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A REVISION OF ISERTIA (ISERTIEAE: RUBIACEAE)

City University of New York

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A REVISION OF ISERTIA
(ISERTIEAE: RUBIACEAE)

by

BRIAN M. BOOM

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

1983

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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The City University of New York

Abstract

A REVISION OF ISERTIA
(ISERTIEAE: RUBIACEAE)

by

Brian M. Boom

Adviser: Associate Professor Scott A. Mori

Isertia (Isertieae: Rubiaceae) is a genus of shrubs and small trees ranging throughout Central America and northern South America and occurring sporadically in the Caribbean. It is an important floristic element in a variety of habitats ranging from savannas to successional and mature rain forests. This revision is based on herbarium, field, and laboratory studies. Seeds and pollen are surveyed by scanning electron microscopy and wood anatomy is studied by light microscopy. The geographic distributions of the taxa are mapped and their ecologies discussed on the basis of herbarium specimen label data. The phylogeny of the genus is discussed in the context of neotropical paleogeography. Diversification of the genus at the sectional level appears to have resulted from the major uplift of the Andes in the Pliocene. Diversification at the species level can be explained by the climatic fluctuations during the Pleistocene as predicted by the Refuge Theory. In the systematic treatment

the genus is described and a key is given to the 14 species, each of which is discussed. One new species, I. scorpioides B. M. Boom, one new combination, I. laevis (Triana) B. M. Boom, and one new status, I. section Cassupa (Humb. & Bonpl.) B. M. Boom, is proposed. Indices to exiccatae and to local names are included.

ACKNOWLEDGMENTS

I wish to thank especially Dr. Scott A. Mori for his support and guidance during this project. Others who have read and commented on the manuscript include Drs. Thomas S. Jensen, Ghilleen T. Prance, Dennis Wm. Stevenson, Peter Nelson, and Durland Fish.

Donald Black freely gave of his time to help with photography and scanning electron microscopy. Dr. Dennis Wm. Stevenson kindly provided laboratory facilities at Barnard College and Steve Clemants helped with wood anatomical technique. A special thanks goes to Dr. Peter Feinsinger of the University of Florida, Gainesville, for the use of unpublished data on the pollination ecology and phenology of Isertia parviflora. Ms. Bobbi Angel provided the illustration for Isertia scorpioides. Isertia distribution was mapped on the Flora Neotropica base map no. 1, published by the State University of Utrecht, the Netherlands. Wood blocks for anatomical study were provided by the U.S. Forest Products Laboratory, Madison, Wisconsin.

Appreciation is extended to the curators of the following fourteen herbaria for loaning the some 2200 specimens examined in this study: BR, CAY, F, GH, K, L, M, MO, NY, P, RB, U, US, VEN. Logistical support for field work was provided by the Office de la Recherche Scientifique et Technique Outre Mer (ORSTOM) in Cayenne, French Guiana, and by the Univ. Católica, Quito, Ecuador.

The new names proposed in this dissertation are not intended to meet the requirements for formal publication under the International Code of Botanical Nomenclature, but rather to indicate the intent for future publication.

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INTRODUCTION

Kirkbride (1979) in her review of the rubiaceous tribe Isertieae (formerly Mussaendae Hook. f.) for the neotropics, realigned the genera to reflect a more phylogenetic classification. She restricted the tribe to Isertia Schreber, Gonzalagunia Ruiz & Pavón, Amphidasya Standley, Raritebe Wernham, Sabicea Aublet, and Mussaenda L. based on the following characters: absence of raphids, valvate aestivation of the corolla, cordiform or discoid placenta, fleshy indehiscent fruit, and seed coat cells with pitted walls. Of the other genera traditionally assigned to the tribe, eight were excluded and an additional four could not be placed due to lack of material.

Kirkbride's delimitation of the tribe appears generally sound, but there are a few problems which will only be clarified when each genus is revised. For example, Kirkbride's circumscription of Isertieae states that the stipules are interpetiolar, but in three species, Isertia rosea Spruce ex K. Schum., I. spiciformis DC., and I. longifolia (Hoffsgg. ex Roemer & Schultes) K. Schum., they are clearly intrapetiolar. Also, Kirkbride places Cassupa Humb. & Bonpl. in synonymy with Isertia, in keeping with modern practice. As per the original description of Cassupa, that genus is characterized by, among other things, a 2-locular ovary. Kirkbride's key

restricts Isertia to a 5-6-locular ovary. Furthermore, Index Kewensis and the Gray Card Index list several additional probable generic synonyms which she does not consider: Brignolia DC., Bruinsmania Miq., Phosanthus Raf., and Creatantha Standley.

An examination of two recent floristic treatments shows some taxonomic confusion of the species within Isertia. Dwyer (1980) in the Flora of Panama stated that I. hypoleuca Benth. has a 2-locular ovary, while Steyermark in the Botany of the Guayana Highland (1967) and the Flora de Venezuela (1974) listed a 5-6-locular ovary for this species. Discrepancies in the geographic distribution of I. hypoleuca also exist in these treatments. From these and other considerations it was decided that it would be useful to revise Isertia as the first step in a monograph of the tribe Isertieae.

HISTORY OF THE GENUS

1775. Aublet described the first species of Isertia as a Guettarda (G. coccinea), based on his collections from around Cayenne, French Guiana. An excellent illustration of "La Guettarde à fleur rouge" accompanied the description in his Histoire des plantes de la Guiane française. Aublet's assignment of this species to Guettarda was probably due to the pyrenate nature of the fruits. This is only a superficial resemblance, however, because in a true Guettarda each nutlet contains only one seed; in G. coccinea there are numerous small seeds in each nutlet. Aublet noted that the fruits are sweet and good to eat and that a decoction of the leaves is used by the Creoles in fomentations, in baths, and in showers in order to cure swelling (from infection?). This tree is common on the Ile de Cayenne on terra firme where it grows in secondary forests and at the edge of savannas; it is in flower and fruit almost throughout the entire year.

1789. Schreber in Genera Plantarum described the genus Isertia by referring to Aublet's plate 123 of Guettarda coccinea. He did not, however, actually make the new combination.

1791. Gmelin was the first to make the new combination
Isertia coccinea.

1798. In *Eclogae Americanae*, Vahl treated Isertia coccinea as the only species of the genus. Vahl cited Aublet's and Schreber's works, but was apparently unaware of that of Gmelin. Perhaps as a consequence of this omission, Index Kewensis later incorrectly attributed the combination I. coccinea to Vahl; many authors have subsequently followed this attribution.

1798. Also in *Eclogae Americanae*, Vahl described I. parviflora from Ryan's collections from Trinidad.

1806. Humboldt and Bonpland described the genus Cassupa and a new species, C. verrucosa, based on their collections from the Río Negro in Venezuela. Bonpland noted the overall similarity of Cassupa to Isertia, but added that the former differs from the latter by its bi-ocular ovary, 2-lobed stigma, and berries instead of pyrenes. An excellent plate illustrated the new species.

1819. Hoffmannsegg described a species of Isertia as Psychotria longifolia from a Brazilian collection in Willdenow's herbarium.

1820. Rafinesque superfluously described the genus Phosanthus based on Guettarda coccinea.
1820. Jussieu recognized the distinction between Isertia and Cassupa.
1830. De Candolle in his Prodromus also recognized the distinctness of Cassupa, and listed the only known species, C. verrucosa. Under Isertia he recognized four species: I. coccinea (misattributed to Vahl), I. parviflora, and two new species. Isertia haenkeana was described based on a Haenke collection from Mexico, and I. spiciformis was described from French Guiana collections. A new genus, Brignolia (now considered congeneric with Isertia), was described based on B. acuminata from a Trinidad collection by Lockhart. The affinity of the new genus to Isertia was acknowledged, but it was thought necessary to describe a new genus because the fruit was not sufficiently known and the locules were of a doubtful number in the Lockhart collection.
1830. Richard in his Mémoire sur la famille des Rubiacées maintained Cassupa as distinct from Isertia, but noted their similarity: "Pour le port, ce genre (Cassupa) a la plus grande analogie avec l'Isertia; même forme

de corolle, mêmes poils en bouchant l'entrée; même nombre d'étamines et de divisions calicinales. Mais ici le stigmate n'est qu'à deux divisions et le fruit à deux loges, tandis qu'on en compte six dans le genre Isertia." Despite this, he placed Isertia in the tribe Isertieae and Cassupa in the tribe Gardenieae.

1838. In Genera Plantarum Endlicher recognized Cassupa, Brignolia, and Isertia. Under Isertia he listed Phosanthus as a synonym.

1838. Meisner in his Genera Plantarum recognized Brignolia, Cassupa, and Isertia and placed each in a separate tribe: Brignolia in the Hamelieae, Cassupa in the Gardenieae, and Isertia in the Isertieae.

1840. Steudel attributed the name I. breviflora to Martius, but this name was never published. A description for this name on a sheet at BR clearly indicates that the name was coined for I. hypoleuca, a new species soon to be published by Bentham.

1841. Bentham described I. hypoleuca based on a Schomburgk collection from Guiana, and noted its

affinity to I. coccinea. In the same publication he described a second species of the genus Brignolia, B. pubigera, based also on a Schomburgk collection from Guiana.

1843. Miquel described the genus Bruinsmania based on B. isertioides from a collection from Surinam by Focke. The affinity to Isertia was acknowledged, but it differed from that genus by having such features as noncristate corolla sinuses and an undivided stigma.

1844. Miquel described I. flava based on specimens from Surinam. He noted that the new species was similar in most respects to I. hypoleuca.

1851. Miquel maintained Bruinsmania isertioides and acknowledged its affinity to Isertia. He listed I. hypoleuca and I. flava as synonyms of I. coccinea (which he incorrectly attributed to Vahl). He described a new species from Suriman, I. commutata.

1856. Schlechtendal listed Allemaña longifolia Hoffsgg. in synonymy with Psychotria longifolia.

1858. Triana described two taxa of Cassupa from Colombia

based on his own collections: Cassupa laevis var. laevis and C. laevis var. chocoensis. He noted the great resemblance of C. laevis to C. verrucosa. He further commented that the inhabitants of the Chocó used the bark of C. laevis var. chocoensis in the manner of Cinchona, taking that plant for a species of the latter genus.

1864. Grisebach in his Flora of the British West Indian Islands recognized three species of Isertia: I. coccinea, I. haenkeana, and I. parviflora. The genera Brignolia and Bruinsmania were listed as synonyms of Isertia.

1873. Bentham and Hooker in their Genera Plantarum recognized Cassupa as distinct from Isertia. For Cassupa they only referred to one species (C. verrucosa) and were apparently unaware of the taxa described by Triana in 1858. For Isertia they recognized 15 species. They considered Brignolia and Bruinsmania as synonyms of Isertia.

1880. Baillon in his Histoire des plantes was the first author to consider Cassupa, Phosanthus, Brignolia, and Bruinsmania all to be synonyms of Isertia.

1889. Schumann in his contribution to the Rubiaceae for Flora Brasiliensis presented an important synopsis of Isertia and Cassupa. In his key to the genera of the Mussaendeae, Isertia is separated from Cassupa on the basis of ovary locule number (Isertia 4-6-locular, Cassupa 2-locular). For Cassupa he recognized C. verrucosa as the only species occurring in Brazil. For Isertia, he recognized six species: I. rosea, I. coccinea, I. bullata, I. spiciformis, I. parviflora, and I. longifolia. The treatment entailed several new species and combinations. He published Spruce's I. rosea based on Spruce's own collections. He described I. bullata as a new species from Maranhão, distinguishing it from I. spiciformis on the basis of leaf texture and shape. Isertia hypoleuca was treated for the first time as a variety of I. coccinea. Psychotria longifolia was transferred to Isertia. The following synonymy was listed: I. flava Miq. as a synonym of I. coccinea; I. commutata Miq. as a synonym of I. spiciformis; Brignolia acuminata DC., Brignolia pubigera Benth., and Bruinsmania isertioides Miq. as synonyms of I. parviflora.

1891. In Die natürlichen Pflanzenfamilien Schumann

recognized Isertia and Cassupa. He listed Brignolia and Bruinsmania as synonyms of Isertia. Under Cassupa he listed the species C. verrucosa and C. alba K. Schum., the latter being a nomen nudum.

1896. Rusby published Britton's I. reticulata based on collections from the Bolivian Andes.

1905. Sprague described two new species of Isertia. Isertia alba was described based on a Spruce collection from Yurimaguas, Peru (as per Wernham, 1914). The original data given for the type by Sprague were "eastern cordilleras between Pitalito and Mocoa," in Colombia. Isertia purdiei was described from a Purdie collection from Muso, Colombia.

1907. Bartlett described I. deamii based on a collection by C. C. Deam from Puerto Barrios, Department of Izabal, Guatemala.

1908. Schumann and Krause described several new taxa. Isertia humboldtiana was based on a Lehmann collection from Colombia. Cassupa alba was based on Triana and Lehmann collections from Colombia. Cassupa juruana and C. scarlatina were named from

collections by E. Ule from Amazonas, Brazil.

1914. Wernham described I. spraguei from a collection made by Sprague from the eastern Cordilleras in Colombia. He allied the new species to I. purdiei. Wernham noted that in the original publication of I. alba Sprague the type locality was erroneously given as Colombia. He corrected the clerical error to the following: Peruvian Amazonas, Yurimaguas, Huallaga River, in secondary forest, fl. May, Spruce 3878.

1914. Standley described Cassupa pittieri from a collection made by H. Pittier in the Pacific coastal lowlands of the Colombian state of Cauca. He stated that C. pittieri resembled C. alba Schum. et Krause in flower color, but differs in its longer verrucose and puberulent corolla and its green leaf blade undersurface.

1916. Standley described Cassupa panamensis from Pittier's collection in the Province of Colón, Panama. He noted that it is the first species of the genus to be reported north of Colombia. He allied it to C. alba Schum. et Krause, but noted his new species is distinguished by the longer

corollas which are tuberculate and puberulent outside rather than smooth and glabrous.

1916. J. D. Smith described I. deamii var. stenophylla from a Pittier collection made near Boca Culebra, Comarca de Puntarenas, Costa Rica.

1922. Ducke described I. viscosa from Brazil based on one of his own collections. The outstanding feature of the species was the viscous upper leaf blade surface.

1925. Krause described I. hoehnei from Hoehne's collections from the Rio Tapajós region, Brazil.

1925. Ducke described I. glabra from his own Brazilian collections. Regarding the relationships of this species he stated: "cette espèce se rapproche de l'I. parviflora des parties nord de l'hyléa, mais elle est presque complètement glabre et les feuilles ont une forme assez différente."

1926. Standley in his Trees and Shrubs of Mexico listed Isertia haenkeana because the type collection of Haenke specified the locality as Mexico. Standley had not seen any recent collections from Mexico,

however, and he suggested that the Mexican locality may be in error. I must agree with this suspicion as I have seen no collections of Isertia made north of Guatemala.

