (NY).

1b. Serjania communis Cambessèdes var. glabra Radlkofer, Monogr. Serjania 110, 1875. Type. Brazil. Without locality, s.d. (fl), Sellow s.n. (lectotype, F, fragment of B, here designated).

Serjania cuspidata Cambessèdes f. dissecta Radlkofer, Monogr. Serjania, 107. 1875. Type. Brazil. Without specific locality, Pohl s.n. (type, n.v.).

Stems sharply triangular, tomentose ferruginous, especially at angles. Upper leaflet surface foveolate. Plants variously pubescent or glabrescent.

Distribution. Serjania communis var. glabra is restricted to the southeastern states of Brazil (Fig. 30). It has been collected in moist forest as well as in open areas at elevations from sea level to 1000 m.

Specimens examined. BRAZIL. Espírito Santo: Ibatiba, margin of forest, 21 Jul 1982 (fr), Hatschbach & Guimaraes 45160 (F). Minas Gerais: Serra, on road MG 010, from Diamantina to Conceiçao de Mato Dentro, 1000 m, 20 Aug 1986 (fr), Acevedo et al. 1496 (NY, PAMG). Paraná: Guaratuba, Boa Vista, margin of forest, 6 Mar 1980 (fl, fr), Oliveira 252 (GB, MO). Rio de Janeiro: Itatiaia, Lago Azul, 24 Jan 1936 (fl), Campos Porto 2867 (B); Itatiaia forest, 900-1000 m, 20 Oct 1927 (fl, fr), Zerny s.n. (V); Macaé, Pico do Frade de Macaé, 900-1000 m, 22 Oct 1985 (fl), Leitmann et al. 14 (NY); Teresópolis, Granja Mafra, 28 May 1977 (fl), Carvalho 540 (NY). Sao Paulo: Without specific locality, woods, 800 m, 22 Jan 1922 (fl), Holway & Holway 1488 (US); Butantan, 29 Sep 1917 (fl, fr), F.C. Hoehne 556 (NY); Santo Amaro, over shrubs, 750 m, 16 Feb 1922 (fl, fr), Holway & Holway 1565 (US); Ubatuba, Mirim River, gallery forest, 10-40 m, 17 Jul 1979 (fr), Jouvin 465 (RB); Sao Paulo, Cidade Jardim, Nov 1940 (fl, fr), W. Hoehne 13426 (NY); Sao Paulo, in woods, 20 Nov 1941 (fl, fr), Pickel 5513 (US); Sao Paulo, Instituto Botânico, 860 m, 21 Feb 1976 (fl), Davidse 10499 (MO).

1c. Serjania communis Cambessèdes var. alsmithii (Macbride) Acevedo-Rodgz. comb. nov.

Serjania alsmithii Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser. 8, 3A: 298. 1956. Type. Peru. Loreto: Yurimaguas, lower Huallaga river, 135 m, woods, 22 Aug-9 Sep 1929 (fr), Killip & Smith 28301 (holotype, F; isotypes, NY, US).

Stems 3-5-angular, glabrescent. Leaflet margins with recurved teeth (at least the lower ones). Inflorescences up to three times longer than subtending leaves.

Distribution. Serjania communis var. alsmithii is restricted to southern part of Colombia, Ecuador, Peru and eastward into central Brazil (Fig. 30). It has been collected from 100 to 1300 m elevation, from moist forest and disturbed areas.

Specimens examined. COLOMBIA. Caqueta: San José da Fragua, disturbed forest along river, 320 m, 11 Jan 1974 (fl), Gentry et al. 9140 (MO).

ECUADOR. Esmeraldas: Lita, Ibarra-San Lorenzo railroad, wet montane forest, 550-650 m, 11 Jun 1978 (fl, fr), Madison et al. 5220 (AAU, F, NY). Napo: Río Conejo rainforest and roadside, 340 m, 1 Apr 1972 (st), Dwyer & MacBryde 9807 (MO); Hac. Cotapino, 500 m, 19-20 Feb 1968 (fl), Harling et al. 7052 (GB, MO); Río Hollín, ca. 10 km E of Archidona, 16 May 1972 (fl), Lugo 2300 (GB, MO). Napo-Pastaza: Archidona, dense forest, 650 m, 19-25 Apr 1935 (fl), Mexia 7244 (US); Tena, dense forest, 400 m, 2-11 Apr 1935 (fl), Mexia 7183 (F-2 sheets, NY, US). Pastaza: Cushillo Urco, ca 8 km N of Puerto Sarayacu, 6 Oct 1974 (fl), Lugo 3963 (GB, MO); Mera, Colonia Játiva, 1100 m, 17 Jan 1977 (fl), Harling et al. 14729 (GB, MO); Sarayaquillo, ca. 10 km E of Puerto Sarayacu, 8 Oct 1974 (fl), Lugo 3995 (GB, MO) .

PERU. Junín: San Ramón, dry woods, 900-1300 m, 9-12 Jun 1929 (fl), Killip & Smith 24756 (F, NY, US). Loreto: Mishuyacu, ca. Iquitos, 100 m, forest, Feb 1932 (fl), Klug 2557 (F, NY). Ucayali: Pucallpa, in open place, 200 m, 4 Jun 1960 (fl), Woytkowski 5767 (MO, US); Pucallpa, open place in forest, 200 m, 3 Jun 1960 (fl), Woytkowski 5757 (MO, US).

BRAZIL. Amazonas: Upper Rio Negro basin, along Rio Castanho, 100-140 m, 16-24 Feb 1946 (fl), Cardona 1420 (F, NY, US).

2. Serjania leptocarpa Radlkofer, Monogr. Serjania 112, 1875.

Type. Brazil. Amazonas: Margin of Rio Negro as far as confluence with Solimoes river, May 1851 (fl), Spruce 1561 (lectotype, K, here designated; isolectotype, CGE).

Figs. 6; 20.2d & e; 31.

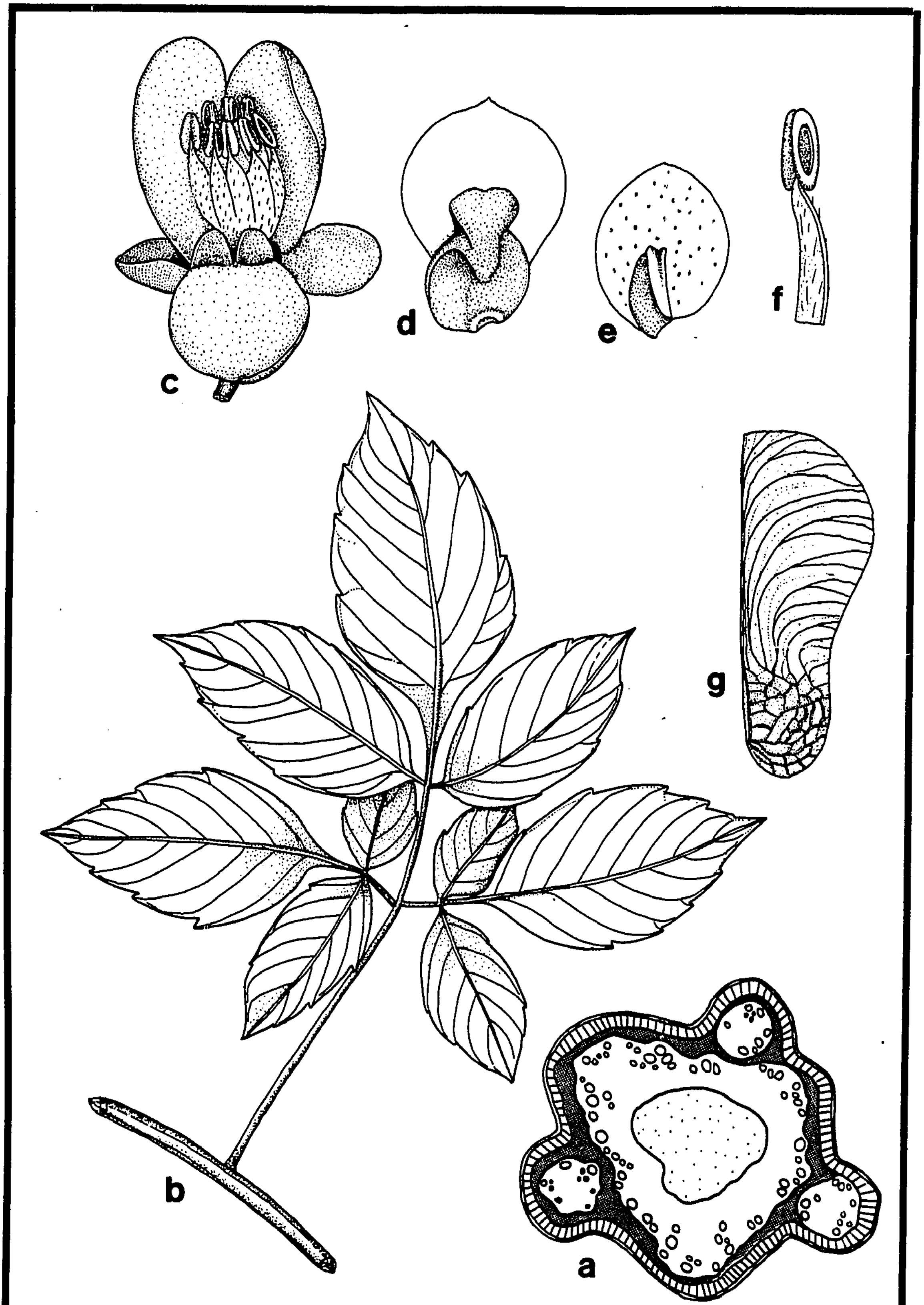
Serjania viridissima Radlkofer, Ergänz. Monogr. Serjania 81. 1886.

Type. Brazil. Rio de Janeiro-Sao Paulo: Without specific locality, 1861-62 (fl), Weir 501 (holotype, K).

Serjania schultesii Cuatrecasas, Revista Acad. Colomb. Ci. Exact. 7: 479. 1952. Type. Colombia. Norte de Santander: La Cabuya, Hoya del río Chitagá, 1300 m, 25 Nov 1941 (fl, fr), Cuatrecasas 13444 (holotype, F; isotype, US).

Semi-woody climber, to 4 m tall. Stems slender, obtusely angular, three-ribbed, glabrescent and smooth, the young stems densely covered with yellowish, straight and curved hairs, 0.3-0.5 mm long; cross section of stem with large, central, obtusely angled vascular cylinder with hollow medulla and three, smaller, subterete, peripheral vascular cylinders slightly included in central one. Stipules deltoid, narrowly deltoid, or subulate, ca 1 mm long. Leaves biternate; petioles not winged, terete, furrowed at adaxial surface, (2.5) 4-6 (7) cm long, glabrous, sparsely or densely covered with small, to 0.2 mm long, curly, yellowish hairs, the main rachis terete, not winged or slightly margined, adaxially furrowed, (1.5) 2.5-5 cm long, with same indument as petiole, the secondary rachis terete, 1-2.5 cm long, with same indument as petiole; leaflets chartaceous, short to long acuminate, often glandular and mucronate at apex, the terminal leaflet larger, 5.5-9 (17.5) x 2-4 (8) cm, ovate, elliptic or lanceolate, with attenuate or abruptly attenuate base, the lateral leaflets 4.5-8 x (1.2) 2-3.2 cm, oblong or lanceolate, with attenuate or obtuse base, the upper surface sparsely to densely covered with minute (0.2 mm long), yellowish, inflexed hairs, the lower surface lighter, densely covered with same type of hairs as upper surface, with dark network of tertiary and quaternary veins, the margins ciliate, remotely and obtusely serrate, the lower serrations glandular, the veins mixed craspedodromus, the primary and secondary veins prominent and densely covered with same type of indument as the upper surface. **Inflorescence** usually longer than subtending leaves, the axis 3-9 (19) cm long, glabrescent, almost terete, the rachis 1-8 (19) cm long, slightly angular and striate, densely covered with small, yellowish, curly hairs; bracts and bracteoles subulate, ca 1 mm long, with same indument as rachis; cincinni alternate, the peduncle 1-2.5 cm long, densely covered with same indument as rachis, 4-7 flowered, the lower peduncles longer; pedicel 4-5 mm long, slightly flattened, with same indument as peduncle, articulate at 1-2.5 mm from base; tertiary bracteoles (prophylls) at base or close to articulation. **Flowers:** sepals 5, the outer sepals 2.5-3 mm long,

Figure 31. Serjania leptocarpa. A. cross section of stem showing a central and three peripheral steles (Breteler 4395). B. Biternate leaf (Cuatrecasas 12101). C. Staminate flower with petals removed (Weir 501). D. Central petal with adnate scale (same as C). E. Lateral petal with adnate scale (same as C). F. Stamen (same as C). G. Fruit merocarp (Tamayo 3818).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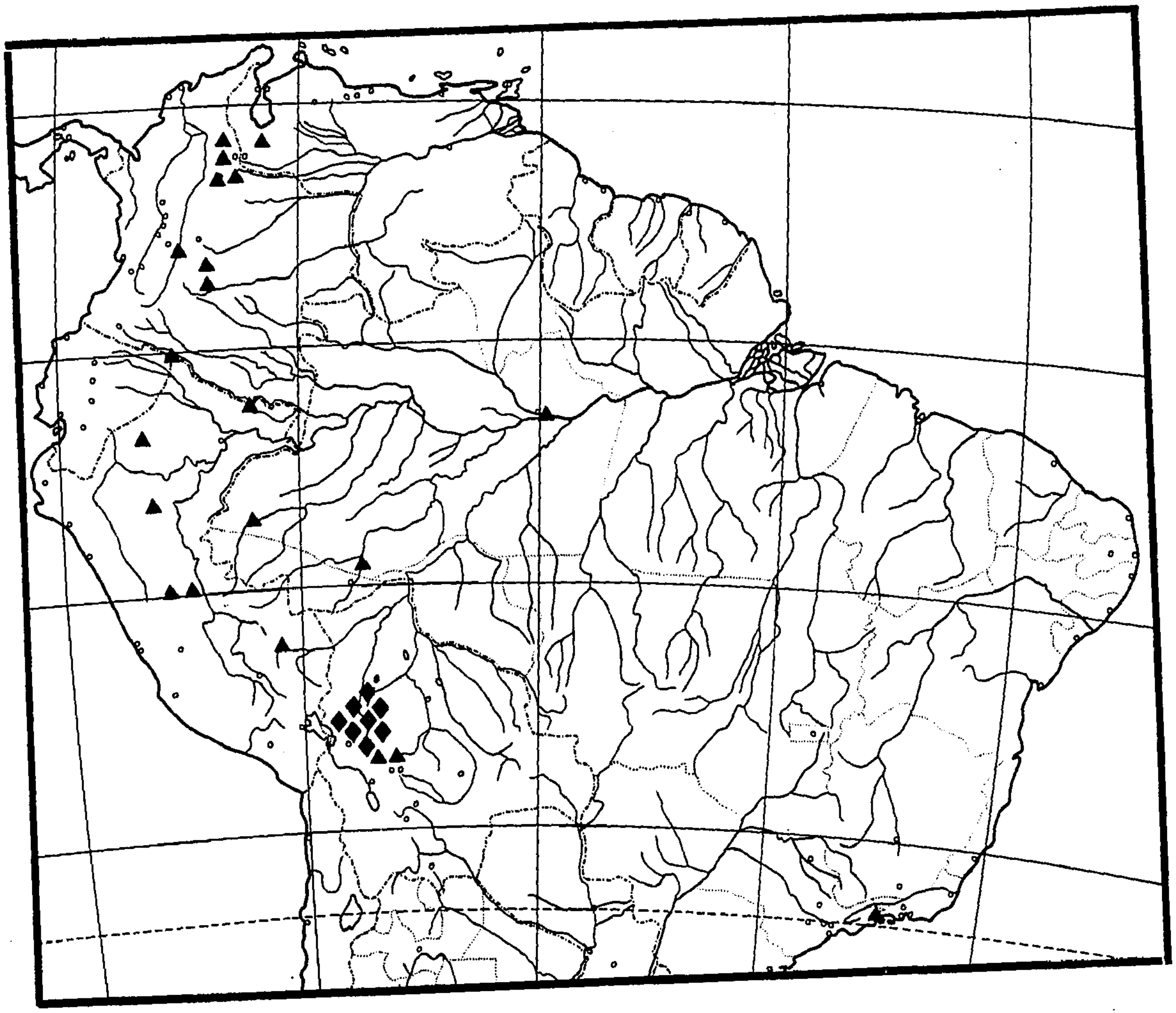
ovate, obtuse at apex, glabrescent, minutely ciliate at margins, the inner sepals 4.5-5.5 mm long, elliptic or obovate, with minute, woolly, yellowish hairs, the third and fifth distinct; petals white, obovate to spathulate, clawed, (5) 6-7 mm long, with minute papillae on adaxial surface; scales 3.5-4.5 mm long, with densely hairy margins, the central ones hood-shaped, with fleshy crown-shaped apex, the lateral ones not fleshy, asymmetric, with outer side bent over disk glands; disk glands two (the laterals obsolete), ovate in outline, periclinally flattened, 1-1.2 mm long; torus slightly enlarged; filaments sparsely covered with small, 0.2 mm long, whitish, inflexed hairs, the anthers dorsifixed, ca 0.75 mm long; ovary spathulate in outline, covered with small papillae and with small, yellowish hairs at edges, the style with same pubescence as ovary, the stigma papillose. Fruit pyriform in outline, 5-6 cm long cm; coccus flat, chartaceous, with reticulate, dark, not-prominent network of veins, not winged dorsally; wings membranous, outline not constricted below coccus, truncate at base. Seeds not known.

Distribution. Serjania leptocarpa is known from Colombia, Venezuela, Ecuador, Peru, Brazil, and Bolivia (Fig. 32). It has been collected in moist, gallery, and secondary forests, as well as in thickets, from 200 to 1600 m elevation. It probably flowers year-round and fruits from August to November.

Specimens examined. COLOMBIA. Magdalena: Magdalena valley,

Figure 32. Distributions of S. leptocarpa and S. dumicola



▲ *S. leptocarpa* ◆ *S.dumicola*

Poponte, 2 Nov 1924 (fl), Allen 788 (MO). Meta: Sierra de La Macarena, Río Guapaya, in dense humid forest, 450 m, 2 Dec 1949 (fl, fr), Philipson et al. 1690 (F, US); dense forest on river bank, 450 m, 29 Nov 1949 (fl),Philipson et al. 1596 (F, US). Norte de Santander: Region del Sarare, La Cabuya, 1300 m, 12 Oct 1941 (fl), Cuatrecasas et al. 12101 (F, GH, US); bet. Toledo & Labateca, 1600 m, 31 Oct 1941 (fl, fr), Cuatrecasas et al. 12829 (BM, F, GH); La Cabuya, 1 Oct 1944 (fl), Garganta 926 (F). Putumayo: Río Putumayo, opposite mouth of Río Gueppi, on border between Ecuador and Peru, 200 m, 19 May 1978 (fl), Gentry et al. 22116 (MO). Tolima: Libano, La Trinidad, by ravine, 1100- 1300 m, 26-29 Dec 1917 (fl), Pennell 3313A (GH, NY).