1927. S. J. Record commented that the wood of Isertia haenkeana was: "brownish, with pink streaks (in specimen), of medium density and weight, fine-textured; pith large and white."

1928. D. A. Kribs discussed the wood anatomy of Isertia hypoleuca based on Persaud collections from British Guiana. He listed the vernacular name as "mamayahooka."

1928. Record listed I. haenkeana as a species of tree collected from Panama.

1929. Record listed I. haenkeana as very frequent in secondary growth near San Luis in northeastern Nicaragua.

1929. Standley described I. weberbaueri based on a Weberbauer collection from the valley of the Río Mixiollo, Peru. He stated that I. weberbaueri is related to I. hypoleuca, but in the latter the

calyx is larger and more conspicuously lobed, and the corolla is 5-8 cm long. He also described I. parvifolia based on a Carlos Schunke collection from the Chanchamayo Valley, Peru. He stated that I. parvifolia is related to I. weberbaueri, but it differs conspicuously from that species in the small, narrow, long-acuminate leaves and much-reduced inflorescence.

1930. Standley listed I. haenkeana as occurring in Honduras.

1930. In The Rubiaceae of Colombia Standley recognized both Cassupa and Isertia as separate genera, separating them in the generic key by ovary locule number. For Cassupa he recognized C. alba, C. pittieri, and C. verrucosa. For Isertia he listed seven species: I. coccinea, I. haenkeana, I. humboldtiana, I. hypoleuca, I. rosea, I. purdiei, and I. spraguei. No key to the species was provided.

1930. Standley described the new species I. leiantha based on a collection by S. Juzepczuk from Peñas Blancas, Dept. de Antioquía, Colombia. He stated that the new plant is similar in most respects to

I. haenkeana, but differs in having a glabrous corolla.

1931. In The Rubiaceae of Ecuador Standley listed I. hypoleuca as possibly occurring in Ecuador. No other species were known from the country at that time.

1931. Standley described the new genus Creatantha with the type species, C. peruviana, collected by Killip and Smith in Puerto Yessup, Dept. de Junín, Peru. He stated that Creatantha is related to Isertia and that it is to be distinguished from the latter only in the length and shape of the corolla tube.

1931. Standley decided that Cassupa was synonymous with Isertia and he transferred the following five species of Cassupa to Isertia: C. pittiei, C. panamensis, C. verrucosa, C. juruana, C. alba. Standley explained his decision: "According to most authorities, Isertia has a 4-6-celled berry and imbricate corolla lobes, while in Cassupa the berry is 2-celled and the corolla lobes valvate.... After careful examination of corollas and buds of the plants referred to the two genera, I am unable to see any essential differences in estivation. All

plants referred to the two genera are exactly similar in general appearance" This reasoning has been followed by all subsequent authors.

1931. Standley in The Rubiaceae of Venezuela listed five species of Isertia: I. haenkeana, I. hypoleuca, I. parviflora, I. rosea, and I. verrucosa. No key to the species was provided.

1932. Standley listed the vernacular name of "coralleira" for Isertia hypoleuca from the Rio Tapajós, Brazil.

1934. Bremekamp described I. coccinea var. pentamera based on a collection by Gonggrijp from the Marowyne River, Surinam. The new variety only differs from the typical situation in having 5-merous instead of 6-merous flowers which are somewhat smaller. Bremekamp disagreed with Schumann's treatment of I. hypoleuca as a variety of I. coccinea; Bremekamp regarded I. hypoleuca and I. coccinea as distinct species.

1936. Standley described Isertia krausei from a collection by Weberbauer from the Dept. Libertad, Peru. He noted "Isertia krausei is a well-marked species,

distinguished particularly by its stiff, narrow leaves, with minute and scant tomentum, which is confined to the bottom of the areoles on the lower leaf surface."

1936. In The Rubiaceae of Peru Standley recognized six species of Isertia: I. alba Sprague, I. hoehnei, I. krausei, I. parvifolia, I. rosea, and I. weberbaueri. He listed Creatantha peruviana in synonymy with I. alba, acknowledging that the corolla character which had prompted him to describe the new genus in 1931 was simply a monstrosity. Unlike his previous treatments of Isertia, this one included a key to the species.

1941. Williams commented on the occurrence of I. parviflora (café negro) in the Caicara region of the middle Orinoco River in Venezuela. He noted: "a tree ca 8 m in height, with a hard, heavy wood of light brown color. Occurs at the lower limit of the forests, adjacent to the savannas. On steep, rocky slopes."

1947. Williams listed Isertia verrucosa as one of the principal understory trees of the Yavita-Pimichín forest, Venezuela.

1957. Bremekamp described a new species, Isertia pterantha, based on a collection by Cowan from Montagne de Kaw, French Guiana. He noted that I. pterantha is similar to I. rosea, but differs in having larger flowers and a 5-6-locular ovary.
1958. Foster listed I. reticulata as occurring in Bolivia.
1958. Brizicky, Stern, and Chambers listed I. haenkeana as occurring on cut-over land in the Canal Zone, Panama.
1967. Steyermark in his treatment of Isertia for the Flora of the Guayana Highland recognized ten species occurring in Venezuela and the Guianas: Isertia hypoleuca, I. verrucosa, I. parviflora, I. pterantha, I. longifolia, I. rosea, I. spiciformis, I. coccinea, I. wilhelminensis, and I. haenkeana. He provided a key to the species, but no descriptions except for the new taxa he described: I. parviflora var. hirta based on a British Guiana Forest Department collection; I. wilhelminensis based on a collection by H. S. Irwin, G. T. Prance, T. R. Soderstrom, and N. Holmgren from Wilhelmina

Gebergte in Surinam; I. haenkeana var. mirandensis based on a Steyermark collection from the Cordillera de la Costa, Miranda, Venezuela. Steyermark incorrectly cited the type species of Isertia as I. parviflora; the type is actually I. coccinea. He also discussed I. alba Sprague which he said occurs in Colombia, Ecuador, and Peru. He incorrectly cited the type of this species as "between Pitalito and Mocoa, Colombia, Sprague s.n." This is understandable since this is the information provided in the original publication. But, as Wernham pointed out in 1914, the type collection of I. alba Sprague was erroneously cited due to a clerical error. The correct citation is as follows: "Peruvian Amazonas, Yurimaguas, Hualluga River, in secondary forest, fl. May, Spruce 3878." I also question Steyermark's citation of the type of I. coccinea as being a collection of von Rohr; the type is an Aublet collection from French Guiana.

1974. Steyermark in the treatment of Isertia for the Flora de Venezuela commented that the genus contained 25 species, 5 of which occur in Venezuela: I. hypoleuca, I. verrucosa, I. rosea, I. parviflora, I. haenkeana. The subspecific taxa recognized are I. haenkeana var. mirandensis and I. parviflora var.

hirta. Illustrations are provided for I. haenkeana and I. hypoleuca. A key to the taxa and descriptions are given.

1975. In the Rubiaceae for the Flora of Guatemala Standley and Williams described and illustrated the only species of Isertia known from that country, I. haenkeana. They listed I. deamii and I. deamii var. stenophylla as synonyms.

1978. Bolten and Feinsinger reported on the pollination ecology and phenology of Isertia parviflora in Trinidad.

1978. Steyermark and Huber in their Flora del Avila (Venezuela) listed Isertia haenkeana var. mirandensis as occurring in cloud forests 900-1000 m in altitude.

1979. M. C. G. Kirkbride in her review of the tribe Isertieae for the neotropics, realigned the genera to reflect her ideas of a more natural classification. She restricted the tribe to Isertia Schreber, Gonzalagunia Ruiz et Pavón, Amphidasya Standley, Raritebe Wernham, Sabicea Aubl., and Mussaenda L. based on the following characters: absence of

raphides, valvate aestivation of the corolla, cordiform or discoid placenta, fleshy indehiscent fruit, and seed coat cells with pitted walls. Of the other genera traditionally assigned to the tribe, eight were excluded and an additional four could not be placed due to lack of material.

1980. Dwyer in his treatment of Isertia for the Flora of Panama listed I. haenkeana and I. hypoleuca. In this treatment he confused I. hypoleuca (an Amazonian-Guayanan plant) for I. alba Sprague (= I. laevis), an Andean-Central American plant.

MORPHOLOGY

Habit. Isertia is a genus of shrubs and small trees growing up to 25 m tall in some species; heights of 10 m are much more common however. The branchlets are either slender and subrotund in cross section or, more commonly, thick and quadrangular. The branchlets may be either glabrous or pubescent (Fig. 1).

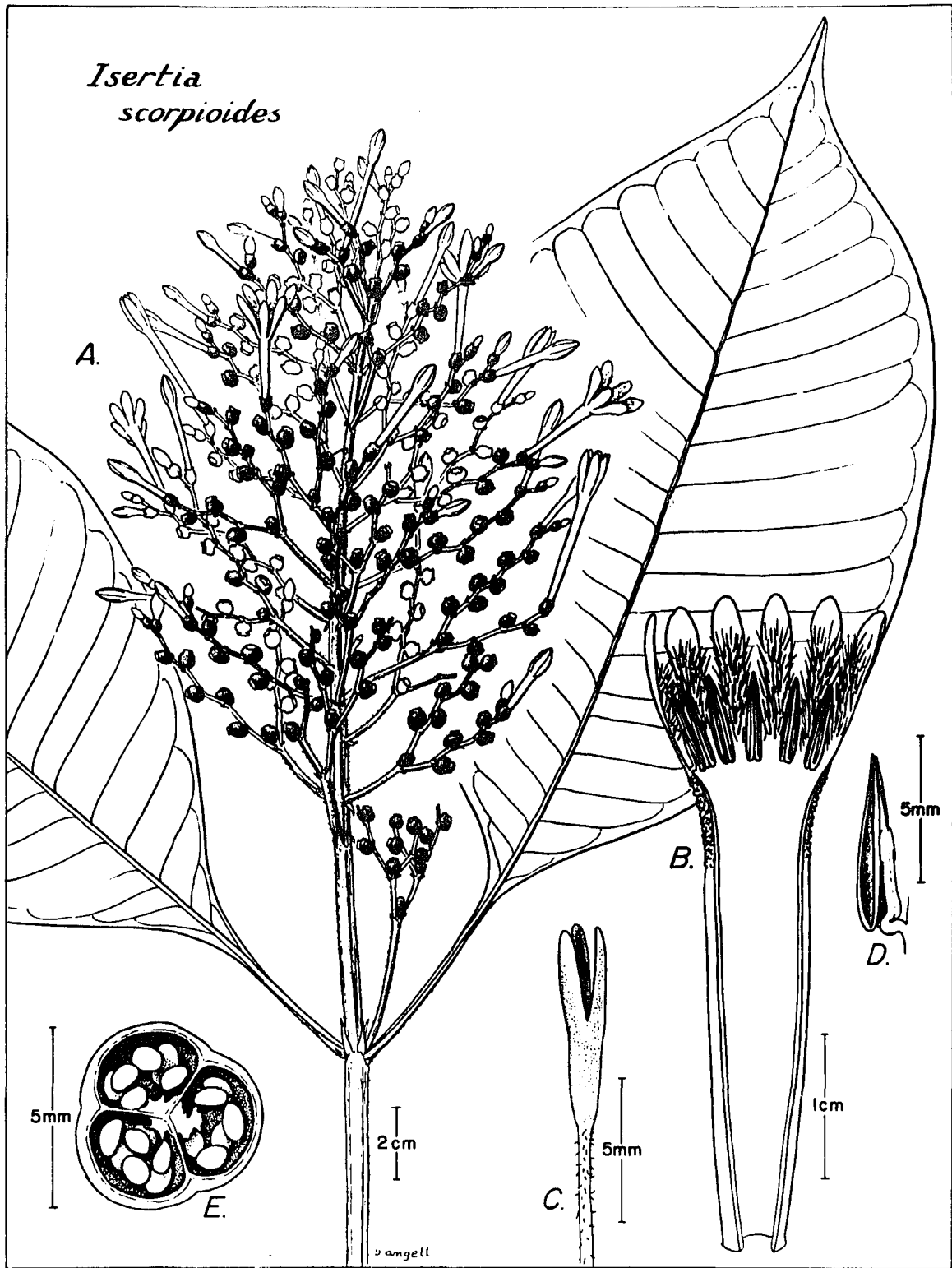
Leaves. All species of Isertia have opposite, petiolate leaves. The major variation of the leaves relates to shape, texture, and tertiary venation. In shape they range from ovate-lanceolate to obovate-lanceolate. In texture they may be membranaceous or coriaceous. In two species (I. krausei and I. reticulata) the tertiary venation of the upper leaf blade is impressed; in all other species this venation is planar.

Stipules. Both interpetiolar and intrapetiolar stipules are found in Isertia. The primitive condition, interpetiolar, is found in the majority of the species. In only three species (I. rosea, I. spiciformis, and I. longifolia--all members of I. sect. Isertia) does the intrapetiolar condition occur. When the stipules are interpetiolar, there are 4 per node; when they are intrapetiolar, there are 2 per node.

Inflorescence. In Isertia the inflorescence is always terminal. The variation encountered has to do with the

Fig. 1. Isertia scorpioides B. M. Boom, drawn from Kirkbride & Hayden 316 (HOLOTYPE: NY). A. Specimen with inflorescence, showing mature fruits. B. Corolla, spread open. C. Stigma and upper portion of style. D. Anther, side view. E. Fruit, x.s., showing seeds detached from placenta.

Isertia
scorpioides



relative degree of inflorescence branching and the disposition of the flowers: either thyrsiform-paniculate or thyrsiform-racemose with secondary rachises terminating in dichasia or scorpioid cymes of sessile or pedicellate flowers.

Flowers. The corolla tubes are all cylindrical, varying in length from 13 mm (I. parviflora and I. longifolia) up to as much as 75 mm (I. pittieri). The throats are always villous inside, but in one species (I. longifolia) this pubescence extends virtually the entire length of the inside of the tube. This pubescence is normally yellow or white, but in I. rosea it is often pinkish-purple. The color of the corolla tube itself varies from white to pink, red, orange, or yellow, and is generally characteristic for each species. The corolla lobes are 5-6 (7) in number, short and spreading; the aestivation is both valvate (3 internal lobes) and imbricate (2 external lobes).

Calyx. The calyx provides few taxonomic characters in Isertia. It is 4-6-lobate, the lobes small, often indistinct, usually more or less equal. The occasional elongation of one or more of the lobes (e.g., in I. coccinea) is of interest due to the regular occurrence of this condition in the genus Mussaenda, a paleotropical member of the tribe Isertiaeae. In some species of Isertia there are red squamose cells produced in small patches

inside around the mouth of the calyx.

Androecium. The stamens vary in number from 4-7, sometimes having such variation in different flowers from the same inflorescence. The stamens are inserted on the corolla tube near the mouth and are included or slightly exerted; the filaments are thus short, not providing any important taxonomic characters. The anthers are loculate.