VENEZUELA. Lara: Guárico, secondary vegetation, Dec 1951 (fl, fr), Tamayo 3818 (VEN). Mérida: Mesa Bolívar, along road to El Vigía, secondary forest, 1000 m, 16 Jan 1964 (fl), Breteler 4395 (G-2 sheets, MO, NY-2 sheets, US).

ECUADOR. Pastaza; Río Curaray, vic Laguna Garzayacu, humid tropical primary forest, 250 m, 20-26 Aug 1985 (fl, fr), Palacios & Neill 676 (NY).

PERU. Amazonas: Mirana; in forest, 250 m, 7 Apr 1960 (fl), Woytkowski 5652 (MO). Junín: Puerto Yessup, in thicket along river, 400 m, 10-12 Jul 1929 (fl), Killip & Smith 26313 (F). Loreto: Florída, río Putumayo, at mouth of río Zubineta, in forest, 200 m, Mar-Apr 1931 (fl), Klug 2080 (F, NY, US); Alto Amazonas, border of río Pastaza between Rimachi and río Witoyacu, 31 Jul 1979 (fl), Díaz et al. 1296 (MO). Madre de Dios: Manu, río Manu, playa 16 km above the mouth, in forest near river, 15 Aug 1976 (fr), Foster & Augspurger 3093 (F, K, MO, NY, US). San Martin: Tarapoto, 27 Aug 1967 (st), Martin & Plowman 1846 (ECON).

BRAZIL. Amazonas: Seringal Aunistella, May 1911 (fl), Ule 9558 (K); along Rio Tarauaca, várzea, s.d.(fl), Krukoff s.n. (MO);

BOLIVIA. Cochabamba: Antahuacama, Espíritu Santo, 750 m, Jun 1909 (fl), Buchtien 2208 (GH, NY-3 sheets, US); Espíritu Santo, 1891 (fl), Bang 1262 (F, GH, K, NY-2 sheets, MO, US, WIS).

Local Name. Peru: Macote.

Field observations. The fresh fruits of S. leptocarpa are red-orange and the inflorescences are pendulous.

Radlkofer's concept of S. leptocarpa was based on the densely hairy specimens available to him. Serjania viridissima was separated from S. leptocarpa by Radlkofer because he felt it to be a closely related but glabrous species. Recent collections show wider variation in pubescence. Some specimens are densely pubescent and others almost completely glabrous. As a consequence, the separation of S. viridissima from S. leptocarpa is not maintained. Typical material of S. schultesii matches perfectly that of S. leptocarpa. An additional name Serjania tamayoi Debrot & Agostini, based on Tamayo 3818 collection is in press in Acta Botanica Venezuelica (Debrot, pers. comm.). I have studied the "holotype" collection, which is in the type collection at VEN, and I have concluded that it is also a synonym of S. leptocarpa.

The vegetative morphology of Serjania leptocarpa is similar to that of S. communis. However, S. leptocarpa has more robust leaves, flowers, and fruits. Serjania leptocarpa differs qualitatively from S. communis in having its third and fifth sepals distinct (not connate 3/4 to entire their length) and by its oblong (not ovate) fruits with the wing outline not constricted (not slightly constricted) below the coccus. These species also differ in their altitudinal distributions. Serjania leptocarpa is mostly found at middle elevations while S. communis occurs at lower elevations.

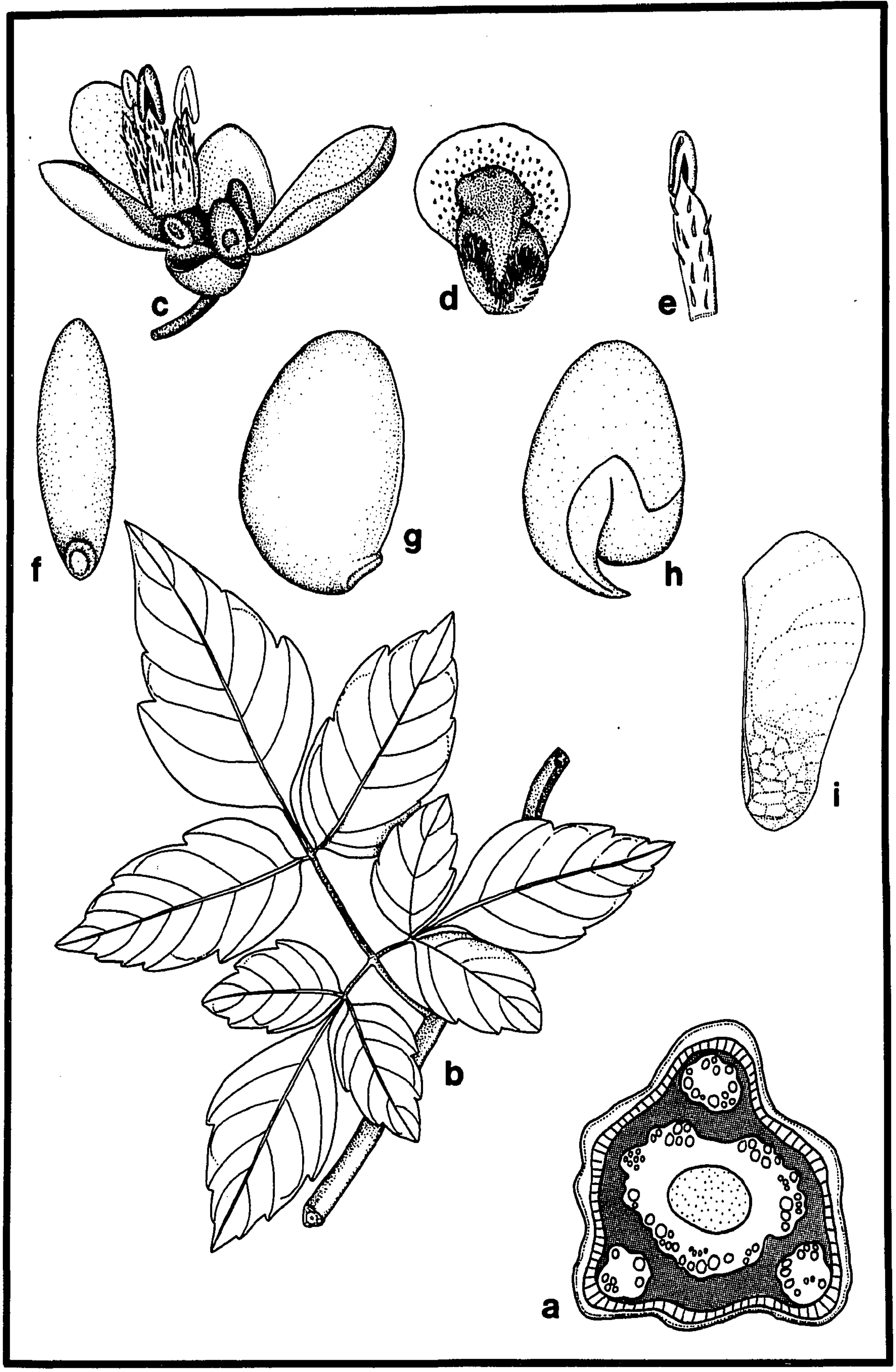
Serjania leptocarpa also resembles S. dumicola, but differs from it by being more robust (i.e., larger leaves, flowers and fruits) and by having yellowish, inflexed (not whitish, erect) hairs.

The name leptocarpa refers to the slender fruits of this species.

3. **Serjania dumicola** Radlkofer, Monogr. Serjania 111, 1875. Type. BOLIVIA. Larecaja: Close to Sorata at Mansamani stream, in thicket, 2650 m, Feb-Mar 1860 (fl, fr), Mandon 775 (lectotype, F, here designated; isolectotypes, F, G, GH, K, MPU-2 sheets, NY-2 sheets). Figs. 7c; 11a; 12d; 15a,c; 33.

Semi-woody climber to 3 m long. Stems slender (less than 1 cm in diam), glabrescent, reddish-brown or gray, obtusely triangular, with three major ribs, the young stems sharply angular, with five ribs, the sulcus densely covered with small (0.5 mm), whitish, erect hairs; cross section of stem with large central, obtusely 5-angled, vascular cylinder and three smaller, elliptic peripheral vascular cylinders slightly included in the central one. **Stipules** deltoid or subulate, 1-1.5 mm long, with same indument as stem. **Leaves** biternate; petioles not winged, sub-terete, adaxially furrowed, (1) 3-5 cm long, densely covered with small (0.5 mm) erect, whitish or yellowish hairs; main rachis margined, sub-terete, adaxially furrowed, 2-3.2 (4) cm long, with same indument as petioles, the secondary rachises sub-terete, adaxially furrowed, 1-1.5 cm long, with same indument as petioles; leaflets chartaceous, obtuse, acute or acuminate, mucronate at apex, the terminal leaflet larger, 3-9 x 1.5-4 (5) cm, ovate or lanceolate, with attenuate, abruptly attenuate or truncate base, the lateral leaflets 2.5-6 x (0.8) 1.7-3.5 cm, oblong or lanceolate, with rounded and oblique base, sessile, the upper surface glabrous to sparsely covered with small (0.3-0.5 mm), whitish or yellowish, inflexed hairs, the veins sparsely or densely covered with same indument, the lower surface lighter (whitish), sparsely covered with whitish, erect hairs 0.5 mm long, especially on veins, the margins ciliate, revolute, remotely and acutely serrate, the teeth glandular-mucronate (glands acute), the veins semicraspedodromus, the primary vein slightly prominent underneath. **Inflorescence** usually longer than subtending leaves, the axis 3.5- 10 cm long, twining, densely covered with same indument as stem, 4-angular, the rachis 1-9 (14) cm long, slightly flattened and angular, densely covered with same indument as stem; bracts and bracteoles subulate, 1.2-1.5 mm long, with same indument as stems; cincinni alternate, the peduncle 0.5-2.6 cm long, with same indument as rachis, 3-8-flowered; pedicels 1.7-3 (4) cm long, slightly flattened, with same indument as peduncle, articulate at middle, with tertiary bracteoles at base. **Flowers:** sepals 5, minutely ciliate at margins, woolly, sometimes with white, inflexed, 0.1 mm long hairs, obtuse at apex, the outer sepals 1.5-2.2 mm long, ovate, the inner sepals 2.5-3.5 mm long, elliptic or ovate, the third and fifth distinct; petals white, spathulate or obovate, clawed, rounded at apex, 3-4 mm long, with minute papillae on adaxial surface; scales ca. 3 mm long, with densely hairy margins, the central ones hood-shaped, with fleshy crown-shaped apex, the lateral ones not fleshy, asymmetric, with outer side bent over disk glands; disk glands four, the central glands ovate in outline, periclinally flattened, ca. 1 mm long, the lateral glands elliptic and smaller, adnate to the slightly enlarged torus; filaments flattened, sparsely covered with inflexed, white, 0.2 mm long hairs, the anthers dorsifixed, 0.7 mm long; ovary spathulate in outline, densely covered with yellowish, inflexed hairs 0.2 mm long, the style with same indument as ovary, the stigma papillose. **Fruits** oblong in outline or slightly wider at base, 2.2-2.7 cm long, notched at apex, subcordate at base, the coccus flat, not winged, with dark, slightly prominent, reticulate network of veins, the wing glabrous, with outline slightly constricted below coccus, the partitioning walls to 2 mm wide. Seeds lenticular, dark brown;

Figure 33. Serjania dumicola. A. Cross section of stem, showing a central stele and three peripheral ones. B. Biternate leaf and stem C. Staminate flower with petals removed. D. Central petal with adnate scale. E. Stamen, filament with inflexed hairs. F. Seed, ventral side. G. Seed, lateral side. H. Embryo, showing cotyledons configuration. I. Fruit merocarp. All drawn from Acevedo & Vargas 1759 except for the seeds and embryo which are from Buchtien 710)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embryo with adaxial cotyledon biplicate and the abaxial cotyledon bent over.

Distribution. Serjania dumicola is known by a few collections from the Bolivian Department of La Paz (Fig. 32). It has been collected in thickets or open areas with shrubby vegetation from 2400 to 2700 m elevation. It flowers from December to June and fruits from February to June.

Specimens examined. **BOLIVIA.** La Paz. Larecaja: Between Guanay and Tipuani, Apr-Jun 1892 (fl), Bang 1450 (F); Sorata, vic. of Sorata, shrubby forest along stream, 2800 m, 4 Dec 1983 (st), Beck 8632 (CTES); 2.9 km from San Pedro along road to La Gruta de San Pedro, 2450 m, 3 Jun 1987 (fl, fr), Acevedo & Vargas 1759 (F, LPB, NY-2 sheets, MO, US); 4.4 km from San Pedro to Consata, rocky hillside with shrubs, 2700 m, 5 Dec 1983 (fl, fr), Beck 8666, 8667 (both LPB, NY), rocky entrance to the gorge, 2780 m, 12 Jun 1950 (fl), Brooke 6493 (F); without specific locality, 2440 m, Feb 1886 (fl), Rusby 518 (F, GH-2 sheets, NY-3 sheets,). Nor Yungas: Milluguaya, 1300 m, Dec 1917 (fl, fr), Buchtien 710 (GH-3 sheets, NY, US); without locality, 1890 (fl, fr), Bang 421 (F, GH-2 sheets, K, MO, NY-5 sheets, US-2 sheets).

Field observations. The stems of S. dumicola produce a watery sap (not milky) when cut and the inflorescences are pendulous.

Serjania dumicola resembles *S. leptocarpa* but differs from it by its: smaller flowers and fruits, whitish erect (not inflexed and yellowish) pubescence, acute glandular-mucronate (not obtusely glandular) teeth, mucronate apex, obtuse mature stem (not sharply ribbed). In overall morphology, *S. dumicola* is very similar to *S. communis*. However, *S. dumicola* has wider fruits with an oblong outline (not slightly constricted below the coccus), the third and fifth sepals are distinct (not connate along most of their length), and the cotyledons are biplicate (not straight). *Serjania dumicola* might represent a vicariant species which evolved from populations of *S. communis* after the uprise of the Andean highlands.

The name *dumicola* means dweller in thickets and refers to the habitat of the species.

4. *Serjania cuspidata* Cambessèdes, in St. Hilaire, Fl. Bras. Mer. 1: 356. 1828. Type. Brazil. Rio de Janeiro: Vic. Rio de Janeiro, on fence and primary forest, 1816 (fl), *St. Hilaire Catal A' 732* (lectotype, P, here designated; isolectotype, MPU, n.v., photo ex MPU at NY).

Figs. 8a; 11b; 14b; 23a; 26c; 34.

Paullinia guarumina Vellozo, Fl. flum, 160, 1829 (1825); Vellozo, Fl. flum. Icon. IV, t. 35, 1831 (1827). Type. Brazil. Rio de Janeiro: Exact locality unknown (lectotype, Tabula 35 in Vellozo, here designated).

Paullinia meyeniana Walpers, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. XIX: 312. 1843. Type. Brazil. Rio de Janeiro, Meyen s.n. (n.v.)

Urvillea ferruginea Lindley, Botanical Register 13: no. 1077, 1827. Type. Brazil. Exact locality unknown (lectotype, Figure 1077 in Lindley, here designated).

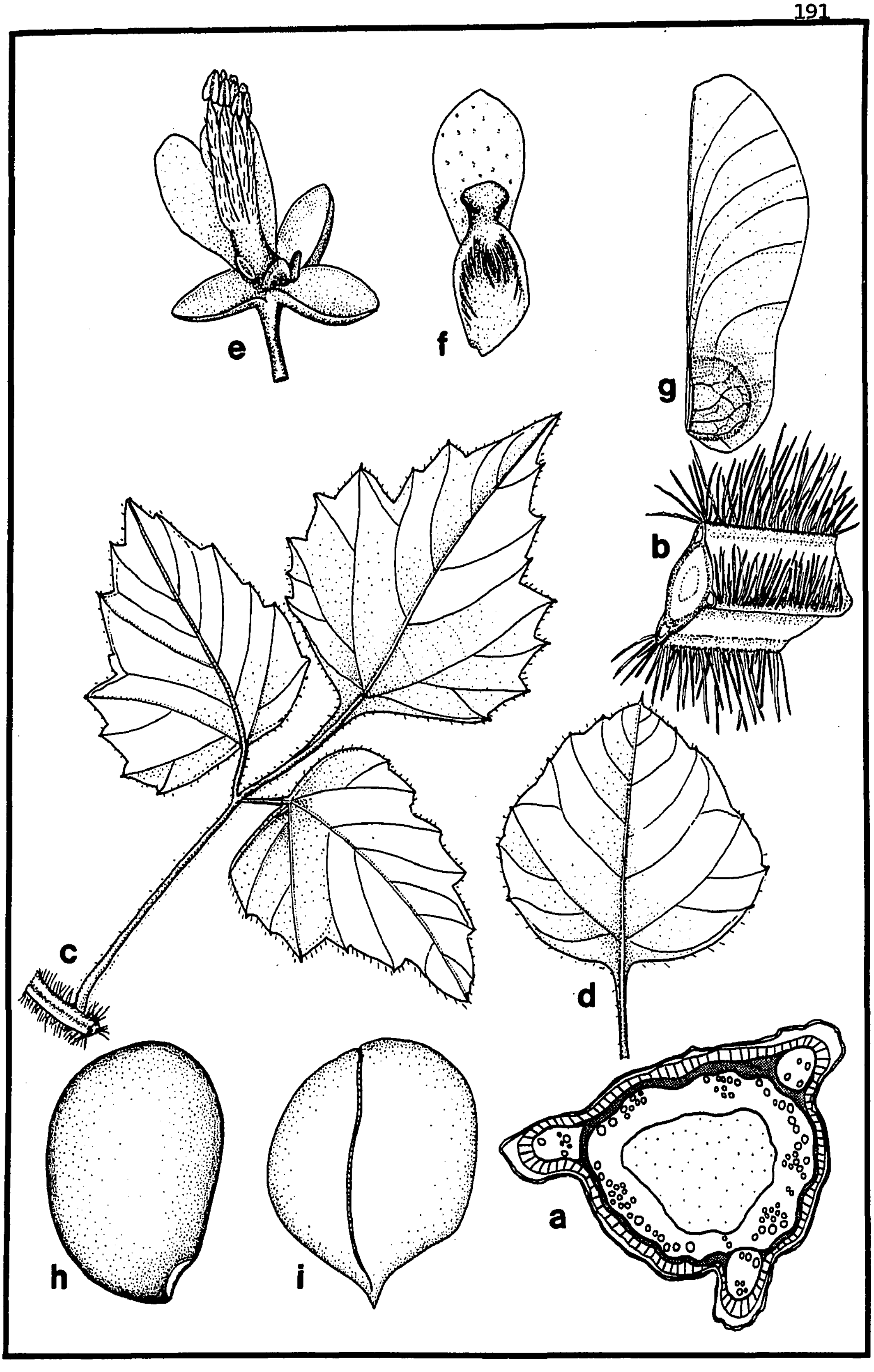
Serjania cuspidata Cambessèdes f. genuina Radlkofer, Monogr. Serjania, 107. 1875. Type. Based on same specimen as S. cuspidata Cambess.

Woody vine to 3 m long. **Stems** sharply triangular, with six ridges, three of which are very much more prominent, the corners covered with stiff, coarse, 2-3 mm long, ferruginous hairs, the sides glabrescent, the young stems with an extra row of hairs on each side; cross section of stem with central, rounded, large vascular cylinder with hollow pith and 3 peripheral, smaller, rounded vascular cylinders. **Stipules** linear, 5 x 0.8 mm, acute, with hirsute margins. **Leaves** ternate, or sub-biternate (fide Radlkofer); petioles not winged, shorter than leaflets, adaxially flattened, densely covered with rusty, curly, 0.2 mm long hairs; leaflets chartaceous, with acute and cuspidate apex, the terminal leaflet larger, ovate, widely ovate, deltoid, trilobate, or 5-lobate, (4.7) 6-8 (10.7) x (4) 5.5-7.6 (10.5) cm, with truncate, attenuate, abruptly attenuate or subcordate base, decurrent onto more or less prolonged (1-4 cm long) petiolule, the lateral leaflets oblong-ovate, (3.6) 4.5-7 (9.1) x (2.5) 3.2-5.1 (6.9) cm, with oblique or subcordate base, shortly petiolulate (1-2 cm long), the upper surface densely to sparsely covered with rusty, prostrate hairs, especially on veins, sometimes glabrescent, the lower surface densely covered with rusty, stiff, erect hairs, especially on veins, the margins serrate and covered with rusty, stiff, erect hairs, the teeth clear glandular, acuminate, obtuse or rounded, the veins craspedodromus, the primary and secondary veins slightly prominent on lower surface. **Inflorescence** axillary, two to three times longer than subtending leaf, the axis 3 to 4-angular, usually twining, hirsute (hairs to 0.3 mm long), the rachis subterete or slightly flattened, with minute (0.2 mm long), whitish or yellowish curly hairs; bracteoles narrowly oblong, with ciliate margins and acuminate apex, the primary bracts 3-3.5 mm long, the secondary bracts ca. 1 mm long; cincinni alternate, 0.4-0.7 (2) cm long, densely covered with small, rusty, curly hairs, usually 5-flowered; pedicels 2.5-3.5 (5) mm long, articulate ca 1.2 mm from base, same indument as peduncle but finer. **Flowers:** sepals with same indument as pedicel, especially on adaxial surface, the outer sepals

2.5-3.2 (4) mm long, ovate or lanceolate, with obtuse apex, the inner sepals (3.2) 3.5-5 mm long, obovate, with obtuse apex, the third and fifth sepals connate from 1/2 to 4/5 of their length; petals white, 5-6.3 mm long, spathulate to broadly spathulate, adaxially minutely papillate, the apex rounded; scales of central petals 3.5-4 mm long, hood-shaped, with fleshy, crown-shaped apex and ciliate margins, the scales of lateral petals 3 mm long, with slightly fleshy apex and ciliate margins; disk glands 2 (the lateral ones obsolete), ca 1 mm long, ovate in outline, obtuse at apex; torus enlarged; filaments densely to sparsely covered with white, inflexed hairs; anthers elliptic, dorsifixed near base, 0.5-0.6 mm long; ovary oblong to elliptic, densely covered with whitish or yellowish, small, curly hairs. **Fruits** 2.7-4 cm long, outline oblong or ovate, sparsely covered with small, erect, yellowish hairs with swollen base, the base truncate, subcordate or cordate, the apex retuse, the cocci flattened, with slightly prominent reticulate network of veins, the outline of wing not constricted or slightly constricted below coccus, the partitioning wall narrow-elliptic, ca 2 mm wide. Seeds lenticular, light brown, ca. 0.7 mm long. Embryo with erect cotyledons.

Distribution. _Serjania_ _cuspidata_ occurs in the Brazilian states of Rio de Janeiro and Sao Paulo. A doubtful collection comes from the state of Bahia (Fig. 36). This species occurs naturally in the coastal restinga and restinga forest but extends into disturbed

Figure 34. Serjania cuspidata. A. Cross section of stem showing central stele and three peripheral steles (Acevedo et al. 1458). B. Stem showing indument and triangular cross section (Guillemin 713). C. Ternate leaf and part of stem stem (Brade 29). D. Oval leaflet (Guillemin 713). E. Staminate flower with petals removed (Lagasa 9). F. Central petal with adnate scale (Lagasa 9). G. Fruit merocarp (Hoehne SPF 16098). H. Seed, lateral side (Hoehne SPF 16098). I. Embryo showing straight cotyledons (Hoehne SPF 16098).



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areas such as along roadsides and open scrubs. It ranges from sea level to 600 m. Flowering collections have been gathered for most parts of the year, however, peak flowering is from March to August. Fruiting mostly occurs from April to August.

Specimens examined. BRAZIL. Without specific locality, 1904 (fl), Anonymous s.n. (MO), cultivated in greenhouse, 24 May 1865 (fl) Anonymous s.n. (NY), 1840 (fl), Armstrong s.n. (NY); s.d. (fr), Burchell 72A (K); s.d. (fr), Gaudichaud 842 (F, a fragment from B); cultivated in greenhouse, 1 Nov 1858 (fl), Gay s.n. (K); s.d. (fl,fr), Hooker s.n. (GH); s.d. (fl, fr), Sellow 247 (F, a fragment from B, GH, MO, photo NY of B). Bahia: Without specific locality, s.d. (fl), Guillot s.n. (NY). Rio de Janeiro: Without specific locality, 24 May, 1865 (fl), Anonymous s.n. (NY), Apr 1838 (fl), Armstrong 77 (K), 1842 (fl), Clausen 49 (GH), s.d. (fl), Douglas s.n. (K), 1837 (fl), Gardner 164 (K), 1832 (fl), Gaudichaud 172 (F), Feb 1874 (fl), Glaziou 6498 (K), 1821-23 (fl, fr), Graham s.n. (K), 1839 (fl), Guillemin 34 (F), 1841 (fr), Hombron s.n. (NY), Feb 1837 (fl), Luschnatt (?), Mart. Herb. Fl. Bras. 70 (F, GH, K, MO-2 sheets, NY), s.d. (fr), Riedel s.n. (NY), Jun-Jul 1832 (fl), Riedel & Luschnatt 502 (NY-2 sheets), 1837 (fl), Tweedie 1260 (K), 1837 (fl) Tweedie s.n. (CGE), 1833 (fl), Vauthier 512 (F, GH), 1844 (fl), Widgren s.n. (US); 24 Nov 1938- 6 Jan 1939 (fl), Wilkes s.n. (GH, NY-2 sheets); Angra dos Reis, 19 Apr 1926 (fl), F.C. Hoehne & Gehrt 17420 (NY); Campo Grande, Serra do Medonha, 400-600 m, 4 Apr 1978 (fl), Lima et al. 321(NY); Magé, Maguá beach on Guanabara Bay, 100 m from shore, mangrove "restinga" scrub, 20 Nov 1966 (fl), Eiten & Eiten 7845 (US-3 sheets); Niteroi, Jurujuba Bay, s.d. (fl), Miers 3720 (K), in thicket, 15 Dec 1901 (fl, fr), Dusén 115 (GH); Rio de Janeiro, s.d. (fl), Schott 5592 (F, NY), 1843 (fl), Weddel 340 (NY), Avenida Nyemeyer, in rocky area, 11 Jul 1961 (fl), Duarte 5901 (BR, NY, US),Corcovado, 1837 (fl), Gardner 164 (CGE), s.d. (fr), Miers 3967 (K), between Furnas and Alto da Boa Vista, 11 Mar 1959 (fl), Duarte & Pereira 4631 (NY, US), Gávea, 90 m, 8 Sep 1921 (fl), Holway & Holway 1097 (US), Gávea Pequena, 7 Mar 1931 (fl), Brade 29 (GH), 22 Mar 1977 (fl), Lagasa 9 (K, US), Pao de Açúcar, 12 Jul 1915 (fl, fr), Rose & Russell 20229 (NY, US), Jacarepaguá, in thickets, 22 Mar 1903 (fl), Dusén 1986 (F, GH, NY, US), over shrubs, 30 m, 16 Nov 1921 (fl), Holway & Holway 1310 (US), Jardim Botânico, 7 Dec 1966 (st), Pereira 10503 (F, K), Leblon, Nyemeyer Ave., 16 Apr 1958 (fr), Pereira et al. 3606 (NY, US), Restinga de Grumarí, margin of restinga, 16 Aug 1986 (fr), Acevedo et al. 1458 (NY, RB), Restinga de Jacarepaguá, margin of flooded formation, 10 Dec 1971 (fl, fr), Sucre 8085 (NY), Tijuca, 12 May 1931 (fl, fr), Lutz 594 (F-2 sheets, W), Vista Chinesa Road, in front of Biological Station, 10 Aug 1960 (fl), Angeli 228 (MO); Rio de Janeiro-Petrópolis, Camboaba, 20 Oct 1938 (fl), Alston-Lutz 102 (BM); Saquarema, Bomsucesso, open woods, 54 m, 13 Sep 1921 (fl), Holway & Holway 1106 (US); Praia de Jacuné-Saquarema, remnant restinga forest, 10 Aug 1986 (fl, fr), Acevedo & Farney 1421 (NY, RB); Restinga de Jacuné, 30 May 1978 (fl), Lima 556

(NY). Sao Paulo: Santo Amaro, 17 May 1932 (fr), W. Hoehne s.n. SPF 16098 (NY).

Local Names. Brazil: Guarumina (Pio Correa, 1931) timbó cabelludo, timbó de peixe (Radlkofer, 1931).

Field observations. The stems of *S. cuspidata* do not produce milky sap when cut, and the inflorescences are pendulous with twining axis.

Serjania cuspidata resembles *S. regnellii* and *S. cardiospermoides* in general morphology. However, *S. cuspidata* differs by the presence of stiff, erects hairs on the stems angle and leaf margins. *Serjania cardiospermoides* var. *subjubata* has similar hairs on the main stem angles but not as long or as abundant. Moreover, the leaflets of *S. cardiospermoides* are chartaceous and almost glabrous.

The name *cuspidata* probably refers to the abruptly acuminate or cuspidate apex of the leaflets of this species.

5. *Serjania morii* Acevedo-Rodríguez, Brittonia 40: 285, fig. 2. 1988. Type. Brazil. Bahia: Santa Cruz de Cabrália, 4-6 km E of ecological station Pau-Brazil (ESPAB), ca 17 km W of Porto Seguro, on old road to Santa Cruz de Cabrália, disturbed Southern-Bahian moist forest, 16°23'S, 39°8'W, 40 m, 19 Oct 1978 (fl), Mori et al. 10855 (holotype, CEPEC; isotype, NY).

Fig. 35.

Woody vine. **Stems** sharply triangular, the angles covered with stiff, coarse, 1.5-2 mm long, hispid, ferruginous hairs; cross section of stem with central, rounded, large vascular cylinder with hollow medulla and 3 peripheral, smaller, rounded vascular cylinders. **Stipules** oblong, 0.2-0.7 cm long, acute, ciliate at margin. **Leaves** ternate, 15-20 X 20-21 cm; petioles not winged, much shorter than leaflets, cylindric, slightly swollen at base, adaxially furrowed and covered with small (0.5 mm), curled, ferruginous hairs; leaflets chartaceous, glabrous except for few hairs on margins and adaxial surface of veins, abruptly acuminate at apex, with repand-denticulate margins, terminal leaflet oval, 11-13 X 7-8.3 cm, the base rounded or obtuse, decurrent into a more or less prolonged (1-2 cm) petiolule, lateral leaflets oval-oblong to obovate, sometimes oblique, base rounded, shortly petiolulate. **Inflorescence** axillary, 3 times longer than subtending leaf, the axis sparsely covered with erect, 1 mm long, rusty hairs; bracts narrowly oblong, 5.2 X 1 mm, margins ciliate, apex acuminate; cincinni alternate, 1-1.5 cm long, densely covered with small, rusty, curled hairs, usually 5-flowered; bracteoles lanceolate, ca 3 mm long; pedicel ca. 4 mm long, articulate near base, densely covered with small (0.15 mm), yellowish, inflexed hairs. **Flowers:** sepals with same indument as pedicel, especially on adaxial surface, the outer sepals ca. 4 mm long, ovate, with obtuse apex, the inner sepals 5-5.5 mm long, ovate-elliptic, with obtuse apex, third and fifth sepals connate from 1/4 to 2/5 of their length; petals white, 6.5-7.5 mm long, broadly spathulate, adaxially minutely papillate,

Figure 35. Serjania morii. A. Cross section of stem showing a central and three peripheral steles. B. Ternate leaf and fragment of stem. C. Detail of stem showing stipules. D. Ciliate margin of leaflet with glandular teeth. E . Staminate flower with petals removed. F. Central petal with adnate scales. G. Lateral petal with adnate scale. All drawn from Morii et al. 10855.

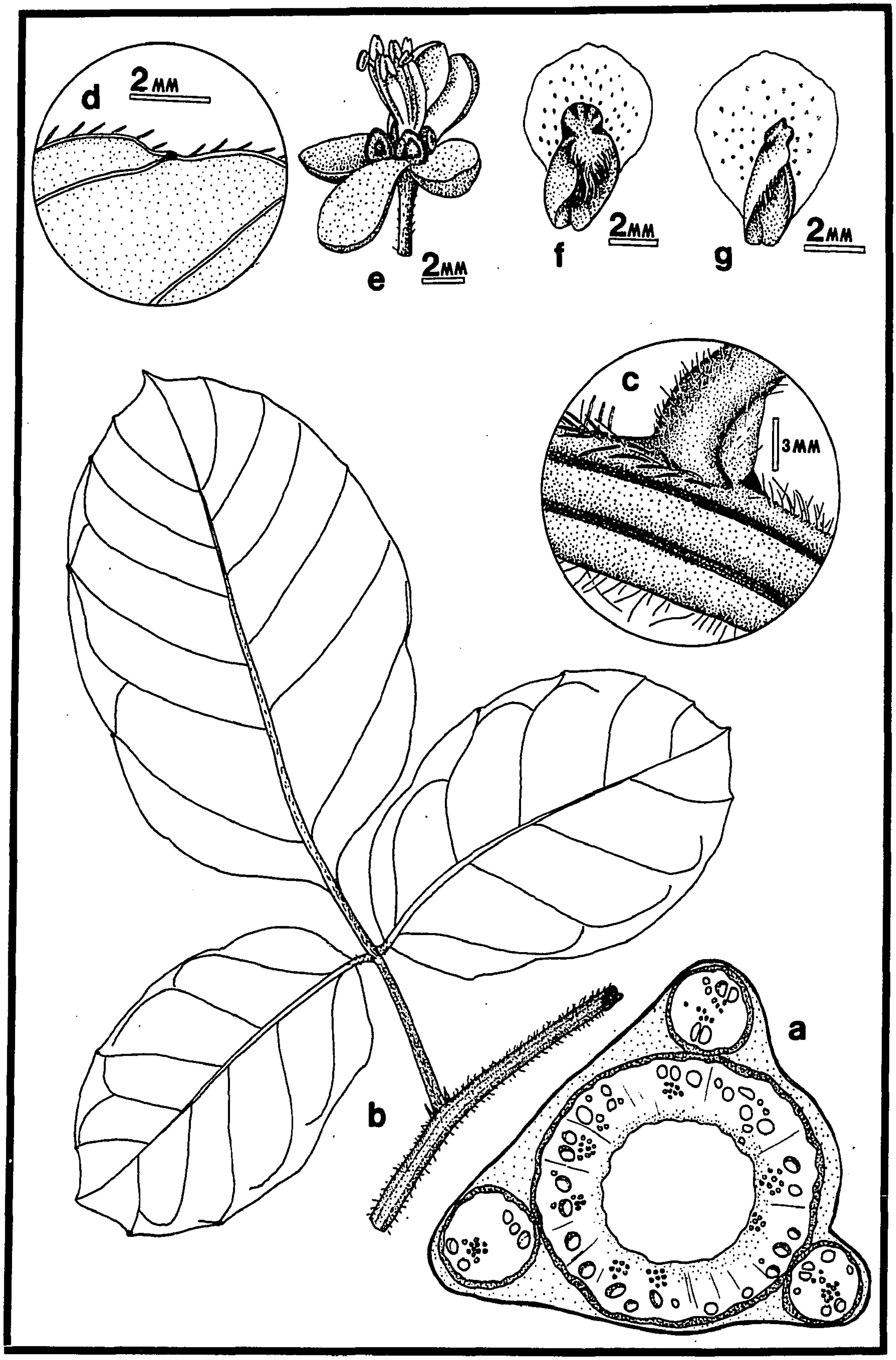
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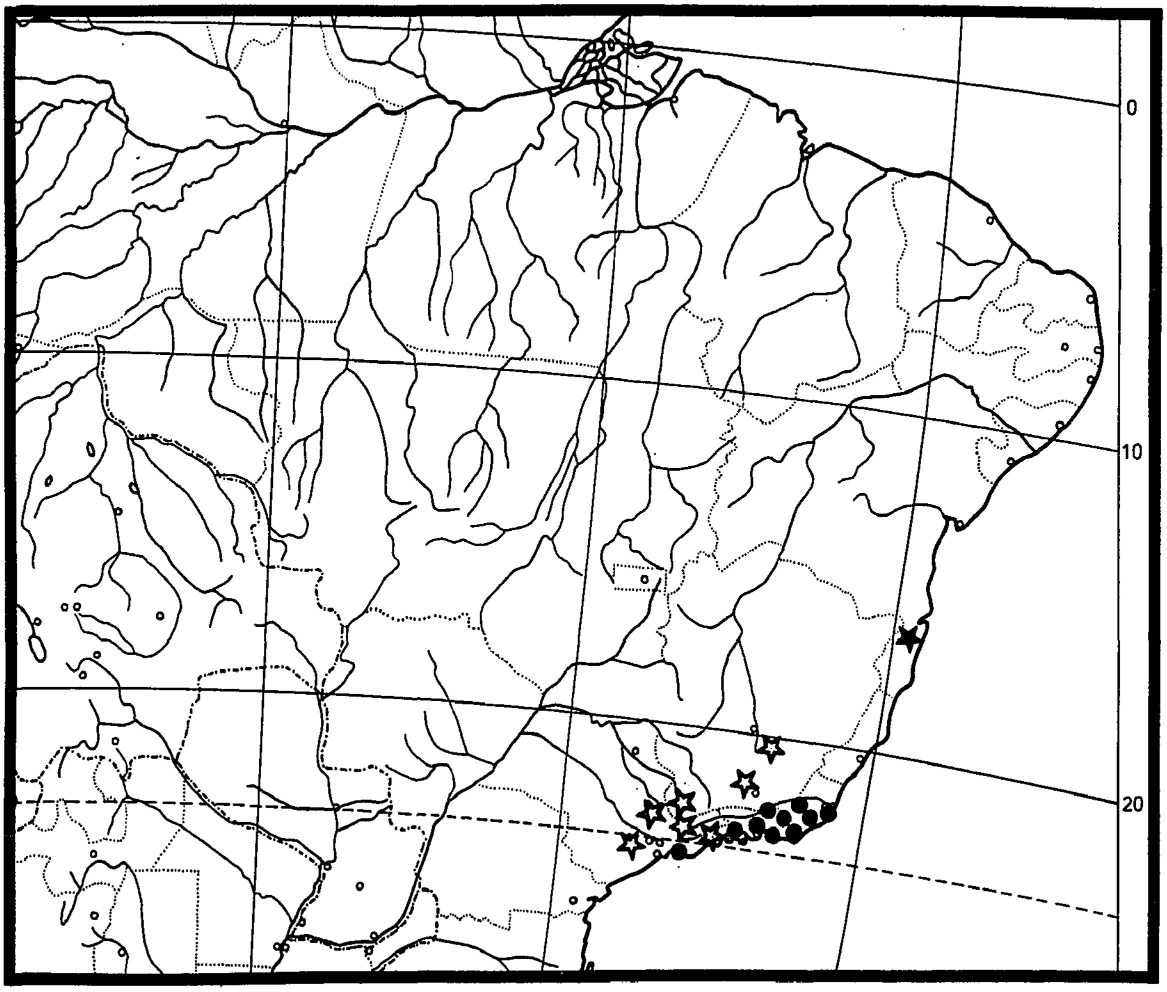
Figure 36. Distribution of three endemic species of section Platycoccus. Serjania cuspidata, S. morii, and S. regnellii.