Gynoecium. The ovary is 2-3 (4)-celled in Isertia sect. Cassupa and (4) 5-6 (7)-celled in Isertia sect. Isertia. In both sections the style is linear, sometimes ciliolate. The stigma has 2-6 (7) narrowly oblong lobes (varying in number again according the section of the genus) which are included or slightly exerted from the corolla mouth. The placentation is axile with numerous ovules being borne on a cordiform placenta.

Fruits. The fruits of Isertia sect. Cassupa are fleshy, 2-3 (4)-loculate berries. The fruits of Isertia sect. Isertia are (4) 5-6 (7)-loculate pyrenes. The distinction of these two fruit types is quite easily observed by cutting into a fresh or re-hydrated fruit. The berries are soft and easily cut, whereas the pyrenes have a bony endocarp that is cut only with difficulty. The number of locules in a pyrenate fruit can often be observed on uncut fruits by noting the ridges of the nutlets. The berries generally give no hint as to the locule number,

the outer surface appearing smooth. The fruits of both sections are globose and vary in size from about 5-10 mm in diameter.

Seeds. The seeds of Isertia vary from 0.5-1.2 mm in length and from 0.2-1 mm in diameter. The seed coat is foveolate with polygonal cells 84-150 um. My observations on Isertia seeds conform with those of Kirkbride (1979) who looked at three or four species.

In the present study the seeds of 13 taxa were examined by Scanning Electron Microscopy (SEM). The specimens examined are listed in Table 1. Seeds were mounted on stubs with double sticky tape and were then coated for two minutes with 60 percent gold and 40 percent palladium in a Technics sputtering coater. The samples were then viewed at 10 Kv in a JEOL JSM-U3 and photographed at 70-100 x with Polaroid Type 55 positive/negative film.

Representative seeds are shown in Figs. 2-13. With the exception of two species, there appears to be few major species-specific diagnostic characters or size differences. The seeds of Isertia pittieri and I. laevis (Figs. 2 & 3) are notable in their rectangular, blocky shape and very irregularly shaped polygonal cells. In most other species of Isertia the seeds have more-or-less rounded-angular shapes. The seeds of the other two species examined in I. sect. Cassupa (I. reticulata and I. verrucosa) are distinguishable from one another in

Table 1. Voucher specimens examined in SEM study of Isertia seeds.*

<u>Taxon</u>	<u>Collector</u>	<u>Country</u>
<u>I. coccinea</u>	<u>Rosa 1030</u>	Brazil
<u>I. haenkeana</u>		
var. <u>haenkeana</u>	<u>Marshall & Neill 6496</u>	Nicaragua
<u>I. wilhelminensis</u>	<u>Irwin et al. 54949</u>	Surinam
<u>I. rosea</u>	<u>Krukoff 7980</u>	Brazil
<u>I. longifolia</u>	<u>Ducke 7610</u>	Brazil
<u>I. parviflora</u>	<u>Graham 541</u>	Trinidad
<u>I. spiciformis</u>	<u>Rosa & Viler 2802</u>	Brazil
<u>I. hypoleuca</u>	<u>Persaud 15</u>	Guyana
<u>I. haenkeana</u>		
var. <u>mirandensis</u>	<u>Steyermark 97527</u>	Venezuela
<u>I. pittieri</u>	<u>Killip & Cuatrecasas</u>	
	<u>38863</u>	Colombia
<u>I. laevis</u>	<u>Maas et al. P12942</u>	Brazil
<u>I. verrucosa</u>	<u>Clark 6563</u>	Venezuela
<u>I. reticulata</u>	<u>Buchtein 64</u>	Bolivia

* All specimens deposited at NY.

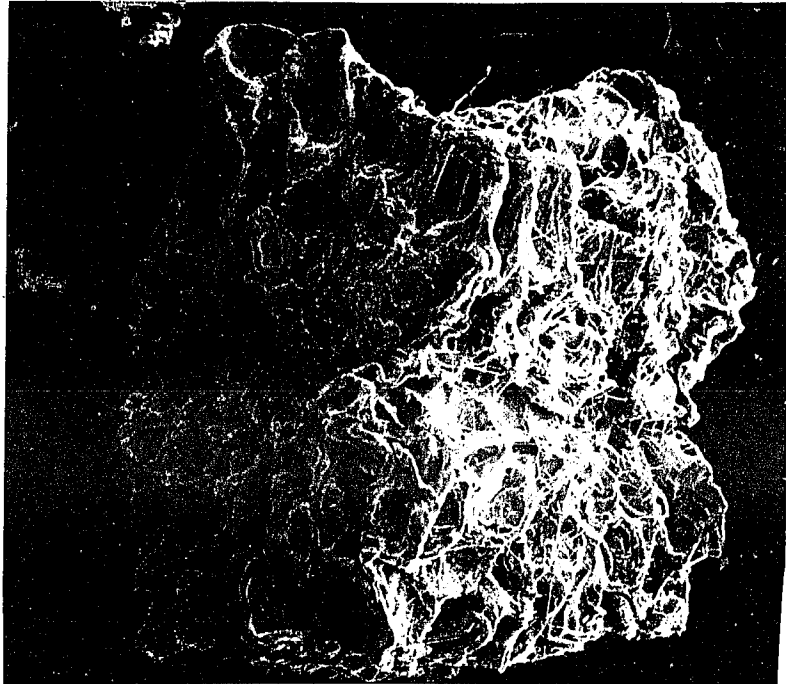


Fig. 2. Seed of Isertia pittieri, 100x.

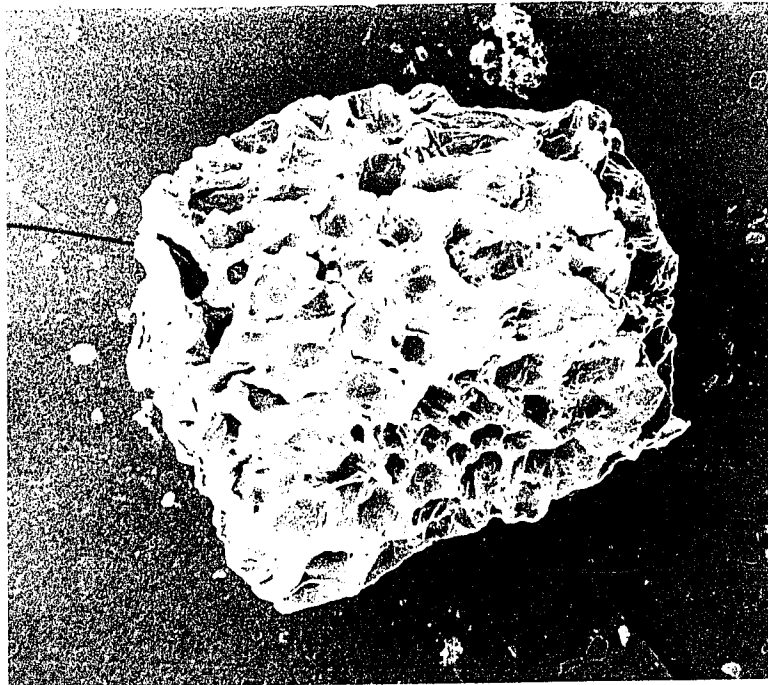


Fig. 3. Seed of Isertia laevis, 100x.

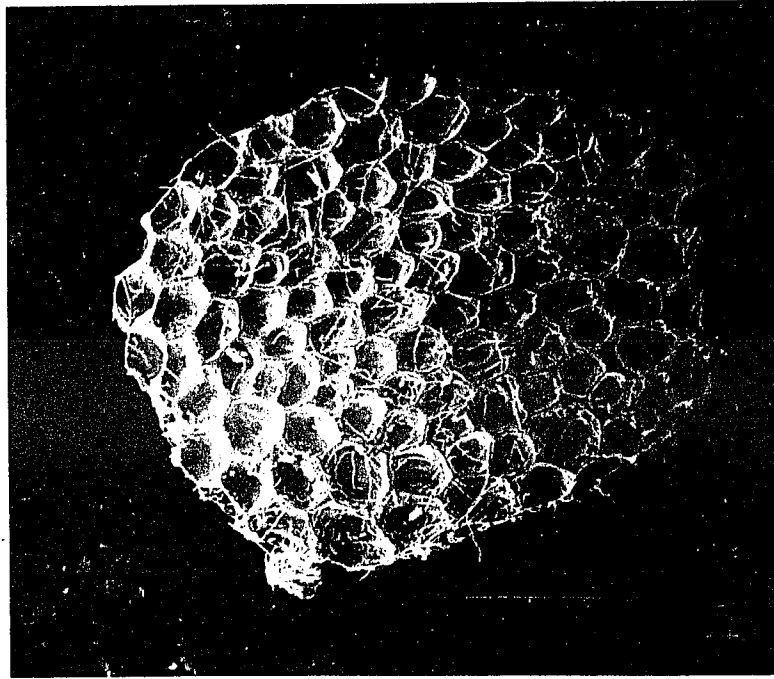


Fig. 4. Seed of Isertia reticulata, 100x.

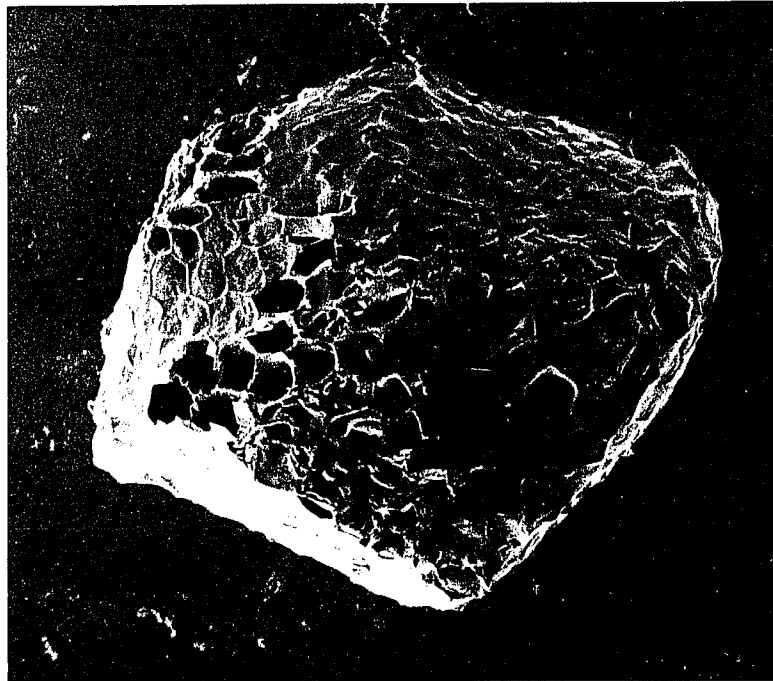


Fig. 5. Seed of Isertia verrucosa, 70x.

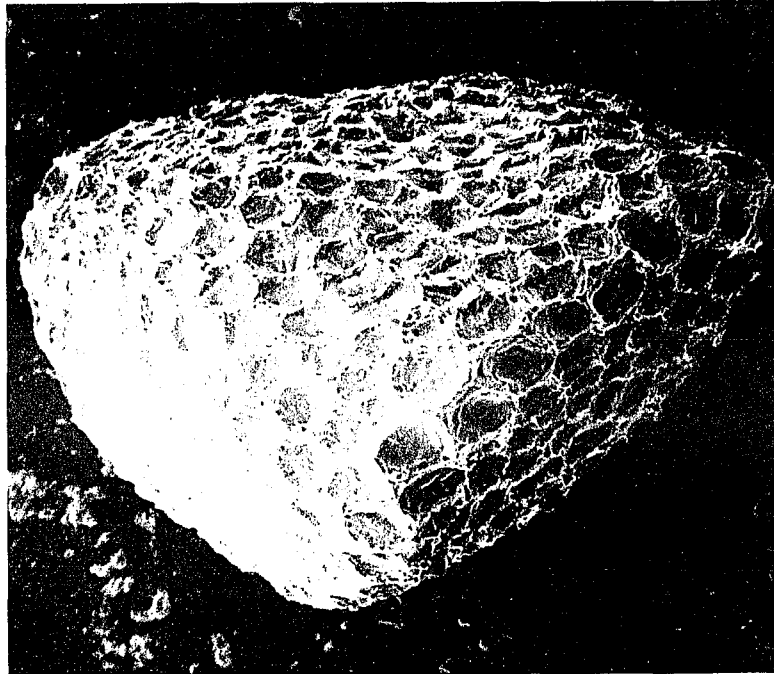


Fig. 6. Seed of Isertia spiciformis, 100x.

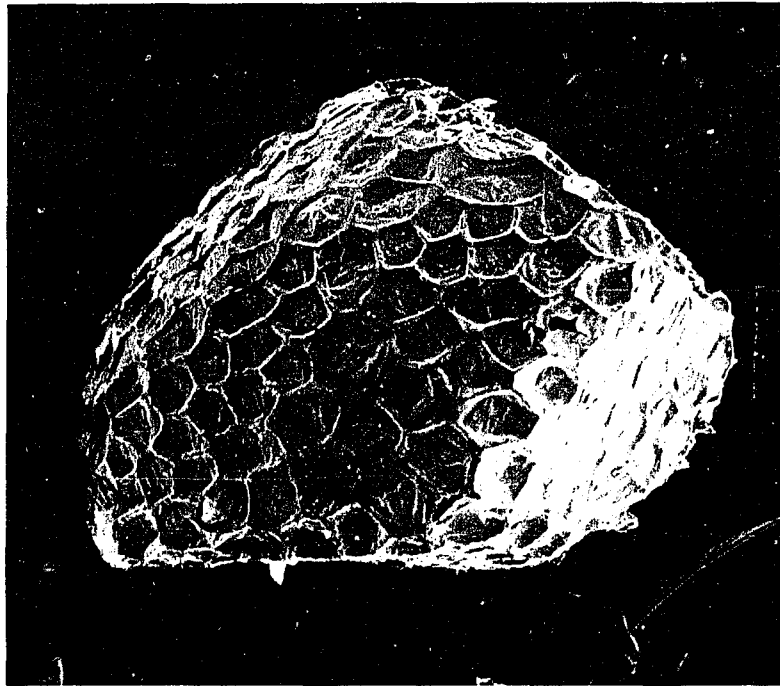


Fig. 7. Seed of Isertia longifolia, 100x.