● **S. cuspidata**
★**S. morii**
✫**S. regnellii**

the apex rounded; the scales of central petals 5 mm long, hood-shaped, with fleshy, crown-shaped apex and ciliate margins, the scales of lateral petals 4 mm long, with slightly fleshy apex and ciliate margins; disk glands 4, the central glands 1.5 mm long, broadly ovate in outline, and obtuse at apex, the lateral glandsreduced, ca. 0.7 mm long, annular; filament puberulent; anthers dorsifixed, elliptic, ca. 1 mm long; ovary not seen. Fruit and seeds not seen.

Distribution. Serjania morii is known only from the type (Fig. 36).

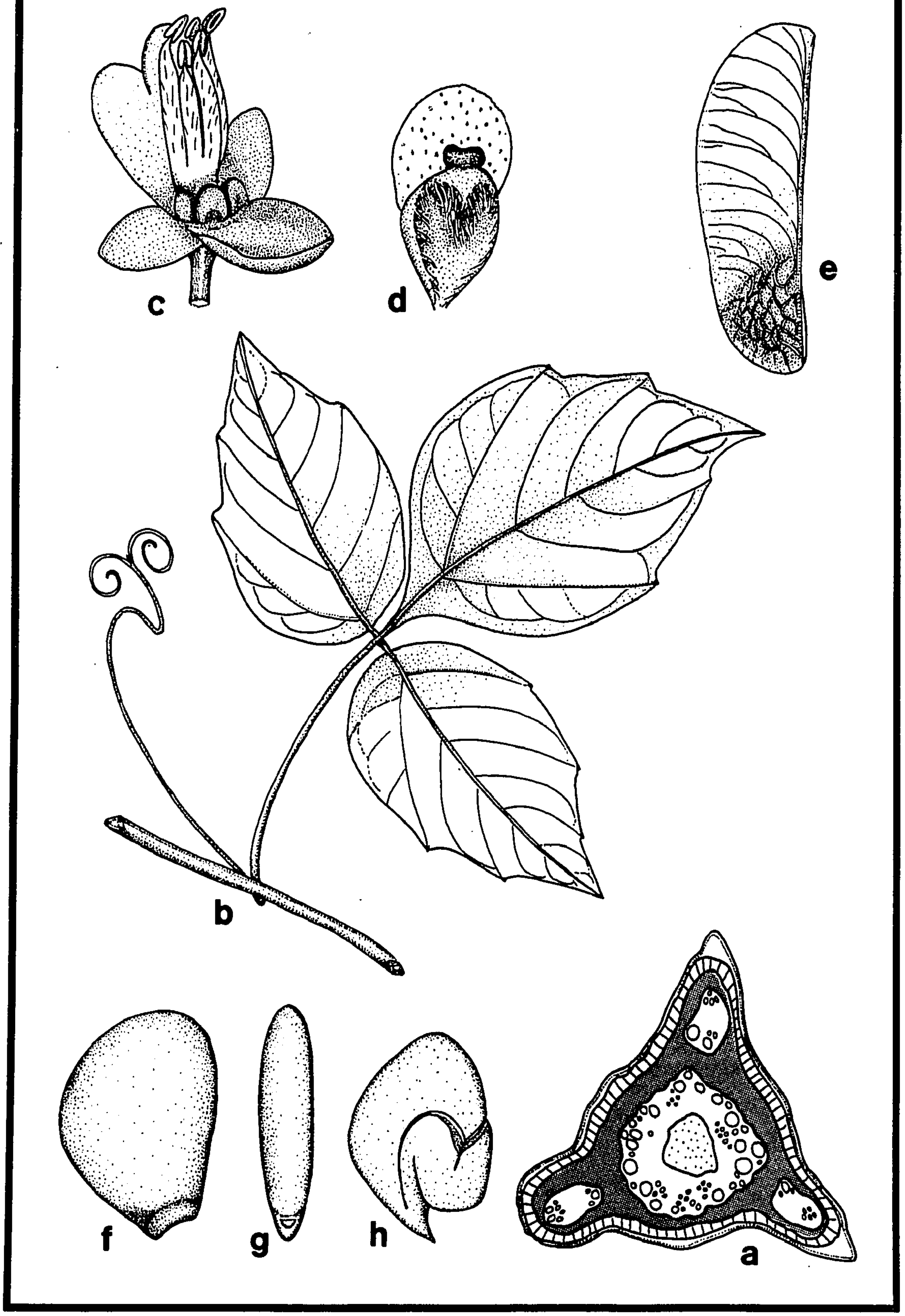
Serjania morii is placed in section Platycoccus even without knowledge of its fruits, because it is very similar to S. cuspidata. These species share similar stem indument and general flower morphology. However, S. morii differs by its oval to oblong-oval (not ovate to subtrilobate) leaflets, repand denticulate (not dentate) margin, essentially glabrous (not tomentose) leaflets, and third and fifth sepals connate 1/4 to 2/5 (not 2/3 to 3/4) of their length.

The name of this species honors Dr. Scott A. Mori, collector of the type and specialist in Neotropical Lecythidaceae.

6. Serjania regnellii Schlechtendal, Linnaea 18: 57. 1844. Type.
Brazil. Minas Gerais: Caldas, s.d. (fl, fr), Regnell I 38
(holotype, HAL 064975). Figs. 26d; 37.

Woody vine to 5 m long. Stems sharply to obtusely triangular at maturity, sides two-furrowed near angles, sparsely covered with yellowish, erect, 0.5-0.8 mm long hairs. Cross section of stem with central, terete, large vascular cylinder and 3 peripheral, smaller, elliptic vascular cylinders, the peripheral cylinders sub-terete and slightly included in central cylinder in old stems. **Stipules** subulate, 1.5-2mm long, scarcely covered with same indument as stems. Leaves ternate; petioles not winged, shorter than leaflets, adaxially and abaxially furrowed, densely covered with erect, rusty, 0.5 mm long hairs; leaflets chartaceous, with acuminate apex, the terminal leaflet larger, ovate, 6.4-9.2 (15) x 3.6-6.5 cm, with attenuate, usually sessile or less often decurrent into more or less prolonged (1-2.7 cm long) petiolule, the lateral leaflets oblong-ovate or lanceolate, 6-9 (11.6) x 3.4-6.4 cm, with oblique, rounded base, sessile or shortly petiolulate (2-6 mm long), the upper surface covered with erect, whitish, or yellowish hairs with swollen bases, ca. 0.2 mm long (longer on veins and margin), the epidermis often with rod-shaped oxalate crystals, the lower surface densely covered with same indument as upper surface, the margins remotely and obtusely serrate and covered with whitish, appressed, 0.5 mm long hairs, the teeth glandular, the veins mixed

Figure 37. Serjania regnellii. A. cross section of stem with a central and three peripheral stele. B. Ternate leaf and fragment of branch. C. Staminate flower with petals removed. D. Central petal with adnate scale. E. Fruit merocarp. F. Seed, lateral view. G. Seed, ventral view. H. Embryo showing cotyledons configuration. All drawn from Acevedo & Laca 1512.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craspedodromus, the lower pair of secondary veins often opposite, primary and secondary veins slightly prominent on both surfaces. **Inflorescence** axillary, 1.5 times longer than subtending leaf, the axis 4-angular, usually twining, sparsely covered with same indument as stem, the rachis sub-terete or slightly flattened, striate, densely covered with same indument as stem; bracteoles narrowly subulate, with same indument as rachis, the margins with glandular hairs, the primary bracteoles 1.5 mm long, the secondary bracteoles ca. 0.7 mm long; cincinni alternate or subopposite, 0.4-1 cm long, with same indument as stem, 4-6 flowered; pedicels ca. 1.5 mm long,articulate at base, same indument as peduncle. **Flowers:** sepals obtuse at apex, ciliate, with same indument as pedicel, the outer sepals 1.2-2.5 mm long, ovate, the inner sepals 2-3 mm long, obovate or wide ovate, third and fifth sepals connate from 2/3 to 3/4 of their length; petals white, 2.5-3.2 mm long, spathulate, adaxially minutely papillate, the apex rounded; scales of central petals 1.5-2 mm long, hood-shaped, with fleshy, crown-shaped apex and ciliate margins, the scales of lateral petals 1.5 mm long, with slightly fleshy apex and ciliate margins; disk glands four, the central glands ca. 0.5 mm long, widely oblong in outline, with obtuse apex, the lateral glands narrower; torus reduced; filament scarcely covered with white, inflexed hairs; anthers elliptic, dorsifixed, ca. 0.4 mm long. **Fruits** 2.7-3.3 cm long, outline oblong or elliptic, sparsely covered with small, erect, yellowish hairs with swollen bases, the base subcordate, the apex retuse, the cocci flattened, with slightly prominent veins, outline of wing not constricted below coccus. Seeds lenticular, light brown, 0.5-0.6 mm long. Embryo with biplicate, smaller, adaxial cotyledon and curved, larger abaxial cotyledon.

Distribution. Serjania regnellii is known only from the states of Minas Gerais and Sao Paulo, Brazil (Fig. 36). It has been collected in campo rupestre as well as in open disturbed areas. It flowers from April to May and fruits in August.

Specimens examined. BRAZIL. Minas Gerais: Caldas, 28 Mar 1847 (fl, fr), Regnell I 38 (S), 18 May 1866 (fl), Regnell I 38 (MO), 28 May 1866 (fl), Regnell I 38 (S), 10 Apr 1877 (fl), Regnell I 38 (F); Ouro Preto, Rod. MG-BR 356, 5 km W of Cachoeira do Campo, 22 Aug 1986 (fr), Acevedo & Laca 1512 (NY-2 sheets, PAMG, US); Santo Antonio do Leite, campos, 9 Apr 1976 (fr), Badini 23379 (NY-3 sheets). Sao Paulo: Cunha, Serra do Monjolo, 14 Apr 1939 (fl), Viegas et al. 3860 (US), Serra da Cantareira, 11 May 1979 (fl), Nakaoka 5785 (F).

Field observations. The stems of S. regnellii produce a watery sap (not milky) when cut, and the fruits are reddish at maturity.

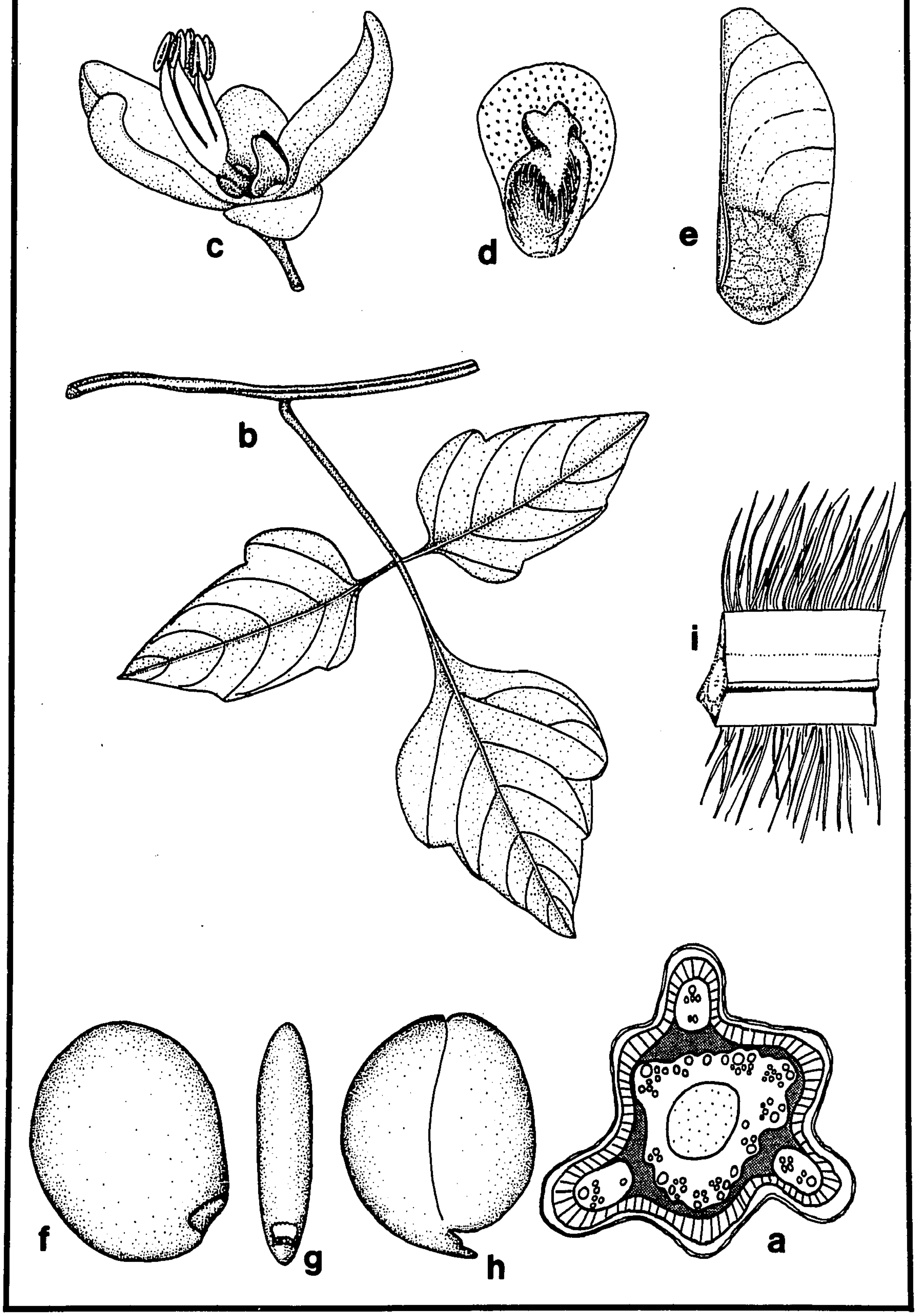
Serjania regnellii is morphologically similar to S. cuspidata. Stems of both species, Serjania regnellii and S. cuspidata are sharply triangular when young, but the latter has long stiff erect hairs in the main angles while the first does not. These species also differ in the shape of their leaflets as those of S. regnellii are narrower (oblong or lanceolate) while those of S. cuspidata are wider (ovate or sub-trilobate).

This species honors Regnell, collector of the type, who lived for several years in Caldas, Minas Gerais, Brazil.

7. Serjania cardiospermoides Schlechtendal & Chamisso, Linnaea 6: 418, n. 1290. 1831. Type. Mexico. Veracruz: Papantla, Dec 1828 (fr), Schiede s.n. (lectotype, HAL, here designated; isolectotype, HAL). Figs. 8a-b, d; 38.