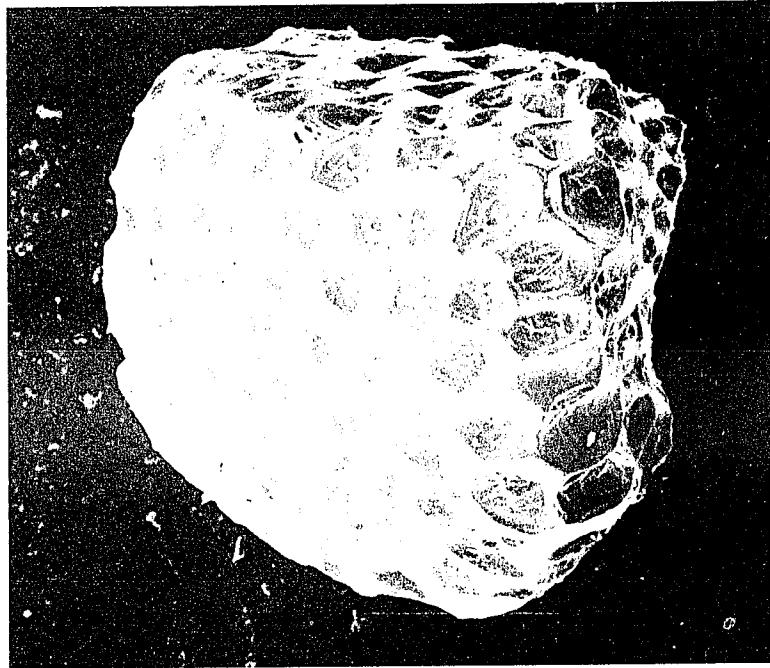


Fig. 8. Seed of Isertia haenkeana var. haenkeana, 100x.

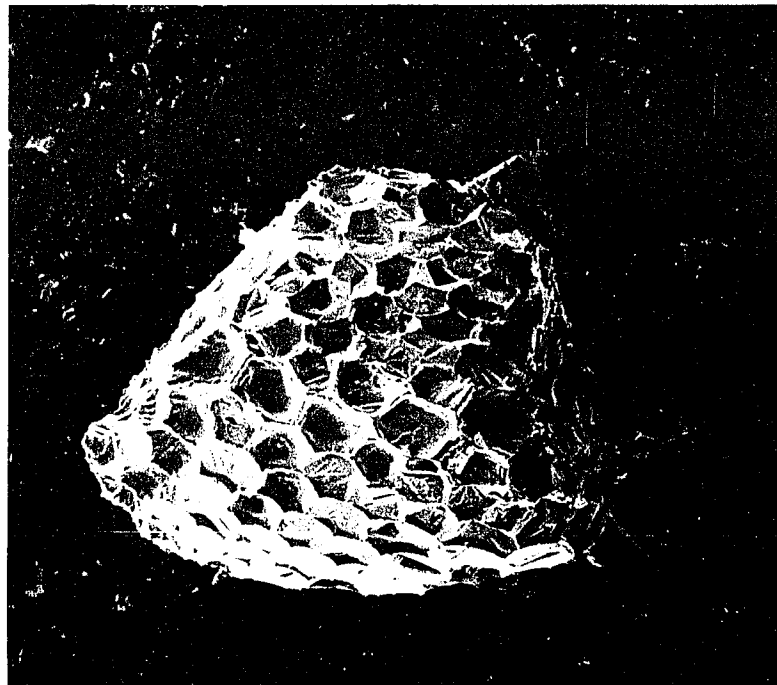


Fig. 9. Seed of Isertia haenkeana var. mirandensis, 100x.

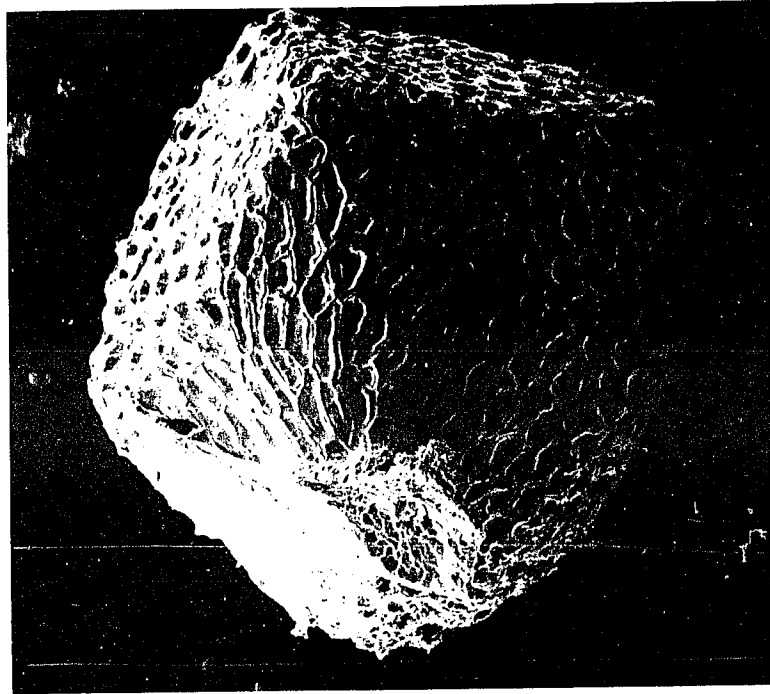


Fig. 10. Seed of Isertia parviflora, 100x.

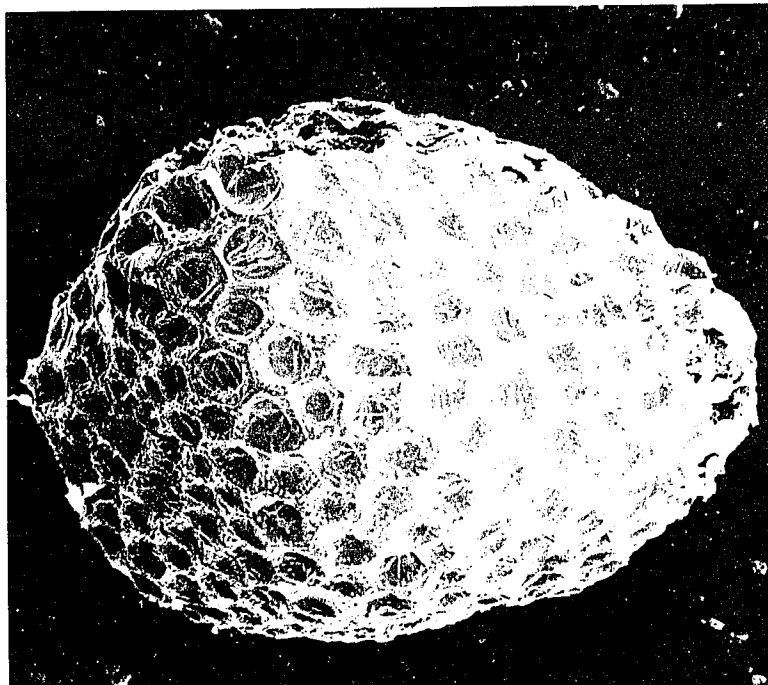


Fig. 11. Seed of Isertia rosea, 80x.

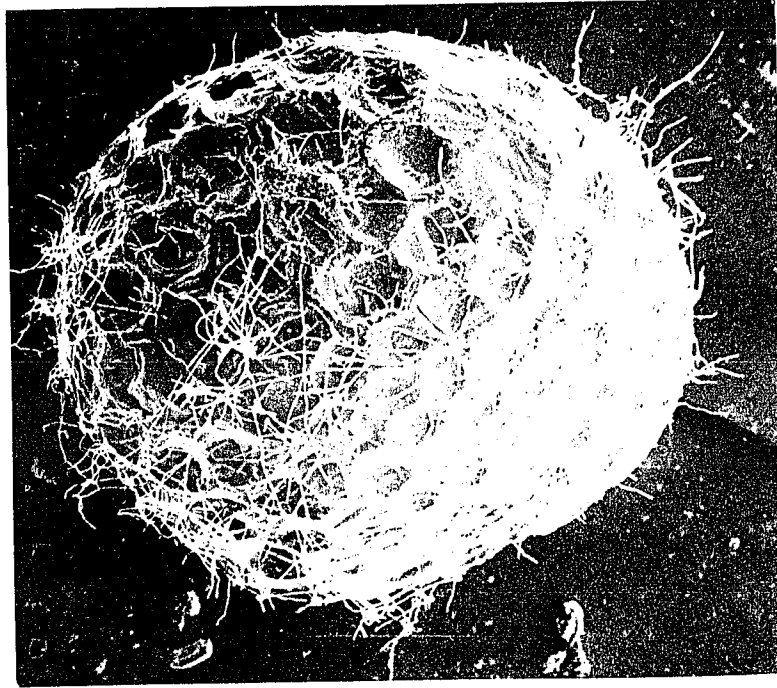


Fig. 12. Seed of Isertia hypoleuca, 100x.

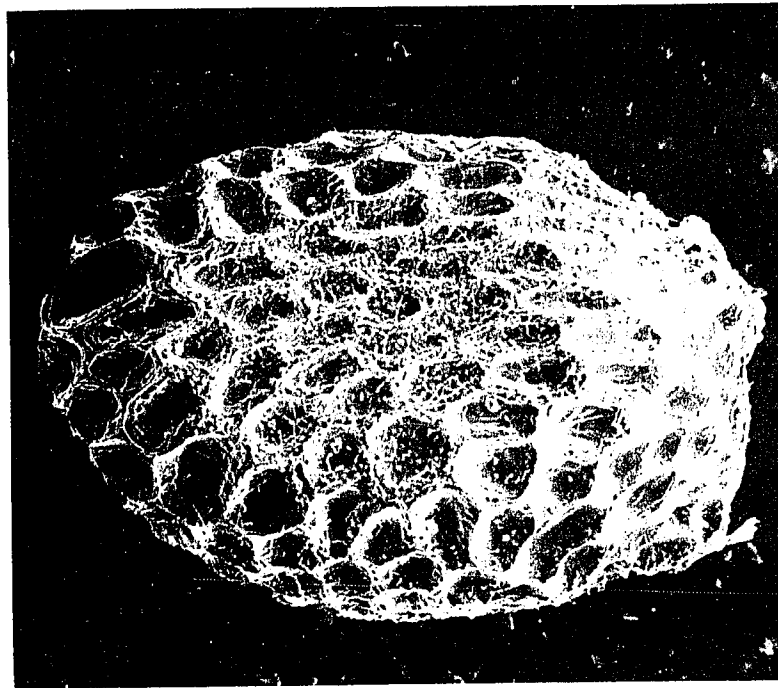


Fig. 13. Seed of Isertia coccinea, 80x.

size and in depth of the polygonal cells: Isertia reticulata (Fig. 4) being smaller and having deeper polygonal cells than I. verrucosa (Fig. 5) with its larger size and shallower polygonal cells.

The seeds of the taxa of I. sect. Isertia (Figs. 6-13) show less variation than those of the taxa in the other section. Of particular note is the small seed size of I. haenkeana var. mirandensis (Fig. 9), and the relatively thick-walled polygonal cells of I. parviflora (Fig. 10). The significance of seed shape is only apparent and is not in reality very important due to the infraspecific variation observed.

Pollen. Isertia pollen is tricolporate and angulaperturate. The grains are small to medium-sized (22-30 μ m in diameter) and the perine is more or less punctitegillate in appearance.

Pollen grains from 11 taxa of Isertia were examined by SEM; the specimens examined are listed in Table 2. Grains were mounted on stubs with double sticky tape and were then coated for two minutes with 60 percent gold and 40 percent palladium in a Technics sputtering coater. The samples were then viewed at 25 Kv in a JEOL JSM-U3 and photographed at 2800-3000x with Polaroid Type 55 positive/negative film.

Representative grains are shown in Figs. 14-24. The perine of all taxa examined is rather unspectacular in

Table 2. Voucher specimens examined in SEM study of Isertia pollen.*

<u>Taxon</u>	<u>Collector</u>	<u>Country</u>
<u>I. haenkeana</u>		
<u>var. haenkeana</u>	<u>Carleton 427</u>	Honduras
<u>I. scorpioides</u>	<u>Hammel 4505</u>	Panama
<u>I. coccinea</u>	<u>Irwin 48706</u>	Brazil
<u>I. hypoleuca</u>	<u>Pinkus 83</u>	Venezuela
<u>I. longifolia</u>	<u>Austin et al. 7204</u>	Brazil
<u>I. parviflora</u>	<u>Fleming 51</u>	Trinidad
<u>I. pittieri</u>	<u>Fosberg 21237</u>	Colombia
<u>I. reticulata</u>	<u>Williams 1480</u>	Bolivia
<u>I. rosea</u>	<u>Wurdack & Adderley</u>	
	<u>43013</u>	Venezuela
<u>I. spiciformis</u>	<u>Frões 11744</u>	Brazil
<u>I. verrucosa</u>	<u>Clark 6563</u>	Venezuela

* All specimens deposited at NY.

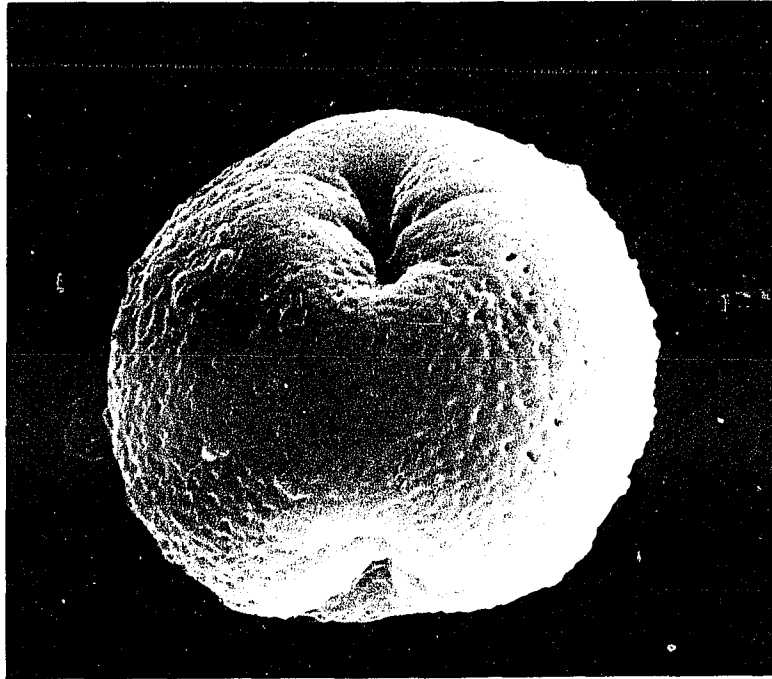


Fig. 14. Pollen grain of Isertia verrucosa, 3000x.