Woody vine to three m long. Stems obtusely 3-5-angular, with five ribs, three of which are more prominent; cross section of stem with central, subterete to angular, large, vascular cylinder and three smaller, elliptic, peripheral, vascular cylinders, these not included in the central one which becomes terete when old. Stipules deltoid, 1 mm long, with ciliate margins. Leaves ternate; petioles shorter than leaflets, not winged, sub-terete, adaxially flattened, sparsely to densely covered with light yellow, curly, 0.1-0.3 mm long hairs, these swollen at base; leaflets chartaceous, with long acuminate or cuspidate apex, the terminal leaflet wider, ovate, widely ovate, or trilobate, (4.6) 6-9 (12) x 3.5-7 (11) cm, with rounded or abruptly and short-attenuate base,

Figure 38. Serjania cardiospermoides var. cardiospermoides. A. Cross section of stem showing central stele and three peripheral steles (Purpus 8661). B. Ternate leaf and fragment of stem (Purpus 2063). C. Staminate flower with petals removed (Nee 23640). D. Central petal with adnate scale, petal densely papillose (Nee 32640). E. Merocarp (Purpus 8681). F. Seed lateral side (Calzada 4247). G. Seed ventral side (Calzada 4247) H. Embryo with straight cotyledons (Calzada 4247). I. S. cardiospermoides var. subjubata, fragment of stem showing hirsute hairs (Steyermark 50908).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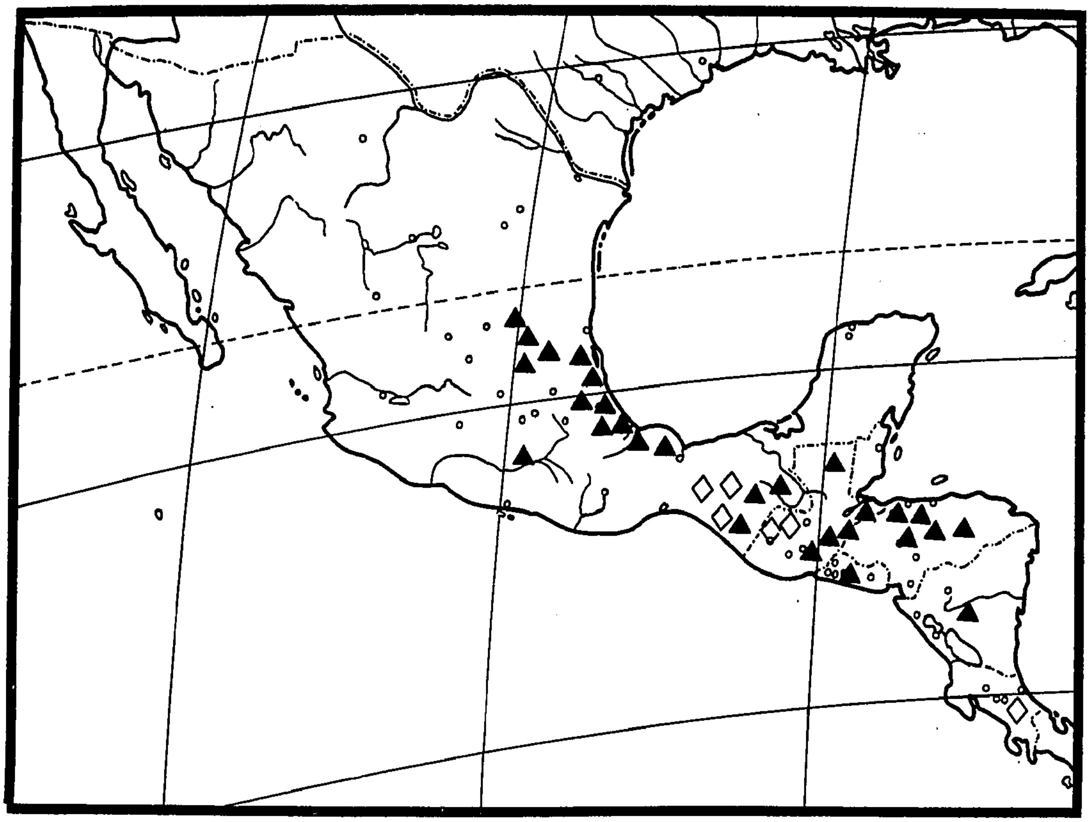
decurrent onto petiolule 1.5-3 (4) cm long, the lateral leaflets lanceolate, (3.5) 5-7 (10) x 2.5-5 (7) cm, with oblique truncate base, shortly petiolulate (1-1.5 cm long), the upper surface densely to sparsely covered with yellowish, prostrate hairs, especially on veins, sometimes glabrescent, the lower surface densely to scarcely covered with yellowish, prostrate or erect hairs, especially on veins, the margins remotely serrate, ciliate and scarious, the teeth clear glandular, acute, obtuse or rounded, the veins mixed craspedodromus, the primary and secondary veins slightly prominent on lower surface. **Inflorescence** axillary, as long as or three times longer than subtending leaf, the axis 4-angular, usuallytwining, with yellowish, 0.5-1 mm long hairs, the rachis angular, furrowed, with similar indument as axis, but the hairs shorter (0.3mm long); bracteoles subulate or lanceolate, 1.5 mm long, margins ciliate, with glandular hairs, secondary bracteoles shorter; cincinni alternate or opposite, 0.3-0.7 (0.9) cm long, with same indument as rachis, usually 5-flowered; pedicels 2.5-5 mm long, articulate at 1-2 mm from base, with same indument as peduncle but finer. **Flowers:** sepals densely covered with whitish, fine hairs, the outer sepals (1.5) 2-3 mm long, ovate and obtuse at apex, the inner sepals (2.5) 3-4 mm long, obovate, with obtuse apex, third and fifth sepals connate from 2/3 of their length; petals white, 4-5 mm long, broadly spathulate or obovate, adaxially densely and minutely papillate, the apex rounded, the scales of central petals ca. 3.5 mm long, hood-shaped, with fleshy, crown-shaped apex and ciliate margins, the scales of lateral petals 3 mm long, with slightly fleshy apex and ciliate margins; disk glands four, the central glands 0.8-1 mm long, ovate in outline, and obtuse at apex, the lateral glands smaller or reduced, elliptic; torus more or less enlarged; filaments densely to sparsely covered with white, inflexed hairs; anthers elliptic, dorsifixed, 0.6-0.7 mm long; ovary obovate, sparsely covered with whitish, short, inflexed hairs. Fruits 2.4-4 (4.7) cm long, outline oblong or ovate, glabrous, the base truncate, subcordate or rounded, the apex retuse, the cocci flattened, with slightly prominent, reticulate network of veins, outline of wing not constricted below coccus; partitioning wall narrowly elliptic, 0.7-0.8 x 0.2 cm. Seeds lenticular, light brown, ca. 0.6 mm long. Embryo with erect cotyledons.

Distribution. Serjania cardiospermoides occurs in the lowlands of Mexico, Guatemala, Honduras, El Salvador, Nicaragua, and Costa Rica (Fig. 39). It has been collected in primary tropical rainforest, deciduous forest, pine forest, gallery forest, thickets, and in disturbed areas such as secondary forest and roadsides at elevations from 30 to 1600 m. It flowers year-round and usually fruits from September to March.

Serjania cardiospermoides is disjunct from the remaining species of section Platycoccus. It is morphologically similar to S. cuspidata and S. regnellii, but the extensive gap in distribution casts some doubts on their close relationship.

Figure 39. Distribution of the varieties of *Serjania cardiospermoides*.



▲ ***S. cardiospermoides cardiospermoides***

◊ ***S. cardiospermoides subjubata***

The name cardiospermoides refers to the vegetative similarity of this species with some species of Cardiospermum.

Key to varieties of Serjania cardiospermoides.

1. Stems hirsute (only one kind of hair).
   ....S. cardiospermoides var. subjubata.

1. Stems glabrescent or pubescent (with pilose and hirsute hairs).
   ....S. cardiospermoides var. cardiospermoides.

7a. Serjania cardiospermoides Schlechtendal & Chamisso var. cardiospermoides. Fig. 38 a-h.

Serjania cardiospermoides Schlechtendal & Chamisso f. genuina Radlkofer in J.D. Sm., Enum. pl. guatem. 4: 21. 1895. Type. Mexico. Veracruz: Papantla, Dec 1828 (fr), Schiede s.n. (lectotype, HAL; isolectotype, HAL).

Serjania cardiospermoides Schlechtendal & Chamisso f. leptothyrsa Radlkofer in J.D. Sm., Enum. pl. guatem. 4: 21. 1895. Type. Honduras. Santa Barbara: San Pedro de Sula, Río Chamelecón, 16 Dec 1838 (fl), Thieme 5177 (lectotype, US, here designated; isolectotypes, F, K).

Stems sharply triangular to five-angular, glabrescent or densely covered with curly, whitish hairs ca. 0.3 mm long along the sides and rusty, erect, 0.8-1.2 mm long hairs along main angles.

Distribution. Variety cardiospermoides occurs from southern Mexico to Nicaragua (Fig. 39) at elevations from 30 to 1600 m. It is found in dense forest as well as in disturbed and open areas.

Specimens examined. MEXICO. Without state: Monte Cristo, Jan 1938 (fl), Matuda 1916 (F, NY). Chiapas: Angel Albino Corzo, along Cuztepeques river, ca. Fca. Cuztepeques, 730 m, 26 Mar 1968 (fr), Ton 3833 (F, LL); Fca. Prusia, steep wooded slope, 730 m, 23 Jan 1968 (fl), Ton 3594 (F, LL); Escuintla, 16 Jan 1936 (fl), Matuda 565 (MO), Fca. Zuarez, 12 Aug 1937 (fl), Matuda 1742 (K, LL); Villa Corzo, Colonia Vicente Guerrero on road to Fca. Cuxtepec, 1100 m, 3 Nov 1981 (fl, fr), Breedlove 54655 (LL). Guerrero: Temisco, second barranca E of Stamp Mill, 350 m, 6 Nov 1937 (fl), Mexia 8759 (F, K, LL, MO-2 sheets, NY). Oaxaca: Juchitan, 20 km N of Ventosa on road to Matias Romero, 12 Dec 1980 (fr), Trigos & Lorence 522 (NY-2 sheets). Queretaro: Pinal de Amoles, 3 km S of Escanelilla, La Cuesta, 1100 m, 2 Jul 1985 (fl), Fernández 3004 (NY). San Luis Potosí: Antiguo Morelos, vic. of El Salto, pine forest, 200 m, 13 Jan 1987 (fl, fr), Croat & Hannon 64982 pro parte (NY); Aquismon, Tampaxal, managed forest, 5 Jun 1979 (fl), Alcorn 3139 (TEX); East slope of Sierra Madre Oriental, 39 km NE of Ciudad Madre Maiz, on hwy. 80 at km 223, 1200 m, 1 Oct 1965 (fr), Roe & Roe 2293 (F, WIS);

San Antonio, 0.5 km W of San Antonio, 9 Oct 1978 (fr), Alcorn 1938 (TEX), Tanjasnec, managed forest, 3 Nov 1979 (fr), Alcorn c12 (TEX); San Dieguito, 13-16 Jun 1904 (fl), Palmer 105 (NY, US); Xilitla, 4 km W of Y Griega, disturbed forest, 270 m, 5 Jun 1982 (fl, fr), Tenorio & Romero 571 (MO). Veracruz: Baños del Carrizal, Aug 1912 (fl), Purpus 6063 (F-2 sheets, GH, MO, NY); Barranca de los Baños, Oct 1918 (fl, fr), Purpus 8280 (NY, US); Remulatero, Jan 1922 (fr), Purpus 8681 (NY); San Andrés Tuxtla, Salto Eyipantla, 3 km from Comoapan, tall primary evergreen forest, 12 Jan 1973 (fr), Calzada 935 (F-2 sheets, WIS), Vic. of Laguna Encantada, 450 m, 2 Nov 1971 (fl), Beaman 5226 (F); Salto Eyipantla, 5 km S of San Andrés, forest of gorge and disturbed edges of river, 150 m, 18°23'30"N, 95°12'30"W, 4 Dec 1981 (fl), Nee 23640 (LL); 8 km from Sihuapan, tall evergreen forest, 250 m, 26 Jan 1978 (fr), Calzada 4247 (F); Zapuacan, Barranca de Tenampa, Aug 1906 (fl), Purpus 2063 (F, GH, MO, NY); Zapuacan, s.d. (fl), Coulter 877 (K); Between cerro de Los Metales and cerro Monte do Oro, secondary vegetation, 11 Jul 1972 (fl), Dorantes et al. 1320 (F).

GUATEMALA. Chiquimula: Quebrada Shusho, above Chiquimula, 480 m, 14 Oct 1940 (fl, fr), Standley 74325 (F); along Tacó river, between La Laguna and Chiquimula, 500-1000 m, 27 Oct 1939 (fr), Steyermark 30753 (F). Gualán: Specific locality not known, in ravine, 190 m, 20 Jun 1909 (fl), Deam 6366 (F, MO-2 sheets, NY, US-2 sheets), On bushes along road, 16 June 1909 (fl), Deam 6308 (US). Petén: Cadenas, in forest, 14 Mar 1964 (fl), Lundell 18295 (LL, MO). Zacapa: Lower slopes of Sierra de las Minas, along trail to

Río Hondo, 250-900 m, 11 Oct 1939 (fl), Steyermark 29557 (F).

BELIZE. Toledo: Balsam Hill, Edwards road, on ridge, 15 Nov 1950 (fl), Gentle 7156 (LL).

HONDURAS. Cortés: San Pedro Sula, montane rainforest, 190 m, 28 Nov 1950 (fl), Molina 3425 (F). Santa Barbara: Between Chamalecón and Cofradía, semi-humid thickets, 150 m, 21 Dec 1950 (fl), Molina 3847 (F). Lempira: Foothills of Montaña Puca, between Guatán and Cuábanos, mixed forest, 1600 m, 25 Sep 1963 (fl), Molina 12916 (F, LL, NY). Yoro: Ca. Progreso, wet thicket, 30 m, 24 Jan 1928 (fr), Standley 55045 (F, US).

NICARAGUA. Matagalpa: Road to El Tuma at El Hular, 13°00'N, 85°48'W, thicket, 500 m, 22 Jan 1982 (fl), Moreno & Elmquist 21421 (MO, NY).

Local Name. Mexico, San Luis Potosí: Oox kekel

Radlkofer based forma leptothyrsa on the size of the inflorescence and the shape of the leaflets. However, examination of more collections indicates that these characters are variable. Therefore, the variety can not be maintained.

7b. Serjania cardiospermoides Schlechtendal & Chamisso var. subjubata Radlkofer, Bull. Herb. Boissier 5: 319. 1905.

Type. Costa Rica. San José: San Mateo, 300 m, 12 Feb 1892 Biolley 7049 (holotype, G, n.v.). Fig. 38i.

Serjania phaseoloides Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 171. 1944. Type. Guatemala. Huehuetenango: Along Río Cuilco, between Cuilco and Aldea of San Juan, 1200-1300 m, 18 Aug 1942 (fl), Steyermark 50908 (holotype, F; isotype, US).

Stems sharply triangular, the angles densely covered with ferruginous hirsute hairs ca 1.5 mm long, the sides glabrous.

Distribution. Serjania cardiospermoides var. subjubata is known from Southern Mexico, Guatemala, El Salvador, and Costa Rica (Fig. 39). It has been collected from gallery and deciduous forests as well as from roadsides at elevations from 800 to 1600 m.

Specimens examined. **MEXICO.** Chiapas: Between Mazapa and Motozintla, 1200 m, 19 Jul 1941 (fl), Matuda 4870 (F); Ocozocoautla de Espinosa, canyon at Río de la Venta ca. Derma, deciduous forest, 800-100 m, 24 Aug 1972 (fl) Breedlove 27356 (MO, NY); Soyalo, steep rocky canyon between Soyalo and La Bombana, 1200 m, 7 Sep 1974 (fl, fr), Breedlove 37194 (MO).

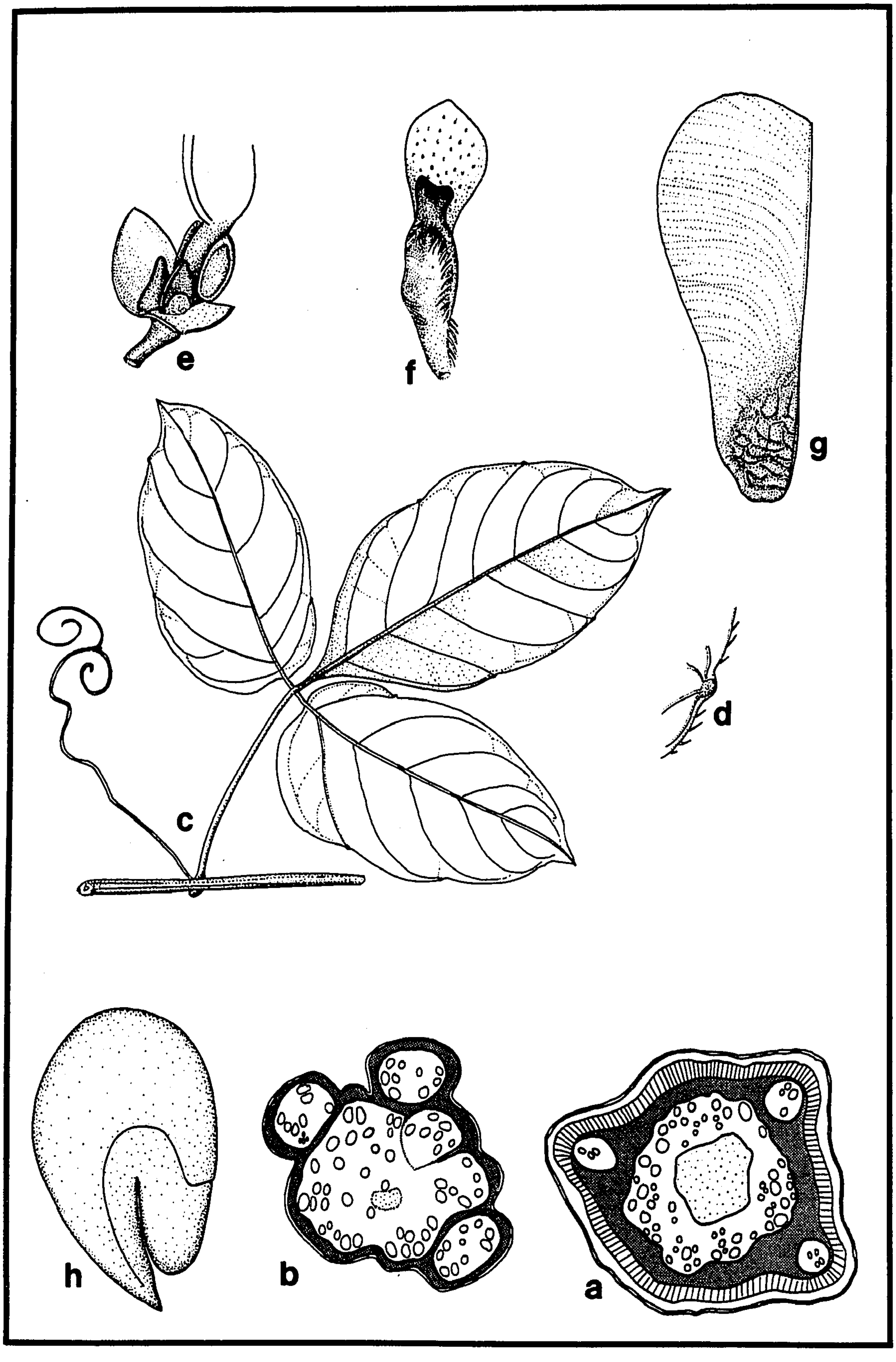
GUATEMALA. Huehuetenango: Trail between Democracia and Santa Ana Huista, Sierra de los Cuchumatantes, 800-1000 m, 25 Aug 1942 (fl), Steyermark 51305 (F).

EL SALVADOR. Sonsonante: Low forest along road to San Julián, 1600 m, 30 Jun 1971 (fl), Montalvo et al. 3603 (MO).

8. Serjania tenuis Radlkofer, Monogr. Serjania 98, 1875. Type Brazil. Rio de Janeiro: Rio de Janeiro, s.d. (fl), Martius 1245 (lectotype, NY, here designated; isolectotypes, CGE, F, GH, K, MO-2 sheets). Fig. 40.

Woody vine. Stems obtusely five-angular, with three to five prominent ribs, glabrous and smooth; cross section of stem with a central, obtusely triangular, large vascular cylinder and 3 peripheral, smaller, terete or subterete vascular cylinders, these not included in central one. Stipules deltoid, 0.9-1.5 mm long, glabrous. Leaves ternate; petiole not winged, terete, as long or shorter than leaflets, adaxially furrowed, glabrous except for few erect or inflexed hairs, 0.5 mm long, on adaxial surface; leaflets membranous to chartaceous, with acuminate or mucronate apex, the terminal leaflet larger, ovate, elliptic or oblong-lanceolate, (3) 6-11 x 2.1-5.2 cm, with attenuate base, the laterals oblong or lanceolate, (3) 4.2-7.5 (9) x 1.6-3.5 (4.2) cm, with oblique, rounded base, sessile or shortly petiolulate (1-1.5 mm long), the upper surface glabrous, except for a few erect or inflexed hairs, 0.3-0.5 mm long on midvein, the lower surface glabrous, the margins entire, scarious, crenate or remotely and obtusely serrate, ciliate and slightly revolute, the teeth glandular, the veins mixed craspedodromus, the primary and secondary veins slightly prominent on both surfaces. Inflorescence axillary, 1.5 times longer than subtending leaf, the axis 4-angular, usually twining, glabrous, the rachis subterete or angular, striate, sparsely covered with minute,

Figure 40. Serjania tenuis. A. Cross section of young stem with a central and three peripheral steles (Eiten 6258). B. Cross section of mature stem (Riedel 505). C. Ternate leaf with branch fragment (Eiten 6258). D. Glandular tooth on leaflet margin (Eiten 6258). E. Pistillate flower with sepals and petals removed (Schüch s.n.). F. Central petal with adnate scale (Duarte 5824). G. Fruit merocarp (Duarte 5824). H. Embryo showing cotyledons configuration (Duarte 5824).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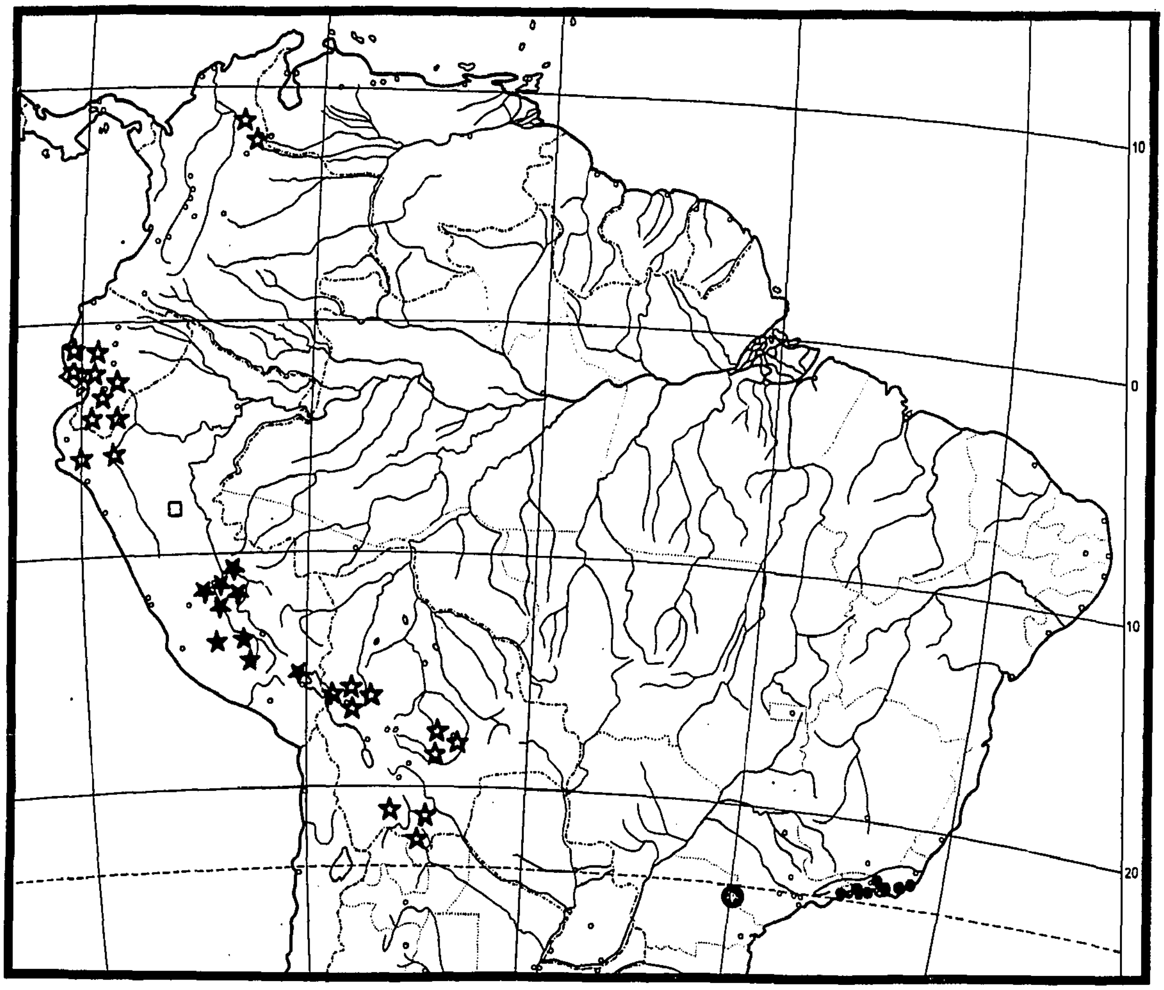
ca. 0.2 mm long, yellowish or whitish, curly hairs; bracts and bracteoles subulate, ca. 1 mm long, margins with glandular hairs; cincinni alternate, 0.5-3 mm long, with same indument as rachis, 3-6-flowered; pedicels 2-4 mm long, articulate close to base, sparsely covered with minute whitish hairs. **Flowers:** sepals obtuse at apex, the outer sepals 1.2-2.5 mm long, ovate, the inner sepals (2.5) 3-4.6 mm long, oblong or wide ovate, third and fifth sepals connate 7/8 of their length; petals white or light yellow, 4-5.5 mm long, spathulate or oblanceolate, sparsely covered with minute papillae on adaxial surface, the apex rounded; scales of central petals 3-4 mm long, basally connate with petal up to 2 mm, hood-shaped, with fleshy, crown-shaped apex and ciliate margins, the scales of lateral petals 3 mm long, with slightly fleshy apex and ciliate margins; disk with two or four glands, the central glands ca. 0.8 mm long, ovate in outline, with obtuse apex, the lateral glands obsolete or less often slightly developed; torus enlarged; filaments densely covered with white, inflexed hairs; anthers elliptic, dorsifixed, ca. 0.5 mm long; ovary oblong or elliptic, densely covered with white, inflexed, minute hairs. **Fruits** 2.1-3.2 cm long, outline ovate, sparsely covered with minute, erect, whitish hairs with swollen bases, the base cordate, the apex retuse, the cocci flattened, with slightly prominent veins, the outline of wing not constricted below coccus, endocarp densely covered with whitish, floccose hairs. **Seeds** flattened, with oblong outline, dark brown, ca. 3 mm long (immature). **Embryo** with biplicate, smaller, adaxial cotyledon and curved, larger, abaxial cotyledon.

Distribution. Serjania tenuis is endemic to the state of Rio de Janeiro, Brazil (Fig. 41). It is naturally distributed along coastal open areas from where it invades secondary formations. It has been collected from sea level to 950 m elevation. Serjania tenuis flowers mostly from January to July and fruits in May.

Specimens examined. Without locality, ex Miers herbarium (fr), collector unknown (BM), ex Miers herbarium (fl), collector unknown (BM). BRAZIL. Without specific locality, s.d. (fl), Burchell 2781 (K), s.d. (fl), Shüch s.n. (NY) . Rio de Janeiro: Itaguaí, Baía de Sepetiba, Ilha Furtada, along coast, 30 Mar 1968 (fl), Martinelli 1543 (NY, RB-2 sheets), coastal area, 30 Mar 1968 (fl), Sucre & Braga 2549 (NY), 31 Mar 1988 (fl) Sucre & Braga 2626 (NY); Parati, Parati, ca. sea level, roadside, 21 Apr 1965 (fl), Eiten & Eiten 6258 (MO, NY); Resende, Itatiaia, Oct 1872 (fl), Glaziou 5772 (K); Rio de Janeiro, May-Jun 1822 (fl, fl), Forbes s.n. (BM), 1852 (fl), Riedel & Luscnatt 505 (A, NY-2 sheets), s.d., (fl), Schott 713 (F, K, NY), Apr 1883 (fl, fr), Glaziou 13694 (K), Gávea, 6 Apr 1943 (fl), Silva s.n. RB 48002 (RB-2 sheets), Grumarí, in secondary formations, 8 May 1969 (fr), Sucre 4980 (MO, NY-2 sheets, RB-2 sheets), 8 May 1969 (fl, fr), Sucre 4968 (RB-2 sheets), 80-100 m, 23 Mar 1972 (fl), Sucre 8744 (MO, NY-2 sheets, RB), Lagoa Rodrigo de Freitas, 16 May 1961 (fl, fr), Duarte 5824 (F, NY, U, US), Guaratiba, roadside s.d. (fl), Almeida & Laroche 1349 (RB-2 sheets), s.d. (fl), Gaudichaud 834 (F-2 sheets); Teresópolis, Serra dos Orgaos, ex Miers herbarium, Anonymous 2129 (BM-2 sheets).

Figure 41. Distributions of S. tenuis, S. hatschbachii, S. ampelopsis, S. schunkei, and S. squarrosa.



● **S. tenuis**

⊙ **S. hatschbachii**

☆ **S. ampelopsis**

□ **S. schunkei**

★ **S. squarrosa**

Field observations. The inflorescences of S. tenuis are pendant.

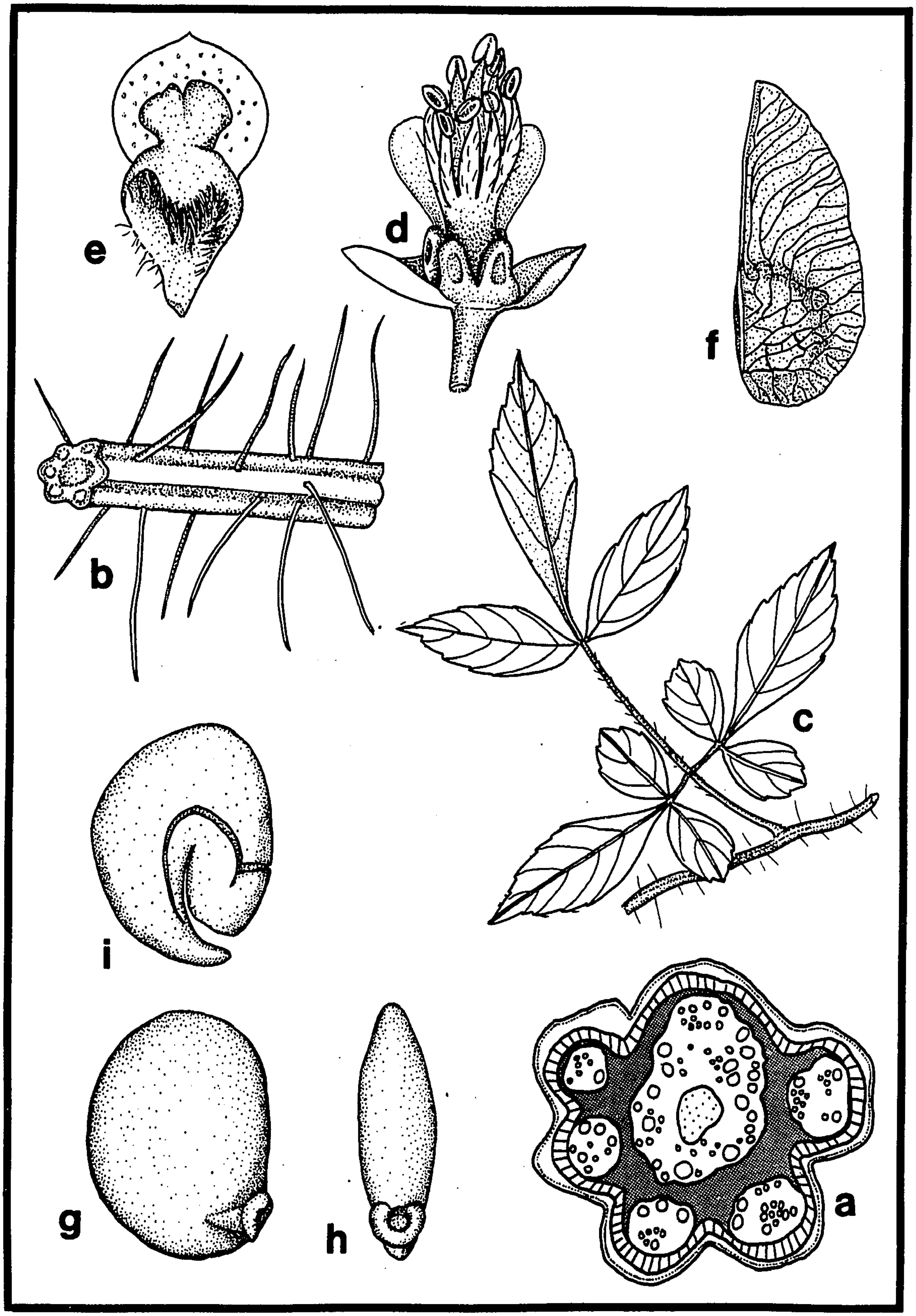
Serjania tenuis is morphologically similar to S. communis. However, it differs form this species by its ternate leaves (not biternate), essentially glabrous parts (not variously pubescent), and embryo with biplicate cotyledons (not straight).

The name tenuis means thin or slender and probably refer to the herbaceous nature of this species.

9. Serjania hatschbachii Ferrucci, Bonplandia 5: 243, 1983. Type. Brazil. Paraná: Adrianápolis, barra Rio Pardo, margin of forest, 4 Apr 1976 (fl, fr), Hatschbach 38522 (holotype, MBM, isotype, CTES). Figs. 11c; 21b; 42.

Woody vine. Stems subterete, with 6 prominent ribs, sparsely covered with 2-3 mm long, setulose yellowish hairs, glabrescent; cross section of stem with central, subterete, large vascular cylinder and (3) 4 or 5 peripheral, smaller, terete or subterete vascular cylinders, these not included in central one. Stipules deltoid to subulate, ca. 1 mm long, with setulose and glandular hairs on margin. Leaves biternate; petiole and rachis not winged, subterete, adaxially furrowed, densely to sparsely covered with same indument as stems, petioles shorter than primary rachis; leaflets chartaceous, with acuminate and mucronate apex, the terminal leaflet larger, lanceolate or elliptic, (3) 6-11 x 2.1-5.2 cm, with long attenuate base, the lateral leaflets lanceolate or elliptic, (3) 4.2-7.5 (9) x 1.6-3.5 (4.2) cm, with rounded base, sessile, both surfaces glabrous, except for a few hairs on midvein of upper surface, the margins revolute, scarious, remotely and acutely serrate, ciliate when young, the teeth glandular, the veins semicraspedodromus, the primary and secondary veins slightly prominent on lower surfaces. **Inflorescence** axillary, longer than subtending leaf, the axis 4-angular, glabrous, usually twining, the rachis subterete, glabrous and striate; bracts and bracteoles subulate, ca. 1 mm long, margins with glandular hairs; cincinni whorled, 0.8-1.2 cm long, glabrous, 5 to 7-flowered; pedicels 2-4 mm long, articulate close to base, sparsely covered with minute, whitish hairs. **Flowers** sepals obtuse at apex, the outer sepals 1.7 mm long, ovate, the inner sepals 2.5 mm long, oblong or widely ovate, third and fifth sepals completely distinct; petals 3-3.5 mm long, spathulate, sparsely covered with minute papillae on adaxial surface, the apex rounded, the scales of central petals cream color, ca. 2.5 mm long, hood-shaped, with fleshy, crown-shaped apex and ciliate margins, the scales of lateral petals 3 mm long, with slightly fleshy apex and ciliate margins; disk with four glands, ca. 0.7 mm long, ovate in outline, with obtuse apex; torus reduced; filaments sparsely covered with white, inflexed hairs; anthers

Figure 42. Serjania hatschbachii. A. Cross section of stem showing central and five peripheral steles. B. Section of stem with hirsute indument. C. Biternate leaf. D. Staminate flower with petals removed. E. Central petal with adnate scale. F. Fruit merocarp with reduced wing. G. Seed, lateral side. H. Seed, ventral side. I. Embryo showing biplicate adaxial cotyledon and bent abaxial one. All drawn from Hatschbach 2957.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elliptic, dorsifixed, ca. 0.4 mm long. **Fruits** 2.2-2.5 cm long, heart-shaped in outline, glabrous, the base obtuse, the apex retuse, the cocci flattened, with slightly prominent veins, the wings reduced toward the base. Seeds flattened, lenticular, light brown, 7 mm long. Embryo with biplicate, smaller, adaxial cotyledon and curved larger abaxial cotyledon.

Distribution. Serjania hatschbachii is known from two collections from Adrianápolis-Ribeira at the border of Paraná and Sao Paulo (Fig. 41). It has been collected in flower and fruit in January and April.

Specimen examined. BRAZIL. Sao Paulo: Ribeira, on cliff, 15 January 1953 (fl, fr), Hatschbach 2957 (US).