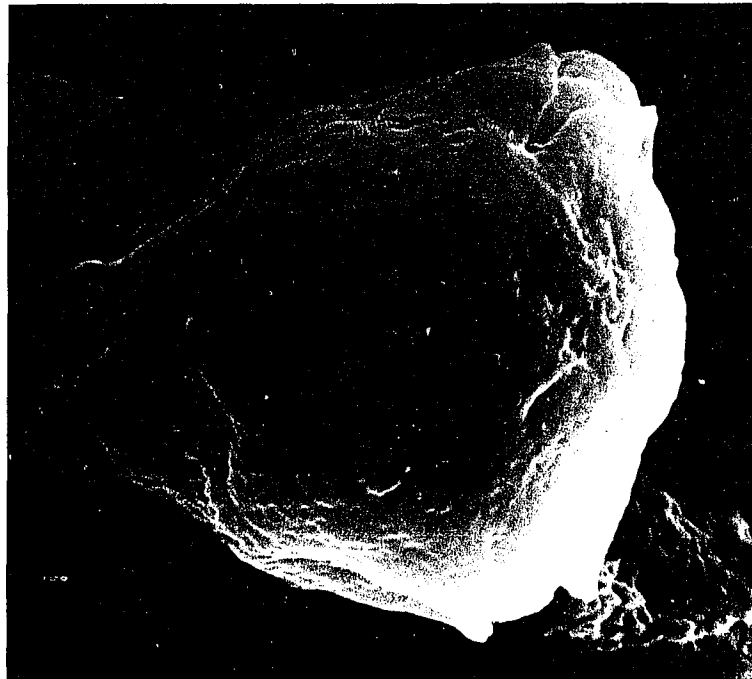


Fig. 15. Pollen grain of Isertia reticulata, 3000x.

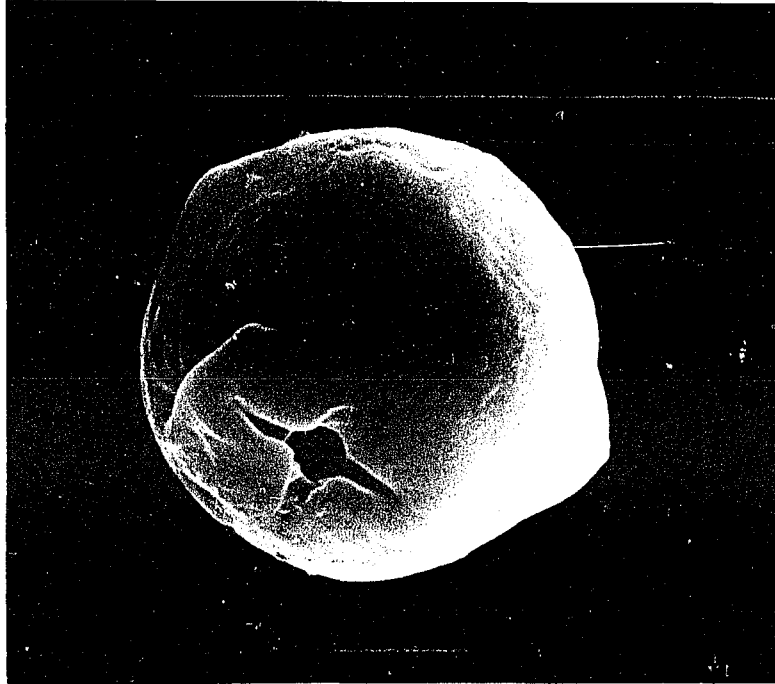


Fig. 16. Pollen grain of Isertia pittieri, 3000x.

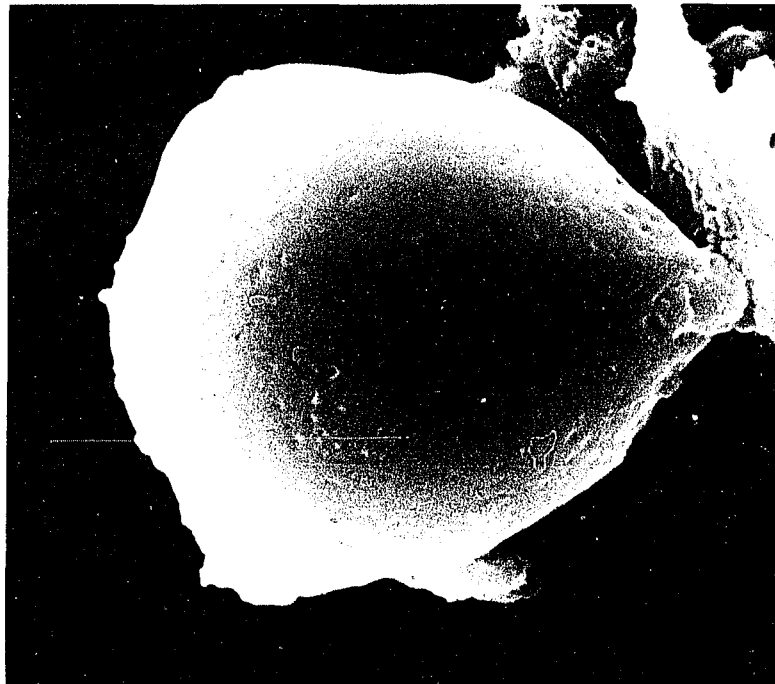


Fig. 17. Pollen grain of Isertia scorpioides, 3000x.

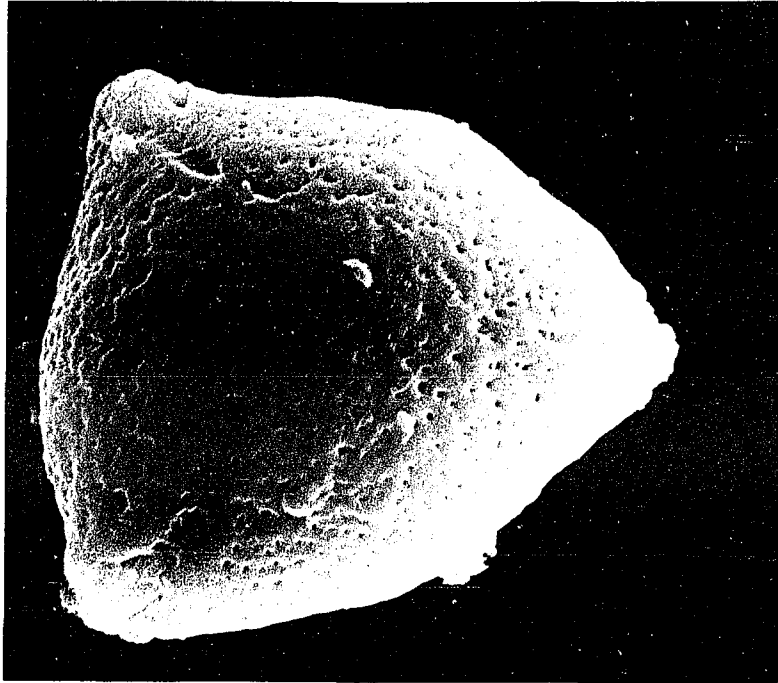


Fig. 18. Pollen grain of Isertia parviflora, 3000x.

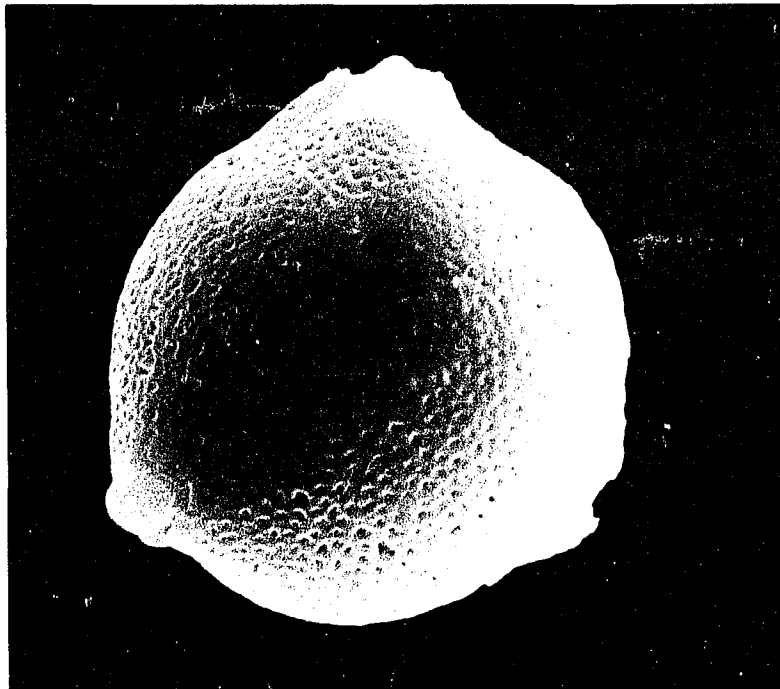


Fig. 19. Pollen grain of Isertia hypoleuca, 2800x.

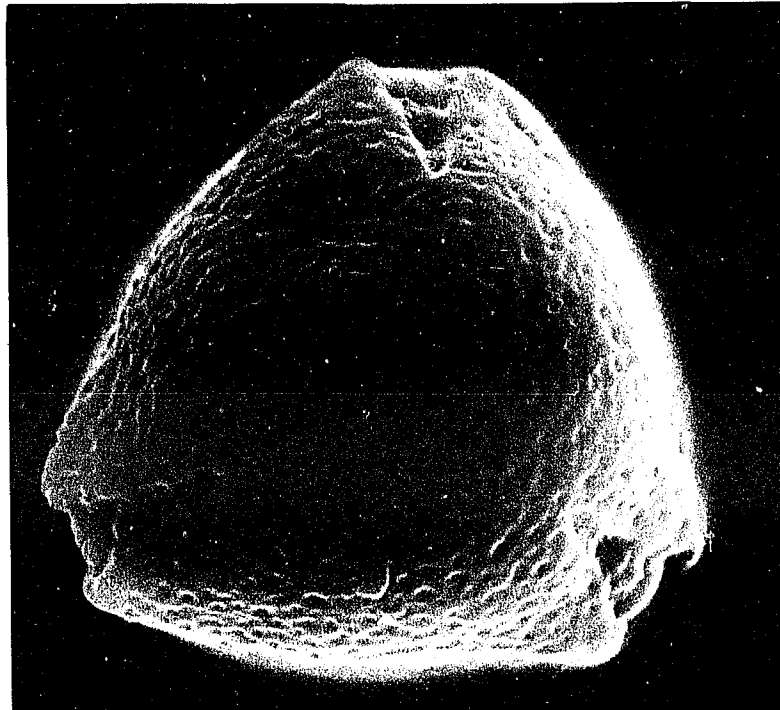


Fig. 20. Pollen grain of Isertia coccinea, 3000x.

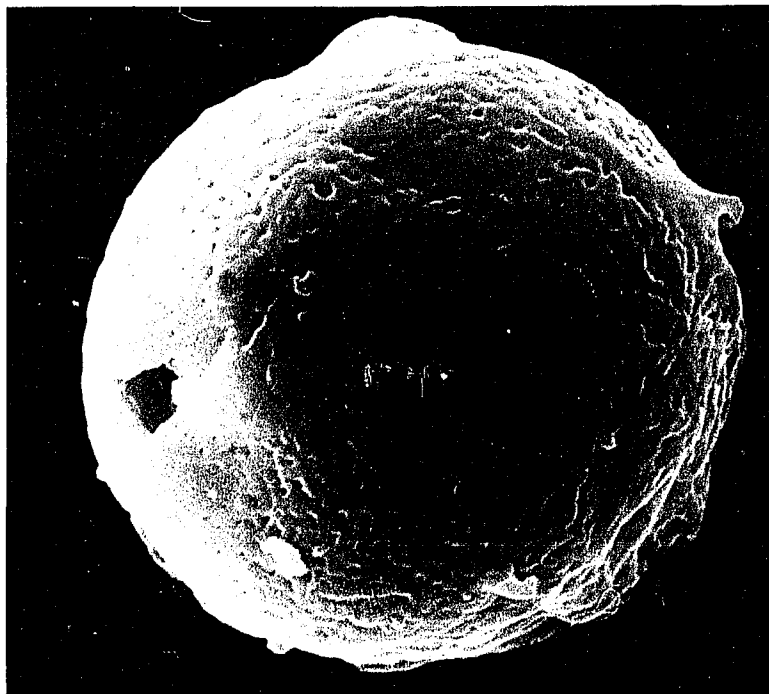


Fig. 21. Pollen grain of Isertia spiciformis, 3000x.

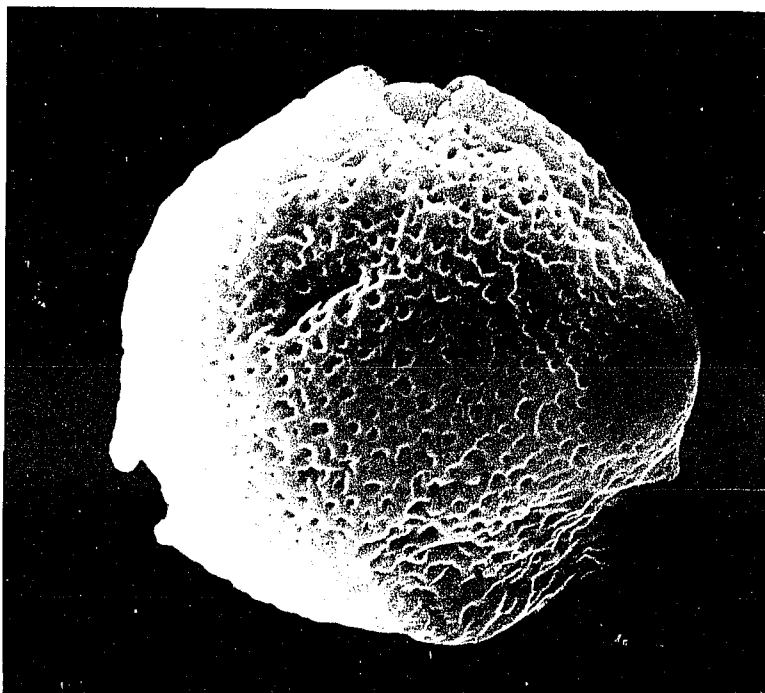


Fig. 22. Pollen grain of Isertia longifolia, 2800x.

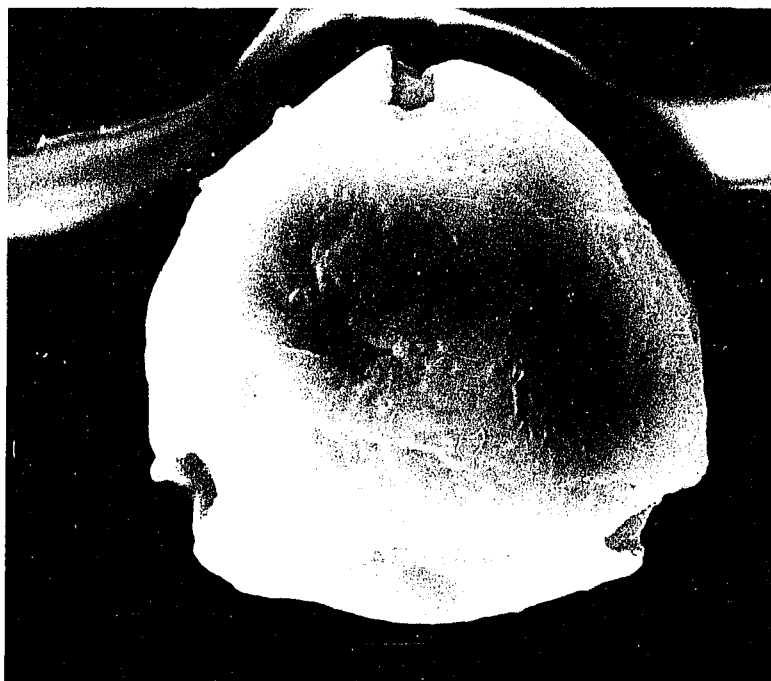


Fig. 23. Pollen grain of Isertia rosea, 2800x.

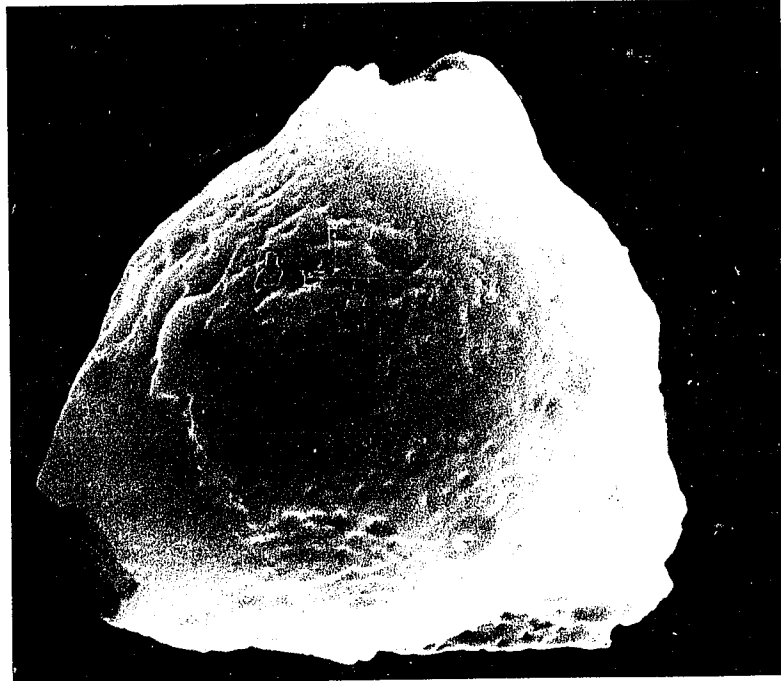


Fig. 24. Pollen grain of Isertia haenkeana var. haenkeana, 3000x.

terms of ornamentation. The only features of note are the small punctations. The degree of punctations, however, vary considerably within a species, and are consequently of no value in helping to distinguish between species.

The anomalous appearance of the only available pollen of I. verrucosa (Fig. 14) is possibly due to the collapse of apertures. On the other hand, the pollen of this species is salmon colored--a unique condition in a genus of otherwise yellow pollen. This correlates well with the other anomalies of this species--verrucations on the corolla tube, unusual inflorescence, and its isolated distribution in the upper Río Negro basin. More material of this species is needed to resolve the problem.

WOOD ANATOMY

Introduction. The wood of Isertia has been investigated anatomically by several workers. Kribs (1928) described the minute anatomy of I. hypoleuca. Later, Metcalf & Chalk (1950) reported that the vessels in Isertia wood are solitary and that the elements are 1 mm or more longer. The rays are usually 4 or more cells wide, and many rays have fewer than 4 marginal rows; the greater part of the ray is composed of procumbent cells.

The most comprehensive study of Isertia wood was undertaken by Koek-Noorman (1972). She made a broad survey of the tribes Gardenieae, Ixoreae, and Mussaendae (=Isertieae). The genera of Isertieae she studied which are relevant to this discussion are Gonzalagunia, Mussaenda, and Isertia. A consideration of Gonzalagunia and Mussaenda wood is important for out-group comparison in the cladistic analysis of Isertia to be presented in a later chapter.

Of Isertia, she studied wood from I. coccinea, I. hypoleuca, I. parviflora, I. longifolia, and I. hoehnei (= I. hypoleuca). She found the wood of these species to be rather similar. Most of the species showed vessels which are nearly exclusively solitary, fiber-tracheids, rays which are composed of a low, mostly biseriate central part consisting of procumbent cells and high uniseriate margins which are composed of upright cells,

and scanty diffuse strands of axial parenchyma which sometimes form short bands between two rays. Isertia hypoleuca has rays which show only rarely uniseriate margins, whereas the procumbent cells form a 2-4-seriate part which is sometimes more than 1 mm high.

Mussaenda sphaerocarpa, M. zenkeri, and M. sp. (U9258) had fiber tracheids and rather scanty diffuse and slightly reticulate axial parenchyma. More than 50 percent of the vessels were arranged in radial multiples, partly 4-7 cells long. Janssonius (1926) had recorded this arrangement for M. frondosa. Chang (1951) studied three species of Mussaenda (M. hirsuta, M. pubescens, M. villosa) and reported that the radial multiples or chains of vessels are usually formed by 2-5 large vessels, followed by 5 or more smaller ones in tail-like arrangement, the diameter varying from about 150 um to less than 50 um. He described 1- to 6-seriate rays composed mainly of square cells occasionally with sheathing upright cells, and occasionally with procumbent cells which are not much radially flattened.

In Gonzalagunia Koek-Noorman (1972) studied only one species, G. spicata. The wood anatomy deviated from the samples of Mussaenda and Isertia in the short 2- to 3-seriate parts of the rays, which are composed of square, upright cells. While Metcalf & Chalk (1950) observed septate fibers in Gonzalagunia, she did not observe this.

As in Mussaenda, more than 50 percent of the vessels of Gonzalagunia were shown to be arranged in radial multiples.

Materials and Methods. Wood blocks of fluid-preserved specimens collected by me and of air-dried specimens obtained from the U.S.D.A. Forest Products Laboratory (Table 3) were soaked in a glycerine/ethanol (95 percent) solution for about a week. Air-dried specimens were first boiled in an aerosol solution before placing in the glycerol. The beakers of soaking wood were placed on a slide warming tray set a low temperature to hasten the impregnation of the solution into the block. Transverse, tangential, and radial sections of 25-30 um thickness were then cut on a sliding microtome. The sections were stained in a 0.5 percent solution of hematoxylin and a 1 percent solution of safranin, as described by Radford et al. (1974). Wood macerations were made from selected specimens of eight species supplied by the U.S.D.A. Forest Products Laboratory. The technique of Schmid (1982), a modified method using Jeffrey's Solution (1:1 nitric acid and aqueous chromic acid), was followed.

Measurements of fiber-tracheid length, vessel element diameter and length and ray length were based on a count of 10 cells or cell groups in each sample. Measurements of vessel and ray abundance (number per sq. mm in transverse and tangential sections, respectively) were based on a count of 10 fields of view in each sample. The

Table 3. Voucher specimens for Isertia wood examined.*

Taxon	Voucher
<u>I. laevis</u>	SJRw 39751; MADw 38927
<u>I. pittieri</u>	SJRw 42696; Boom 1385
<u>I. verrucosa</u>	SJRw 41429
<u>I. rosea</u>	SJRw 41598; MADw 38928; MADw 35147; MADw 35146
<u>I. haenkeana</u>	SJRw 55115
<u>I. coccinea</u>	SJRw 50902; Boom & Mori 1868
<u>I. hypoleuca</u>	SJRw 35746
<u>I. parviflora</u>	SJRw 35491

* SJRw and MADw are abbreviations used by the U.S.D.A.
Forest Products Laboratory.

range and mean values were determined in each instance.

Results. Tables 4-6 summarize the results and Figs. 25-29 show transverse, tangential, and radial sections. The fiber-tracheids of Isertia have thick to very thick walls with small, slit-like pits 10-15 um long. They range in length (Table 4) from 1165-2688 um. For most of the species examined the fiber-tracheid lengths overlap, but it should be possible to distinguish I. laevis from I. hypoleuca on the basis of the lengths of fiber-tracheids.

The vessel elements (Table 5) show a greater variability than the fiber-tracheids. In transverse sections, the pores range in frequency from 4-120 per sq. mm. The three species examined of I. sect. Cassupa have a range of means of 34-58 (Figs. 25A, D and 26A). In I. sect. Isertia there appears to be two groups of species--I. rosea (Fig. 26D) and I. haenkeana (Fig. 27A) with a high density of pores averaging 88 and 75, respectively, and I. coccinea (Fig. 28A) and I. hypoleuca (Fig. 28D) with a low density of pores averaging 19 and 18, respectively. The remaining species, I. parviflora (Fig. 27D), has an intermediate density of about 52 pores per sq. mm. Regarding the length of vessel elements, the same situation exists as with fiber-tracheids. The ranges of lengths for nearly all species overlap, but it should be possible to distinguish between I. laevis and I. rosea on

Table 4. Results of a wood anatomical survey of eight species of Isertia: fiber-tracheids.*

Taxon	Length (um)	
	Range	Mean
<u>I. laevis</u>	1232-1680	1431
<u>I. pittieri</u>	1344-1747	1543
<u>I. verrucosa</u>	1546-2128	1900
<u>I. rosea</u>	1232-2688	1900
<u>I. haenkeana</u>	1232-1926	1662
<u>I. coccinea</u>	1456-2240	1716
<u>I. hypoleuca</u>	1613-2307	1794
<u>I. parviflora</u>	1165-2464	1718

* Based on counts of 10 cells for each sample.

Table 5. Results of wood anatomical survey of eight species of Isertia: vessel elements.*

Taxon	Frequency		Length, um		Diameter, um	
	Range	Mean	Range	Mean	Range	Mean
<u>I. laevis</u>	16-60	45	630-990	795	63-153	114
<u>I. pittieri</u>	32-100	58	810-1260	1063	63-153	123
<u>I. verrucosa</u>	8-60	34	945-1530	1215	63-108	89
<u>I. rosea</u>	48-120	88	1080-1440	1209	36-90	65
<u>I. haenkeana</u>	36-120	75	810-1620	1082	54-90	68
<u>I. coccinea</u>	8-36	19	891-1665	1132	81-135	107
<u>I. hypoleuca</u>	4-36	18	657-1350	1079	81-171	125
<u>I. parviflora</u>	32-80	52	729-1251	970	36-72	57

* Based on a count of 10 cells for each sample.

Frequency is no. pores/sq. mm in transverse section.

Table 6. Results of a wood anatomical survey of eight species of Isertia: rays.*

Taxon	Frequency		Length (cells)		Width (cells)
	Range	Mean	Range	Mean	
<u>I. laevis</u>	8-20	14	5-17	10	2-4
<u>I. pittieri</u>	8-24	14	5-10	7	2-3
<u>I. verrucosa</u>	8-24	16	6-19	12	3-4
<u>I. rosea</u>	4-24	13	5-12	7	2-3
<u>I. haenkeana</u>	8-16	13	4-13	7	2
<u>I. coccinea</u>	8-12	10	7-21	12	2-3
<u>I. hypoleuca</u>	4-24	13	6-27	16	3-4
<u>I. parviflora</u>	12-24	20	5-10	7	2-3

* Based on counts of 10 rays or 10 fields of view for each sample. Measurements made on bi- or multiseriate portions. Frequency is no. rays/sq. mm in tang. sect.

Fig. 25. Sections of wood of Isertia, 60x. A-C, I.
laevis: A. transverse, B. tangential, C. radial. D-F,
I. pittieri: D. transverse, E. tangential, F. radial.

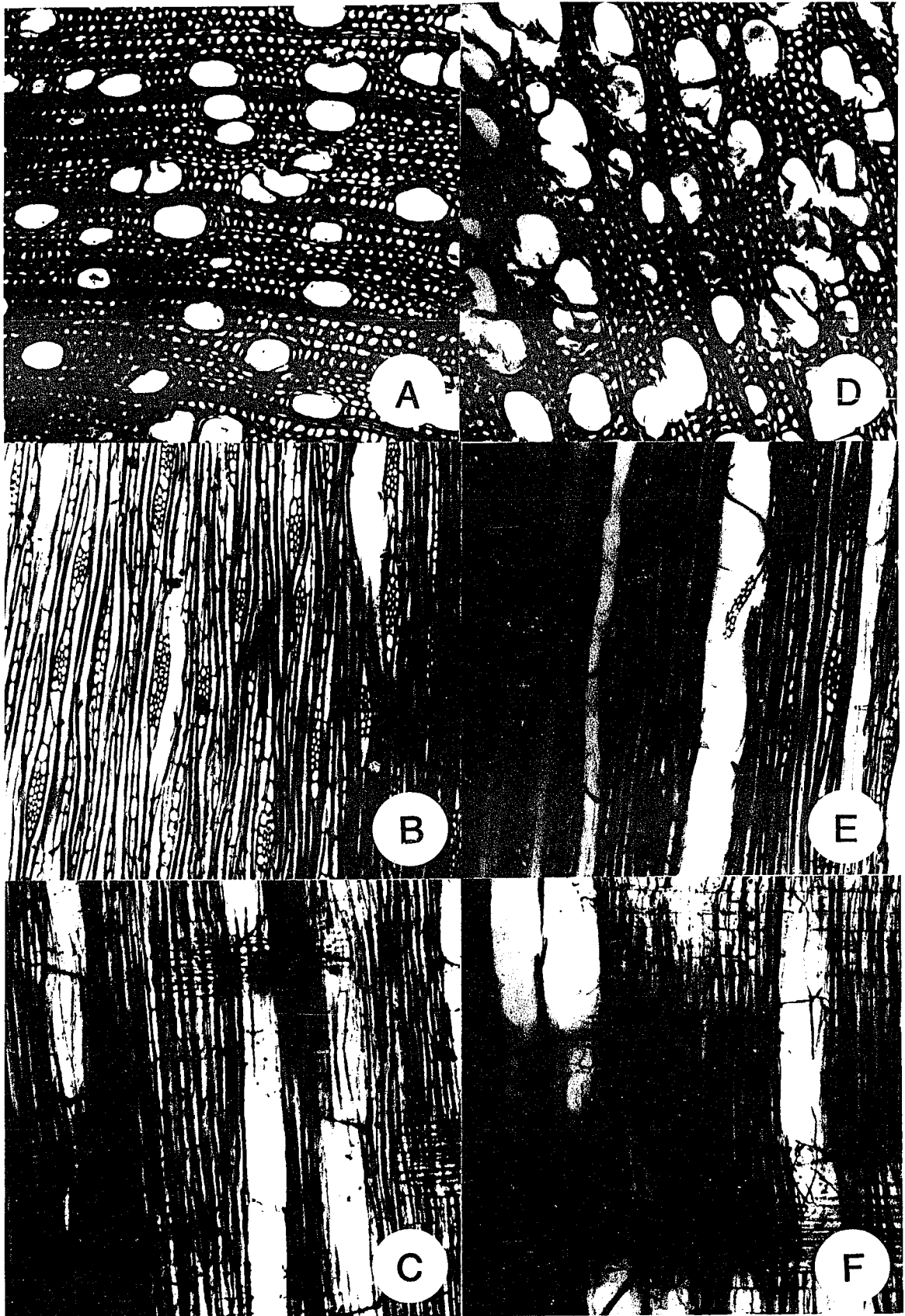


Fig. 26. Sections of wood of Isertia, 60x. A-C, I.
verrucosa: A. transverse, B. tangential, C. radial. D-F,
I. rosea: D. transverse, E. tangential, F. radial.