Serjania hatschbachii is morphologically similar to S. tenuis. However, it differs from this species by its biternate (not ternate) leaves, sparsely hirsute stems (not glabrous), cross section of stem with four to five peripheral steles (not three) and fruits with very reduced wing.

This species honors Gert Hatschbach, who made the only collections of this species as well as many other interesting plants from southeastern Brazil.

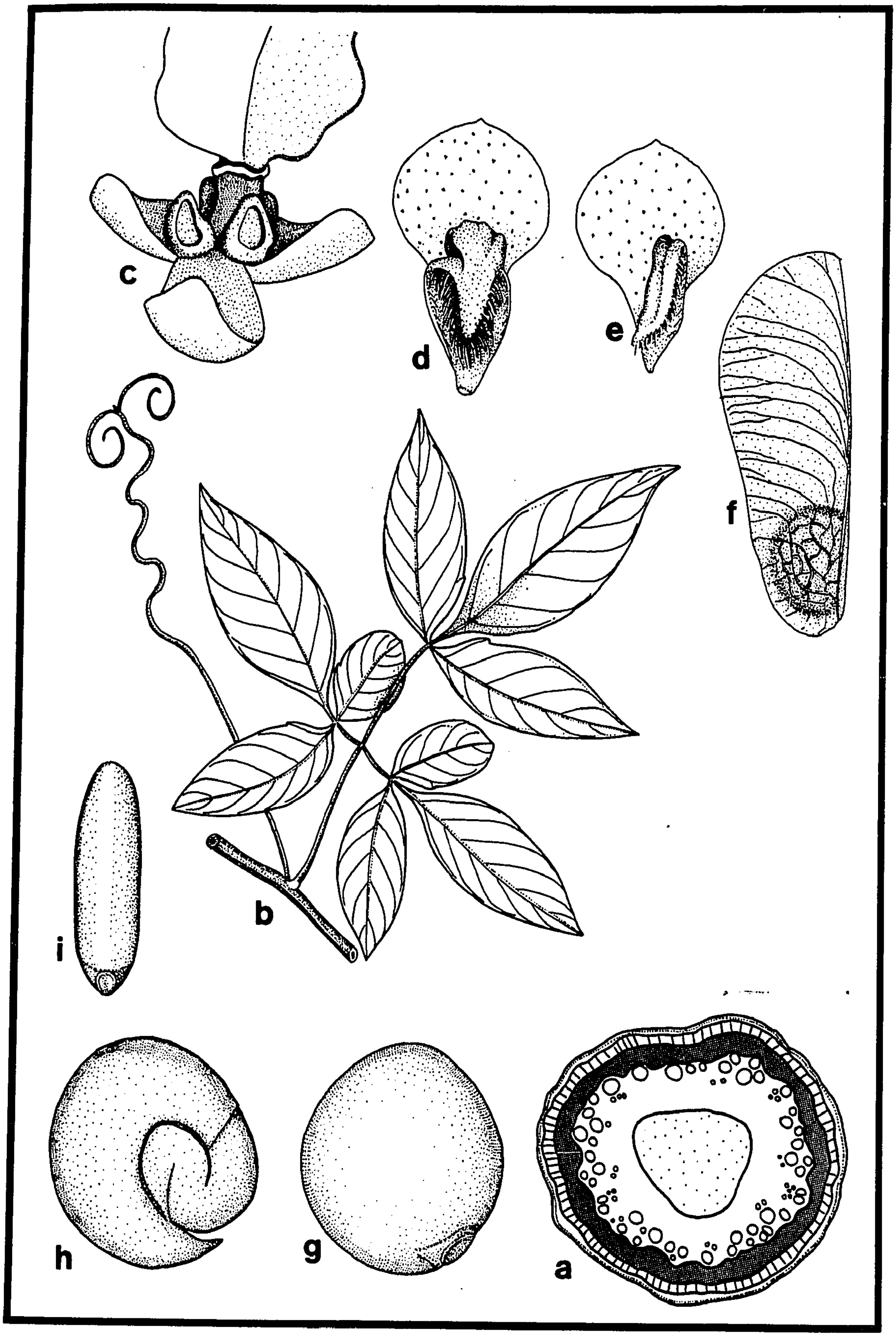
10. Serjania ampelopsis Planchon & Linden in Triana & Planchon, Ann. Sci. Nat. Bot. XVIII: 350, 1862. Type. Colombia. Norte

de Santander: Prov. de Ocaña, Vic. Ocaña, 1390 m, Oct 1850 (fl), Schlim 153 (lectotype, BR, here designated; isolectotypes, BR, F, K). Figs. 19e; 21c; 43.

Serjania areolata Radlkofer, Ergänz. Monogr. Serjania 87, 1886. Type. Bolivia La Paz: Nor Yungas, vic. Coroico, 5000-7000 ft, May 1866 (fl), Pearce s.n. (holotype, K).

Semi-woody climber to 5 (8) m long. **Stems** slender, nearly terete, or 5 to 6-costate, glabrous, the young stems angular; cross section of stem with simple vascular cylinder, the medulla hollow. **Stipules** deltoid, ca 1 mm long, usually covered with small (to 0.3 mm long), whitish hairs. **Leaves** biternate, 11-20 x 12-19 cm; petioles not winged, terete and ridged at adaxial surface, (1.5) 2-6 (7) cm long, the main rachis terete, margined, or narrowly winged, (1.5) 1.7-3.2 (4.2) cm long, sparsely or densely covered with small (to 0.35 mm long), whitish hairs; the secondary rachises 0.5-2.5 cm long, with same indument as main rachis; leaflets chartaceous to membranous, lanceolate, elliptic, oval or ovate, 2-9 (12.5) x 1-3.5 (7) cm, the terminal leaflet larger, the apex acuminate or abruptly acuminate, the base attenuate, obtuse or rounded in terminal leaflet, oblique and shortly petiolulate in lateral leaflets, the upper surface glabrous except for few hairs on veins, covered with whitish, mucilaginous dots, the lower surface lighter (because of whitish glandular projections), with dark network of tertiary veins, glabrous or sparsely covered with small (0.3-0.5 mm long), whitish hairs, the margins revolute, ciliate, entire or remotely dentate to sub-sinuate; veins brochidodromus or mixed craspedodromus, the primary and secondary veins slightly raised on both surfaces. **Inflorescence** 10-20 (35) cm long, usually longer than subtending leaves, the axis 4-12 cm long, glabrous, almost terete, the rachis angular, striate, densely or sparsely covered with small (to 0.15 mm long), whitish, inflexed hairs; primary bracteoles lanceolate, 1.2-2.5 mm long, with same indument as rachis; cincinni opposite, subopposite or alternate, the peduncle 0.5-1.4 (2.5) cm long, glabrous or densely covered with small (to 0.15 mm long), white hairs, 4 to 5 (9)-flowered, the lower peduncles longer; secondary bracteoles lanceolate, ca. 1 mm long, with same indument as peduncle; pedicels 2-5 mm long, slightly flattened, with same indument as peduncle, articulate at 1-2.5 mm from base; tertiary bracteoles (prophylls) narrowly deltoid, 0.5 mm long, close to pedicel articulation. **Flowers:** sepals 5, the outer sepals 2-3.5 mm long, ovate, obtuse at apex, sparsely covered on abaxial surface with small (to 0.1 mm long), whitish hairs, ciliate at margins, the inner sepals 3-5 mm long, oblong-ovate, densely covered with small (to 0.1 mm long), whitish hairs, the third and fifth sepals distinct or connate for up to half their length; petals white, obovate, clawed, 4-5.5 (7) mm long, with small papillae on adaxial surface; scales 3-5 mm long, with densely hairy margins, the central scales hood-shaped, with fleshy crown-shaped apex, the lateral scales not

Figure 43. Serjania ampelopsis. A. Cross section of stem with single stele. B. Biternate leaf with branch fragment. C. Pistillate flower with petals removed. D. Central petal with adnate scale. E. Lateral petal with adnate scale. F. Fruit merocap. G. Seed, lateral view. H. Embryo showing cotyledons configuration. I. Seed, ventral view. All drawn from Acevedo and Vargas 1781.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fleshy, asymmetric, with outer side bent over disk glands; disk glands four, the central glands 1-1.2 mm long, ovate to oblong-ovate and obtuse at apex, the lateral glands 1 mm long, oblong to rounded, laterally adnate to androgynophore; torus enlarged into a small androgynophore; filaments sparsely to densely covered with small, (0.2-0.3 mm long), whitish, inflexed hairs, the anthers dorsifixed, 0.75 mm long; ovary elliptic to oblong, sparsely to densely covered with small, whitish hairs; style 0.5-0.8 mm long, the stigma papillose. Fruits ovate to oblong, chartaceous, glabrous, 3-4.2 x 3 cm, the apex notched, the base cordate; coccus lenticular, flat, with network of slightly raised, dark veins, not-crested or slightly crested, the wings glabrous, with slightly constricted outline below coccus. Seeds dark brown, lenticular, 6-7 x 5.0-5.6 mm; embryo symmetrical in frontal plane, the adaxial cotyledon smaller and biplicate, the abaxial cotyledon larger and curved.

Distribution. Serjania ampelopsis has been collected in Colombia, Ecuador, Peru, and Bolivia (Fig. 41). It occurs in humid to semi-dry forests as well as open or disturbed areas from sea level to 2130 m elevation. It flowers from April to October and fruits from May to December.

Specimens examined. COLOMBIA. Norte de Santander: Prov. de Ocaña, Ocaña to Pamplona, Santa Barbara, open area on fence, 3800 ft, 7 Nov 1878 (fl, fr), Kalbreyer 800 (K).

ECUADOR. Azuay: Machalati-Santa Isabel road, near bridge over río San Francisco, shrubby thicket, 730 m, 11 Jun 1971 (fr), Macbryde 435 (US). Bolívar: Between road to Bucay and Hacda. Rosa Mercedes, lower spurs of Cordillera Central, 600 m, 12 Sep 1943 (fl), Acosta Solis, 5180 (F). Chimborazo: Cañon del río Chanchan, from Naranjapata to below Huigra, 600-900 m, 19 Jun 1945 (fl, fr), Camp E3864 (NY). Guayas: Capera, 23.5 km N of Guayaquil on road to Daule, 150 m, 21 May 1981 (fl, fr), Dodson & Clendenin 11037 (MO); Guayaquil, 0-50 m, 18-20 Jun 1923 (fl), Hitchcock 20148 (GH, NY), 30 Aug-2 Sep 1918 (fl, fr), Rose & Rose 22455 (F, GH, NY, US); 3 km N of Julio Moreno, deciduous forest, 200-300 m, 11 May 1985 (fl, fr), Harling & Andersson 25039 (GB); Vic. del Oro, junct. of rivers Ambocas & Luis, 10 km S of Portovelo, 670-760 m, 6 Oct 1944 (fl, fr), Camp E586 (NY). Junction of Guayas, Cañar, Chimborazo & Bolívar, near Bucay, 300-380 m, 8-15 Jun 1945 (fl), Camp E3711 (F, GH, NY, US). Loja: Alamor-Cazaderos road, 5 km W of El Limo, secondary growth, 800 m, 3 Apr 1980 (fl), Harling & Andersson 17829 (GB, MO); Alamor-Puyango road, semi-deciduous forest, 600-700 m, 7 Apr 1980 (fl), Harling & Andersson 17970 (GB). Manabí: Naranja, N of Paján, 550 m, 16 Jul 1942 (fl), Haught 3405 (F, NY, US).

PERU. Lambayeque: Lambayeque, vic. "El Salvador" restaurant, Mesones-Muro hwy., 28 km E of Olmos, 1150-1200 m, 8 Jan 1964 (fl), Hutchinson & Wright 3467 (F, NY). Cajamarca: Cutervo, Izco, in hedgerow, dry region, 1300 m, 18 Dec 1938 (fr), Stork & Horton 10210 (F).

BOLIVIA. La Paz: Nor Yungas, Coroico, ca. 20 km S of Coroico along roadside, 1660 m, 29 May 1987 (fl, fr), Acevedo & Vargas 1727 (F, LPB, MO, NY, US), ca. 4 km S of Coroico along roadside, 1600 m, 30 May 1987 (fl), Acevedo & Vargas 1731 (F, LPB, MO, NY, US), Sep 1894 (fl), Bang 2444 (GH, MO, NY-2 sheets, US, WIS); Coripata, Hacienda el Choro, 1700 m, 28 Jun 1930 (fl), Buchtien 8124 (NY). Santa Cruz: Florida, Río Bermejo, after bridge Agua Blanca, 1 Jun 1963 (fl), Legname & Cuezo 4020 (CTES), Yerba Buena, stream side, 1300 m, 14 Jun 1966 (fl), Steinbach 291 (NY); 63 km W of Santa Cruz de la Sierra along road to Samaipata, humid, open roadside, 1200 m, 13 Jun 1987 (fl), Acevedo & Vargas 1778, 1779 (both F, LPB, MO, NY, US); 35 km E of Samaipata along road to Santa Cruz de la Sierra, 1500 m, 13 Jun 1987 (fl), Acevedo & Vargas 1781 (F, MO, LPB, NY, US). Tarija: Ipa, 30 km N of Villa Montes, Thainguate stream, 3 Jun 1971 (fl), Krapovickas et al. 19476 (NY); Arce, 29.2 km S of Emboroza-Sidras road, on road to Bermejo, 12.7 km S of Naranjo Agrio, disturbed moist subtropical forest, 600 m, 21-23 April 1983 (fl), Solomon 10017 (MO, NY); O'Connor, 6.8 km NW of Entre Ríos, disturbed moist tropical forest, 1400 m, 3 May 1983 (fl), Solomon 10435 (MO, NY).

Field observations. The stems of S. ampelopsis produce a watery sap (not milky) when cut, and the inflorescences are pendulous.

Serjania areolata was separated from S. ampelopsis by Radlkofer because of its larger flowers with the third and fifth sepals distinct from one another, and its glabrescent parts. However, S. areolata represents the extreme in variation in these characters and, therefore, I consider it a synonym of S. ampelopsis.

Serjania ampelopsis is morphologically similar to S. schunkei. Both have similar fruits although those of S. schunkei are much larger. Serjania ampelopsis differs vegetatively from S. schunkei by its smooth stems (not warty) and biternate, chartaceous leaves (not ternate and coriaceous). Nevertheless, they both have stems with a single stele.

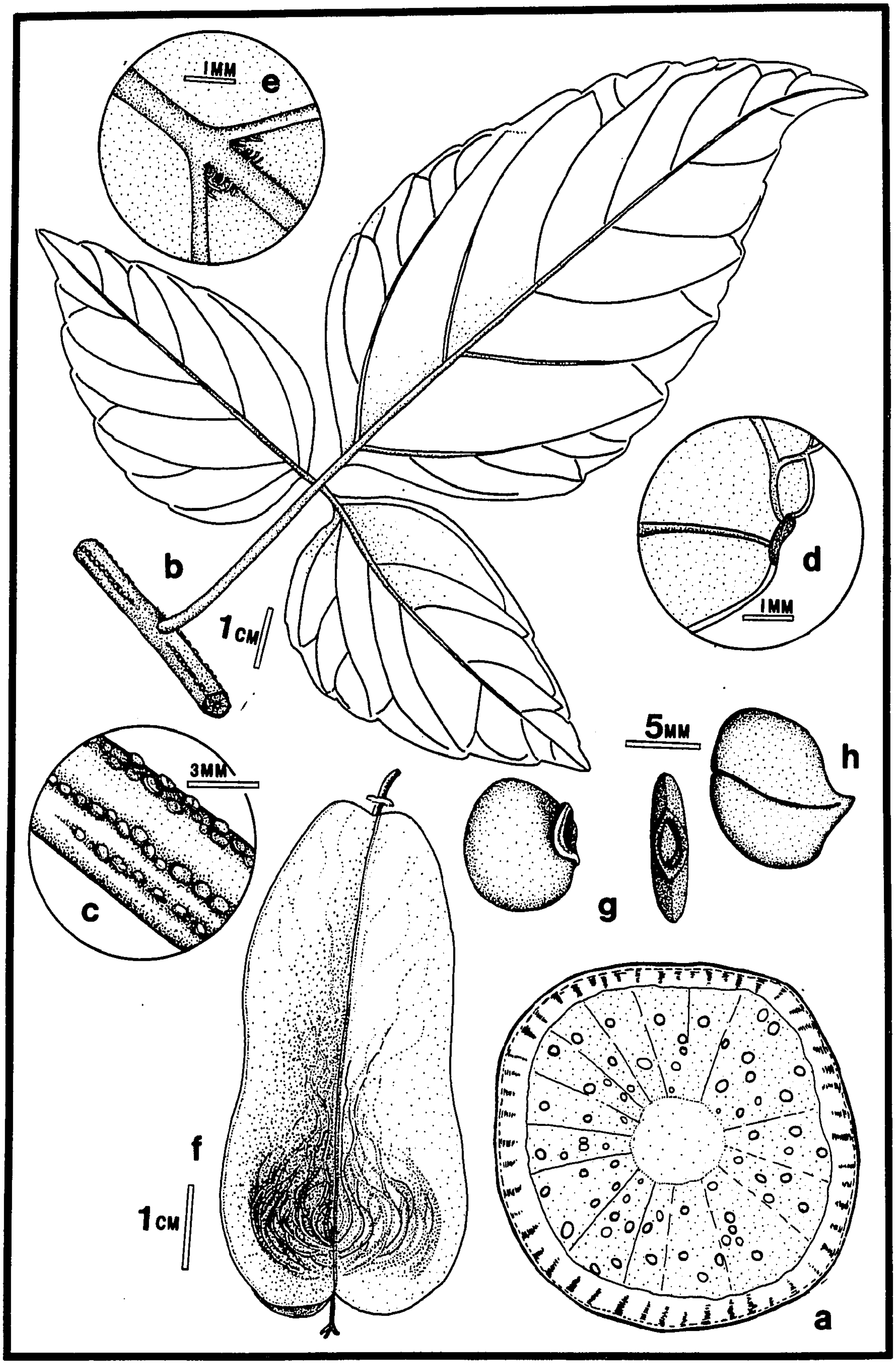
Serjania ampelopsis does not seem to be clearly related to any other member of section Platycoccus except for S. communis, with which it share many vegetative characters. Serjania ampelopsis might represent a vicariant species which evolved from isolated populations of S. communis after the recent geological uprise of the Andes.

The name ampelopsis means grapevine-like and refers to the climbing habit of this species.