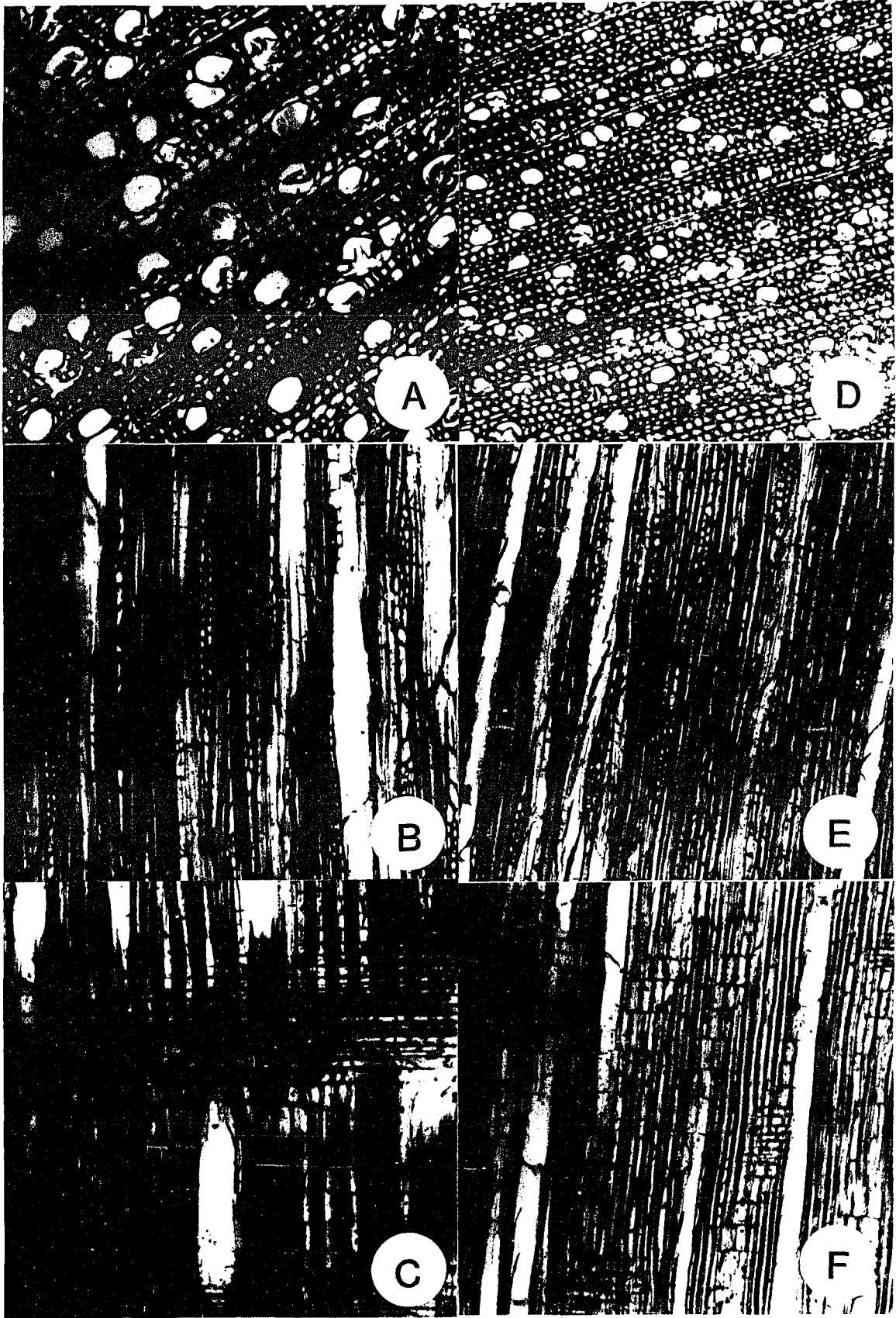


Fig. 27. Sections of wood of Isertia, 60x. A-C, I.
haenkeana var. haenkeana: A. transverse, B. tangential,
C. radial. D-F, I. parviflora: D. transverse, E.
tangential, F. radial.

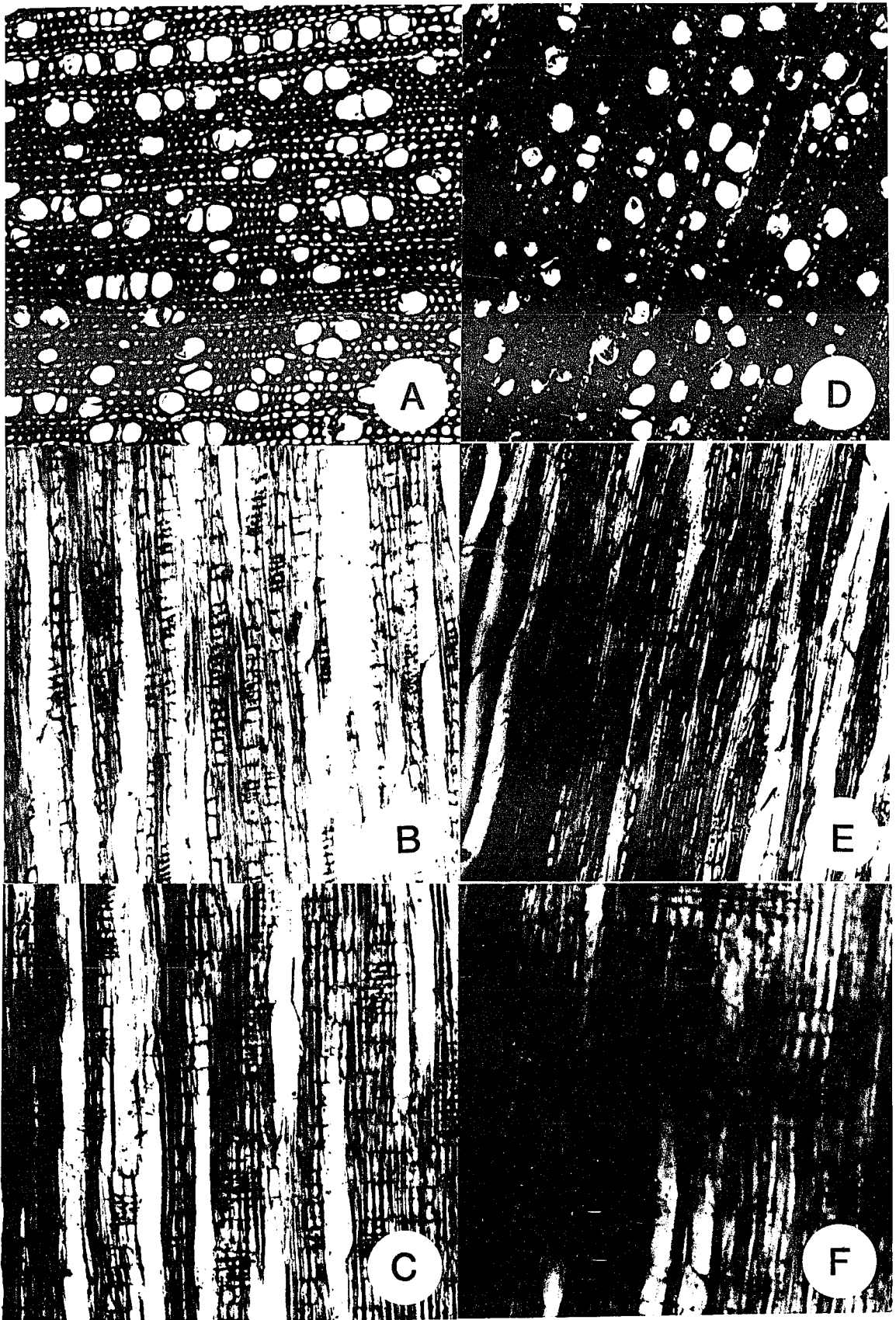


Fig. 28. Sections of wood of Isertia, 60x. A-C, I.
coccinea: A. transverse, B. \pm tangential, C. \pm radial.
D-F, I. hypoleuca: D. transverse, E. tangential, F. radial.

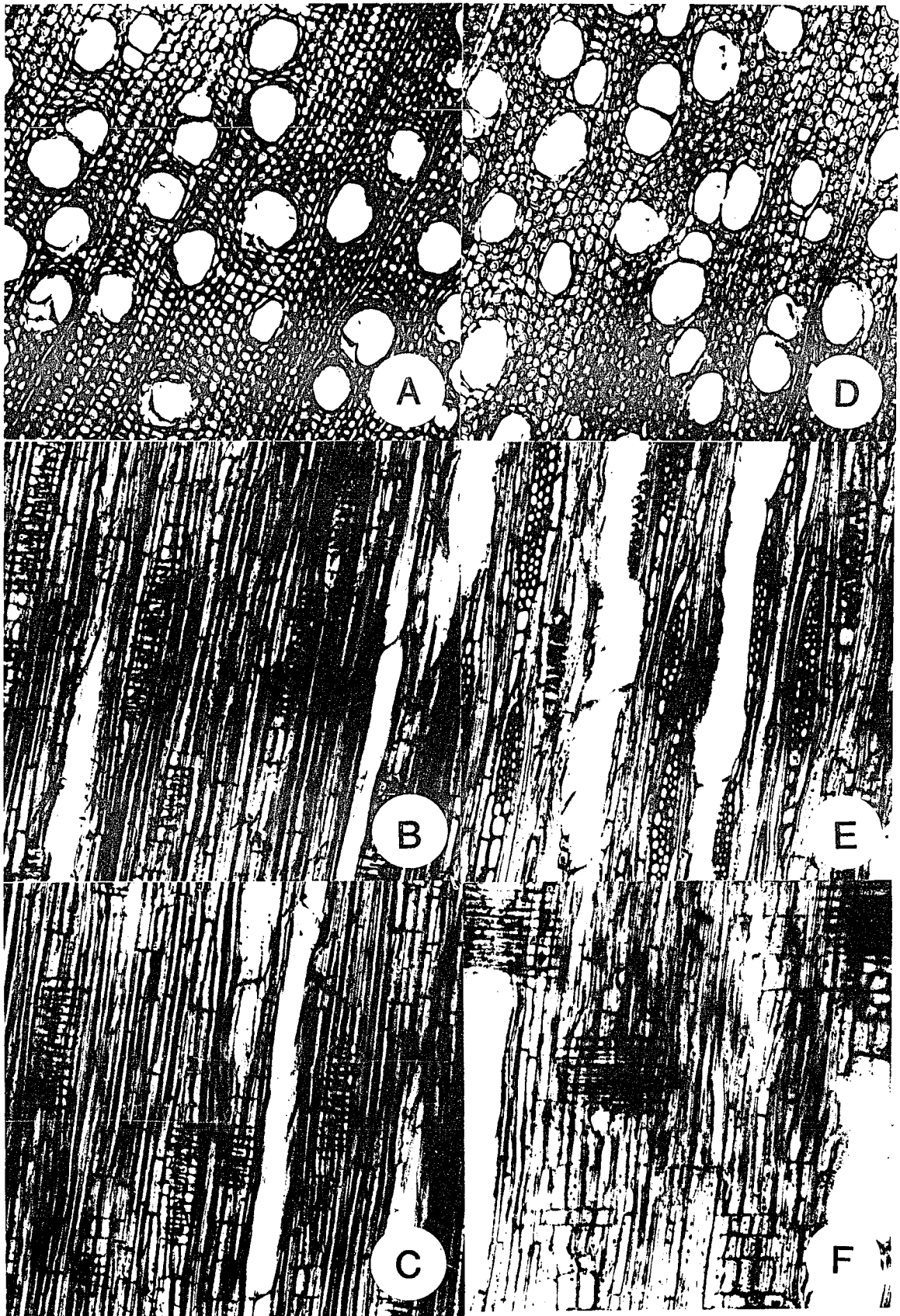
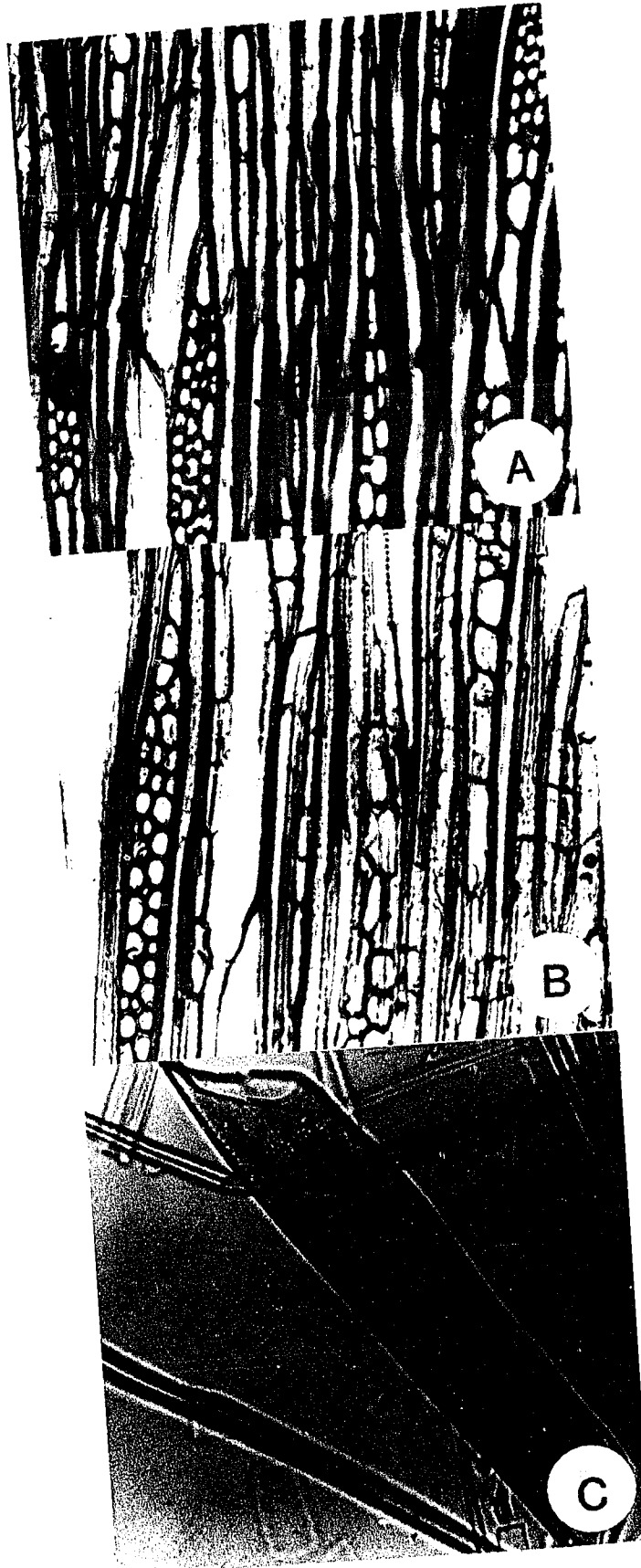


Fig. 29. Details of Isertia wood anatomy, 120x. A. I.
laevis, tangential section. B. I. rosea, tangential
section. C. I. rosea, vessel element, fiber-tracheids,
and ray cells.



the basis of vessel element length. A much simpler method to distinguish some of these woods is to examine the transverse sections and to note the vessel element diameter. Strikingly different mean diameters are indicated for the species examined (Table 5). The vessels are generally solitary, but occasional pore multiples (I. laevis) and pore chains (I. haenkeana) occur. The elements are angular or circular in transverse section and the walls are thin. The oblique end walls are composed of simple perforation plates. The pitting is alternate (Fig. 29C).