11. Serjania schunkei Acevedo-Rodríguez, Brittonia 40: 287-288, Fig. 3. 1988. Type. Peru. San Martín: Mariscal Cáceres, Tocache Nuevo, Quebrada Cachiyacu de Huaquisha, in tall forest, 500-650 m, 3 Jan 1981 (fr), J. Schunke Vigo, 12492 (holotype, NY; isotypes, F, MO). Figs. 3d; 10a; 44.

Woody vine to 17 m long. **Stems** 5-angular, 6-7-striate, glabrescent, the old stems obtusely angled, with many, small, rounded lenticels arranged in lines along stem; cross section of stem with single vascular cylinder. **Stipules** subulate, ca 1.5 mm long. **Leaves** ternate; petiole not winged, cylindric, adaxially furrowed, glabrous or puberulent, 2-4 cm long; leaflets coriaceous, glabrous, acuminate or mucronate at apex, the terminal leaflet larger, 9-13 x 4-6.5 cm, ovate, with rounded base, petiolule 0.5-1 cm long, the lateral leaflets 5-6 x 3 cm, ovate-lanceolate with rounded oblique base, petiolule 0.3-0.6 cm long, the lower surface with hair domatia at axils of secondary veins, the margins scarious, remotely serrate with obtuse, glandular teeth, the veins craspedodromus, the primary and secondary veins prominent, especially on lower surface. **Inflorescence** longer than subtending leaf, the rachis sub-terete, densely covered with small (0.2 mm long), curly, whitish hairs; bracts and bracteoles 1 mm long, subulate; cincinni alternate, 3-4 mm long, deciduous, with same indument as rachis, 3-flowered; pedicel ca. 2 mm long, articulate at middle. **Flowers** imperfectly known; sepals 5, the outer sepals ca. 2 mm long, the inners sepals 2.2-2.5 mm long, third and fifth sepals completely distinct; petals spathulate, 2.5 mm long; disk with four glands, the central glands larger (0.75 mm long) and ovate, the lateral glands smaller and rounded; torus well developed. **Fruit** straw-colored, glabrous, chartaceous, oblong to oblanceolate, 5.5-6 x 3 cm, retuse at apex, rounded or subtruncate at base; cocci flat with slightly prominent reticulate network, the wing glabrous with

Figure 44. Serjania schunkei. A. Cross section of stem showing single stele. B. Ternate leaf and stem fragment. C. Detail of stem showing warty texture. D. Leaflet margin with glandular tooth. E. Lower leaflet surface with hair domatia. F. Fruit (not yet separated into merocarpic units). G. Seed, lateral and ventral sides. H. Embryo with straight cotyledons. All drawn from Schunke Vigo 12492.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outline not constricted below coccus, the partitioning wall 12 x 2 mm. Seeds lenticular, brown, 0.8 mm long, with large hilum (3.5 mm), inserted near base of coccus. Cotyledons erect.

Distribution. Serjania schunkei occurs in open tall forest. It is known only from the type (Fig. 41).

Local Name. Peru: Mashoshillo huasca.

Serjania schunkei is morphologically similar to S. ampelopsis. However, S. schunkei differs by its ternate, coriaceous leaves (not biternate and chartaceous), larger fruits with pyriform outline (not smaller with oblong outline) and warty stems (not smooth).

This species honors José Schunke Vigo, enthusiastic Peruvian botanist who collected the type and many interesting plants from the Peruvian Amazon.

12. Serjania squarrosa Radlkofer, Monogr. Serjania 115, 1875.

Type. Peru. Locality unknown, 1839-1840 (fl, fr), Gay s.n. (holotype, P). Fig. 45.

Serjania platypetala Radlkofer, Bot. Jahrb. Syst. 54 (117): 42. 1916. Type. Peru. Ayacucho, rocky slopes between shrubs, 3000-3200 m, May 1910 (fl, fr), Weberbauer 5506 (holotype, B, destroyed; lectotype, US, here designated; isolectotypes, F, GH, NY).

Woody vine 2 m long. **Stems** subterete or angular, with 5 prominent ribs, glabrescent, young stems densely ferruginous; cross section of stem with central, subterete, large vascular cylinder and (1) 2 or 3 peripheral, smaller, subterete vascular cylinders, these slightly included in central cylinder. **Stipules** oblong, obtuse, ca. 2 mm long. **Leaves** 4-5-jugate, lower jugae compound, or bipinnate; petiole margined, adaxially tomentose, 1-2.5 (4) cm long; rachises winged, adaxially tomentose, the main rachis 4-6.5 cm long; leaflets chartaceous to coriaceous, with acute, mucronate apex, the terminal leaflets, sub-rhombic, deltoid, lanceolate, oblong-lanceolate, or trilobate, (0.7) 1-3.5 (5.5) x 0.6-2 (3) cm, long attenuate or cuneate at base, the lateral leaflets ovate, oblong or lanceolate 1-2 (4) x 0.5-1.5 cm, obtuse and oblique at base, sessile or shortly petiolulate, both surfaces glabrous or sparsely covered with small (0.1-0.6 mm long), whitish hairs with swollen bases, the margins remotely serrate above middle, the teeth obtuse and glandular, the veins mixed craspedodromus, the primary and secondary veins slightly prominent on lower surface, higher order of veins dark, forming a conspicuous network. **Inflorescence** axillary, longer than subtending leaf, the axis angular, sparsely covered with small (0.2 mm long), whitish hairs, the rachis angular and slightly striate, densely covered with same indument as axis; bracts and bracteoles subulate, with glandular hairs on margins, the bracts ca. 2.5 mm long, the bracteoles 0.7 mm long; cincinni alternate, 0.2-2.5 cm long, with same indument as rachis, 5-7-flowered; pedicels 4-5 mm long, articulate close to middle, with same indument as cincinnus or glabrous. **Flowers:** sepals obtuse at apex, lineolate on abaxial surface, glabrous or densely covered with woolly, yellowish hairs, the outer sepals 2-3.2 mm long, oblong-ovate, the inner sepals 3-5 mm long, obovate, third and fifth sepals completely distinct; petals 4-5.5 mm long, spathulate or obovate, sparsely or densely covered with minute papillae on adaxial surface, lineolate on abaxial surface, the apex rounded; scales of central petals ca. 4 mm long, hood-shaped, with fleshy, crown-shaped apex and ciliate margins, the scales of lateral petals 3 mm long, with slightly fleshy, elongated apex and ciliate margins; disk with two central glands, ca. 1 mm long, ovate in outline, with obtuse apex, the lateral glands usually reduced; torus reduced; filaments sparsely covered with white, inflexed hairs; anthers elliptic, dorsifixed, ca. 0.4 mm long; ovary obovate in outline, glabrous to densely tomentose , the hairs yellowish or whitish, the style longer than stigma. **Fruits** 1.7-2.1 cm long, ovate in outline, glabrous or sparsely covered with yellowish or whitish hairs, the base subcordate, the apex slightly retuse, the cocci flattened, with slightly prominent veins, the wings slightly constricted below the coccus. Seeds flattened, lenticular, light brown, 5 mm long. Embryo with biplicate adaxial and curved abaxial cotyledons.

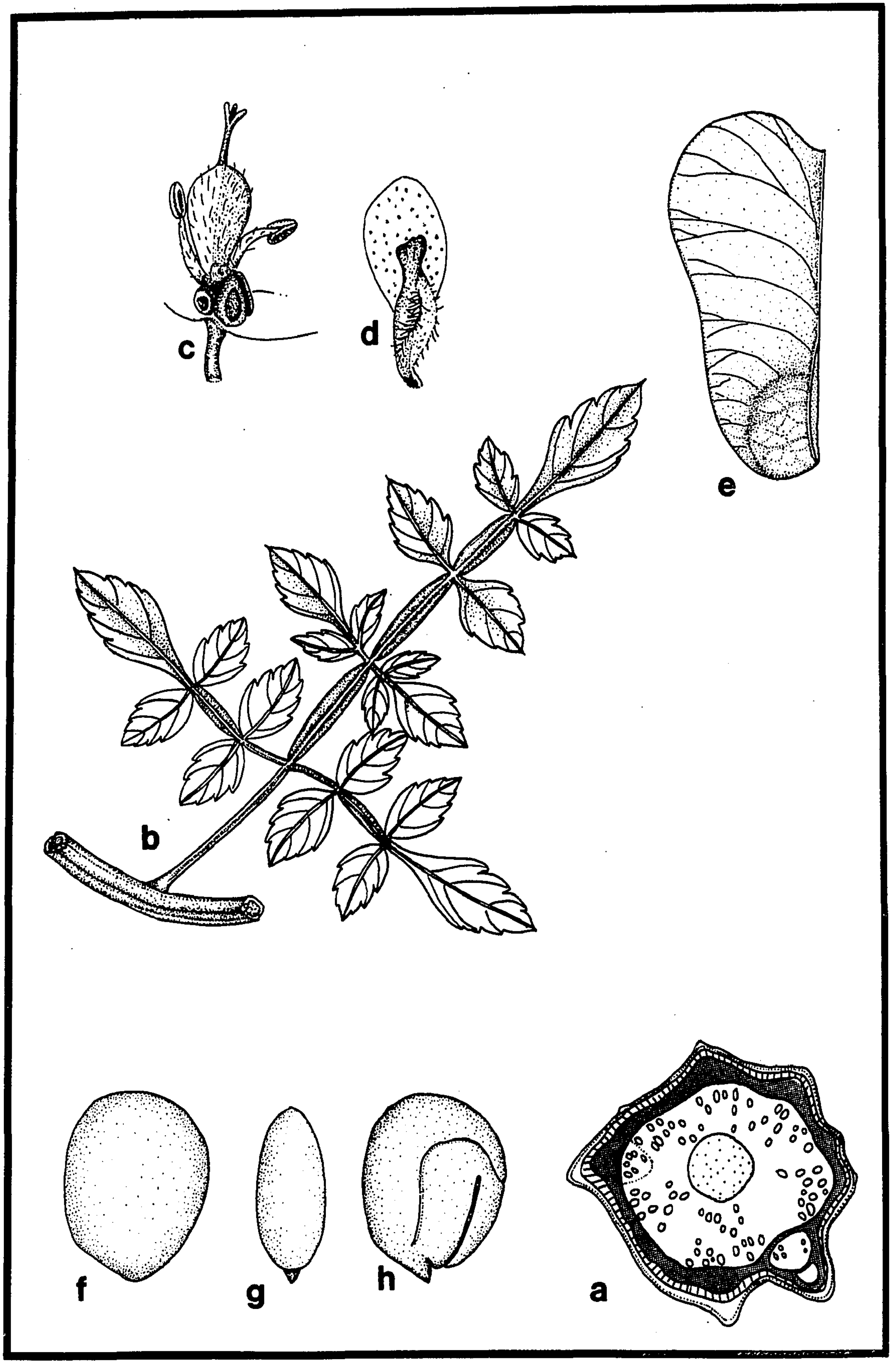
Distribution. Serjania squarrosa is a high elevation

(1200-3200 m) species endemic to Peru (Fig. 41). It has been collected in the Departments of Apurimac, Ayacucho, Cuzco, and Puno, from gallery forests and open areas such as rocky hillsides, dry slopes, and roadsides. It flowers from December to May and fruits from January to June.

Specimens examined. PERU. Without specific locality, Parchar, river-bank, 2900, 26 Apr 1925 (fr), Pennell 13688 (F, GH-2 sheets, NY). Apurimac: Abancay, vic. of Abancay, 2400 m, Apr 1938 (fl), Vargas 943 (A, F, MO); Chalhuanca, vic. Pakayca, dry slopes, 2650-2800 m, 24 Jun 1978 (fr), Gentry et al. 23317 (MO). Ayacucho: Between rivers Huaytata and Ocros, 21 Feb 1968 (fl), Soukup 5600 (US). Cuzco: Huispicanchi, Arapeza, Huasao, 3200 m, May 1925 (fl, fr), Herrera 687 (A, US); Quillabamba, Quintalpata, roadside, 1210-1435 m, 29-30 Dec 1986 (fl), Nuñez 6767 (MO); Urubamba, Ollantaytambo, 3000 m, 27 Apr 1915 (fl, fr), Cook & Gilbert 389 (US-2 sheets), Jan 1926 (fl), Ferrera 849a (US), bank of Urubamba river, 2850 m, 26 Apr 1925 (fr), Pennell 13685 (F-2 sheets); Pumahuanca, rocky hillside, 2900 m, 18 Jan 1949 (fl), Vargas 7603 (MO); illegible vic. Tanccac, roadside, 2770 m, 5 Jun 1964 (fr), Gade s.n. (WIS). Puno: Ollachea, 2725 m, Jan 1937 (fl, fr), Soukup 500 (F).

Serjania squarrosa is a very distinct species not obviously related to any other species of section Platycoccus. The cladistic analysis for the species of section Platycoccus suggests that S. squarrosa may not belong to it. However, it seems better to keep S.

Figure 45. Serjania squarrosa. A. Cross section of stem with a central and a peripheral stele. B. 4-jugate leaf, with lower pinnae compound, and fragment of stem. C. Pistillate flower with sepals and petals removed. D. Central petal with adnate scale. E. Fruit merocarp. F. Seed, lateral view. G. Embryo, ventral view. H. Embryo, lateral view. All drawn from Gentry et al. 23317.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squarrosa in section Platycoccus until more is known about other sections of Serjania.

EXCLUDED TAXA

Serjania confertiflora Radlkofer, Monogr. Serjania. 117. 1875.
Type. Brazil. Rio de Janeiro, s.d. (fl), Schott 712 (lectotype, K, here designated).

Mature fruits of this species have woody cocci with partitioning walls project beyond the coccus. These features place S. confertiflora in its own section.

Serjania grandidens Radlkofer, Bot. Jahrb. Syst. 37: 144, 1905. Type. Colombia. Santa Marta, along open dry water course, 5 miles N of Bondas, 100 ft, Oct 1898 (fl), H.H. Smith, 1538 (lectotype NY, here designated, isolectotypes BR, GH).

Recent collection of this taxon reveals that its fruits are woody, with a marginal rib along the partitioning wall. These features differ from those of section Platycoccus. Therefore, this species should be transferred to section Confertiflora.

Serjania decemstriata Radlkofer, Sitzb. Mat. Phys. Akad. Muech. 8: 223, 1878. Type. Argentina. Buenos Aires: Close to Buenos Aires, s.d. (fl), Didrichsen s.n. (lectotype C, here designated).

Although no fruiting material is known for this species, I tentatively place it in section Confertiflora because of its similar morphology to S. confertiflora, with which it may be synonymous.

Serjania foveata Grisebach, Plantae Lorentzianae, 60. 1874.

Type. Argentina. Tucumán: Close to Siabon, in subtropical forest, Mar 1872 (fl), Lorentz 288 (lectotype GOET, here designated).

This species has woody fruits with globose coccus and wide dissepimentum. Therefore, I consider this species to be a member of section Serjania.

Serjania minutiflora Radlkofer, Repert. Spec. Nov. Regni Veg. 17: 355. 1921. Type. Paraguay. Central: Vic. of Ypacaray lake, Dec 1913 (fl), Hassler 12414 (holotype, B, destroyed; lectotype, NY, here designated; isolectotypes, A, GH, K, US).

Although fruiting material for S. minutiflora is not yet known, it is morphological similar in other features to S. confertiflora. Therefore, S. minutiflora should be transferred to section Confertiflora.

Serjania trichomisca Radlkofer, Monogr. Serjania. 114. 1875.

Type. Brazil. Goiás: Serra Sao Felix to Rio Frairas, s.d. (fl,fr), Pohl 1934 (holotype W).

Although only immature fruits are known from this species, they do not have flat cocci, which indicates that S. trichomisca does not belong tosection Platycoccus. This species is better placed in section Eurycoccus.

Serjania paludosa Cambessèdes in St. Hilaire, Fl. Bras. Mer. 1: 369. 1828. Type. Brazil. Minas Gerais: Vic. Olho d'Agoa and Contendas, marshy area, Oct 1816-21 (fl), St. Hilaire 17 (lectotype, P, here designated).

The fruits of this species are triangular in outline, with partitioning wall projecting beyond the coccus, a character which defines section Confertiflora.

Serjania chartacea Radlkofer, Monogr. Serjania. 114. 1875. Type. French Guiana. Without specific locality, 1833 (fl), Leprieur 331 (lectotype, G, here designated; isolectotypes, F-2 sheets; photo from G at MO, GH).

Fruiting material is not known from this species. However, it is morphologically similar in other features to the S. confertiflora complex and therefore, should be placed in section Confertiflora.

Serjania inscripta Radlkofer, Bot. Jahrb. Syst. 37: 145. 1905. Type. Brazil. Amazonas: Lago de Esperança, Juruá Mirim, Aug 1904 (fl,fr), Ule 5644 (holotype, B, destroyed; lectotype, K, here designated).

Serjania inscripta is clearly a member of section Confertiflora because of its woody fruits with a marginal rib along the partitioning wall.

Serjania brachyptera Radlkofer, Bot. Jahrb. Syst. 37: 145. 1905. Type. Peru. Huanúco: Huamalies, between Punchau and Chiquibamba along valley of Marañon river, 3200 m, Jul 1903 (fl, fr), Weberbauer 3304 (holotype, B, destroyed; lectotype, USM, here designated, isolectotype, F, fragment of B).

Based on recent collections of fruits, this species belongs to section Physococcus.

NUMERICAL LIST OF TAXA

1. S. communis Cambessèdes
    - 1a. var. communis
    - 1b. var. glabra Radlkofer
    - 1c. var. alsmithii (Macbride) Acevedo-Rodgz.
2. S. leptocarpa Radlkofer
3. S. dumicola Radlkofer
4. S. cuspidata Cambessèdes
5. S. morii Acevedo-Rodgz.
6. S. regnellii Schlechtendal
7. S. cardiospermoides Schlechtendal & Chamisso
    - 7a. var. cardiospermoides
    - 7b. var. sujubata Radlkofer

8. S. tenuis Radlkofer

9. S. hatschbachii Ferrucci

10. S. ampelopsis Planchon & Linden

11. S. schunkei Acevedo-Rodgz.

12. S. squarrosa Radlkofer

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Numbers in parentheses refer to species and varieties as provided in the numerical list of taxa. Bold numbers refer to type collections.

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Acevedo, P. & E. Vargas, 1727(10), 1731(10), 1742(1a), 1759(3), 1778(10), 1779(10), 1781(10).

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Guarumina	*S. cuspidata*
Macote	*S. leptocarpa*
Mashoshillo huasca	*S. schunkei*
Oox kekel	*S. cardiospermoides*
Timbó cabeludo	*S. cuspidata*
Timbó de peixe	*S. cuspidata*
Timbó miúdo	*S. communis*

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