Data for rays are presented in Table 6. The rays are heterocellular. The frequency of rays does not appear to vary so much among species; the notable exception being the difference between I. coccinea and I. parviflora. As shown by the tangential sections in Figs. 25-28, the dimensions of the rays are often distinctive for a particular species. The rays are 2-4 seriate in width at the center and taper to uniseriate wings at each end (which often unite to an adjacent ray). The bi-seriate or multiseriate portions vary in length from 4-27 cells. The observable trend seems to be a reduction in ray width and length as taxa become more specialized.

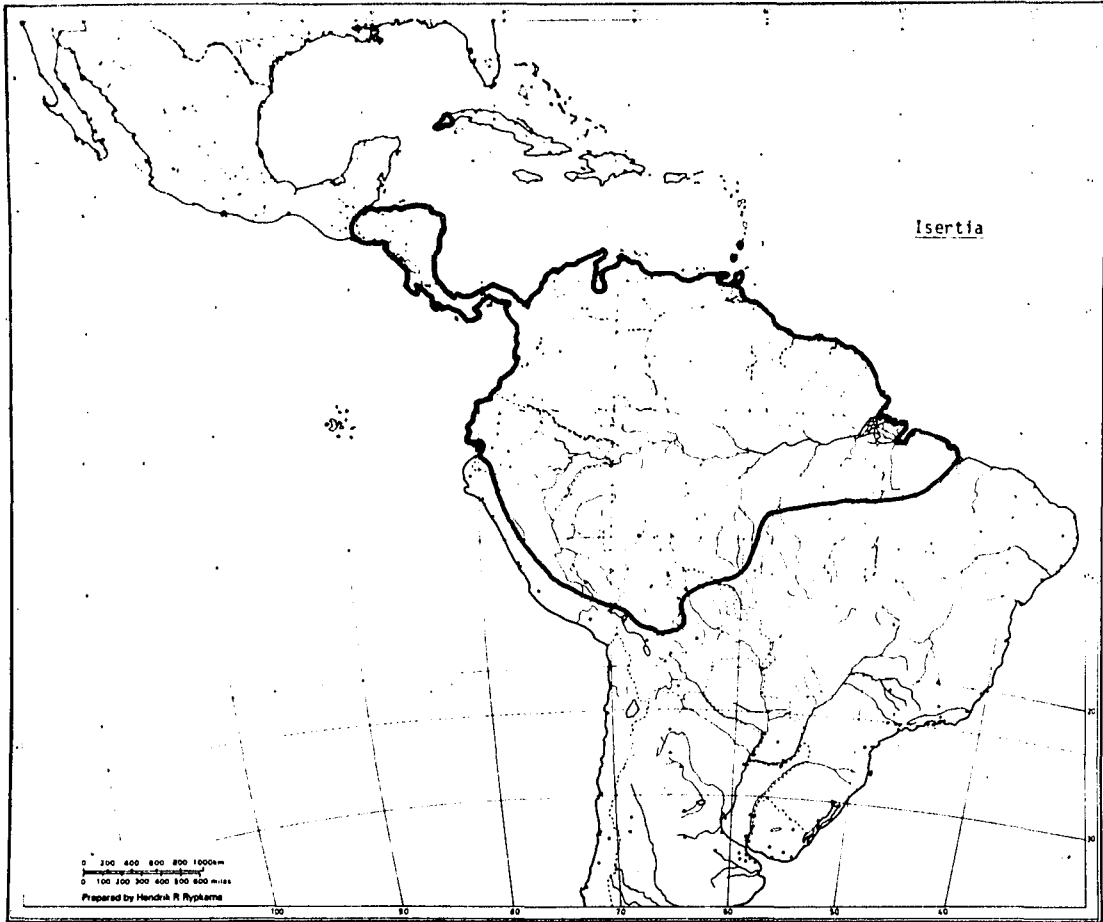
In conclusion, data from wood anatomy suggest that Isertia sect. Cassupa is ancestral to I. sect. Isertia. The primitive condition of the wood must have included

large diameter vessel elements (> 100 um) and long, multiseriate rays. Such conditions are characteristic for I. laevis and I. pittieri. Within I. sect. Isertia, I. coccinea and I. hypoleuca have primitive-state wood; the more advanced taxa (e.g., I. rosea and I. longifolia) have 2- or at most 3-seriate rays which are relatively short in length (5-12 cells). This conclusion is strengthened by the other advanced character-states shared by these taxa (e.g., pyrene fruits and intrape-tiolar stipules).

DISTRIBUTION AND ECOLOGY

Isertia is distributed throughout Central America and northern South America, occurring naturally in the Caribbean only in extreme western Cuba and Guadeloupe (Map 1). Isertia sect. Cassupa has a principally Andean distribution (Map 2), while I. sect. Isertia is principally Amazonian and Guayanan in distribution (Map 3). Species of both sections, however, are sympatric in northern Colombia and Central America as far north as Costa Rica. It may be stated as a generalization about the ecology of the Isertia that the genus is characteristic of secondary or successional forest. Certainly this is true of the several species I have seen in the field, and it can be confirmed for the remainder of the genus on the basis of herbarium specimen label data.

The distributions of the six species of Isertia sect. Cassupa are shown in Map 4. Isertia krausei is known only from the type collection from the valley of the Río Mishiollo in the central Peruvian Andes at an elevation of 1700 m. Isertia reticulata, only slightly better known, is restricted to similar elevations in the Bolivian Andes. In sharp contrast to these two species, I. verrucosa is a lowland species restricted to the upper Río Negro in Venezuela and adjacent Brazil at elevations of 120-140 m. Isertia pittieri is restricted



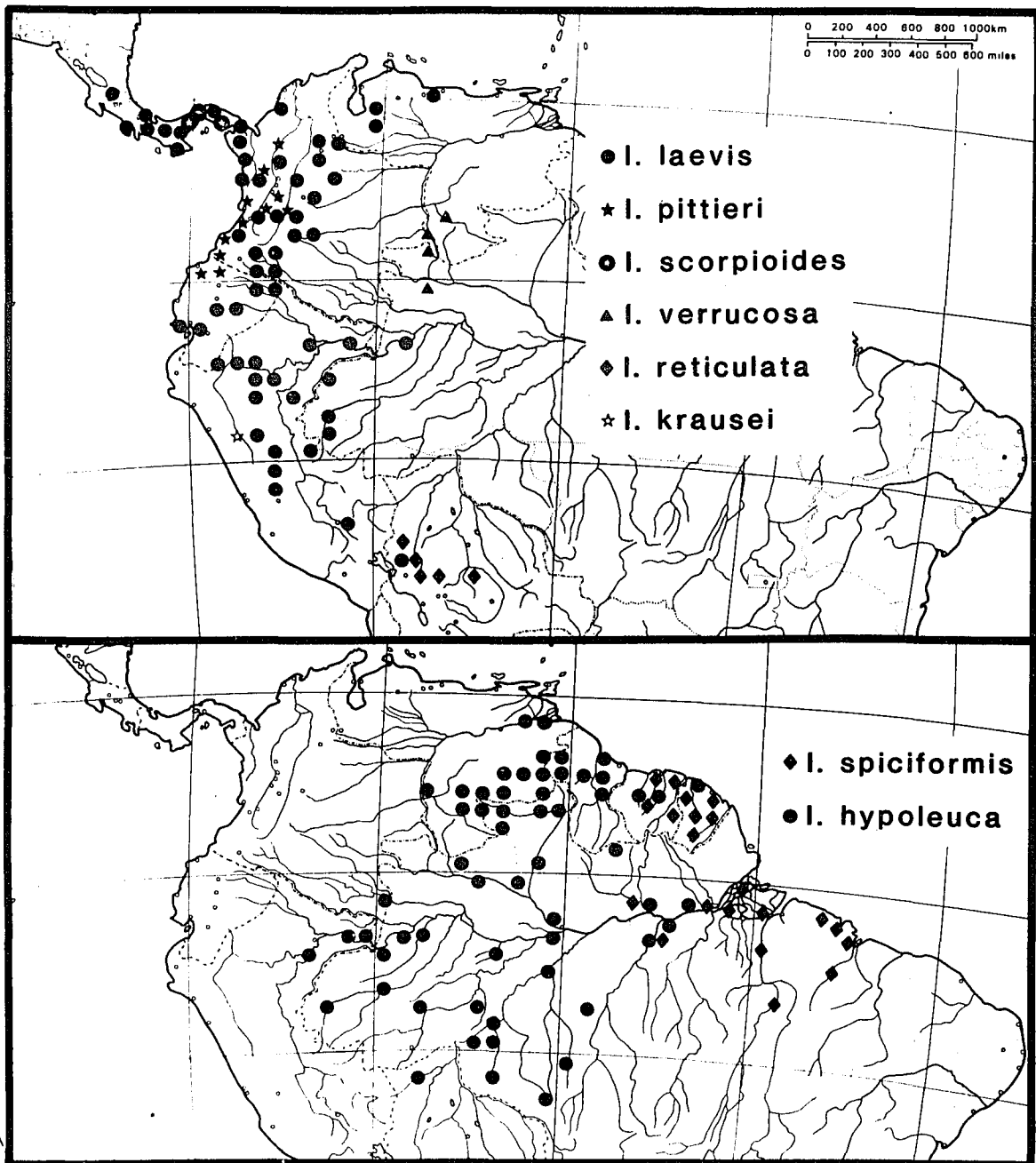
Map 1. Distribution of Isertia.



Map 2. Distribution of Isertia sect. Cassupa.



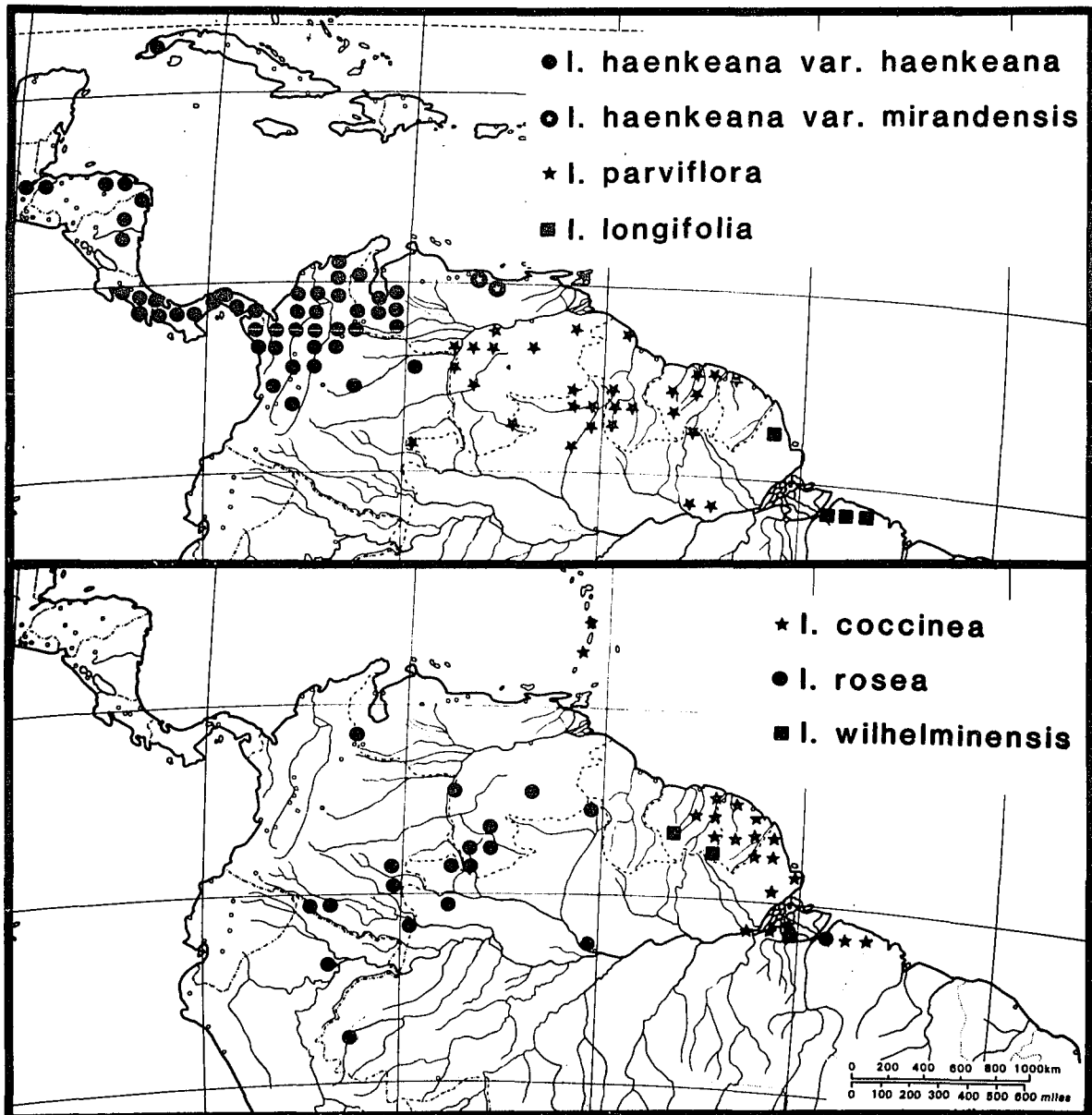
Map 3. Distribution of Isertia sect. Isertia.



Maps 4-5. Map 4. Distribution of *Isertia laevis*, *I. pittieri*, *I. scorpioides*, *I. verrucosa*, *I. reticulata*, and *I. krausei*. Map 5. Distribution of *I. spiciformis* and *I. hypoleuca*.

to the Pacific slope of Ecuador and Colombia; within this area, however, is occurs from mangrove swamps along the Pacific up to 1500 m in the Cordillera Occidental. I have observed this species as being one of the most common trees in northern Esmeraldas Province, Ecuador, along the Ibarra-San Lorenzo railroad. A new species being described herein, I. scorpioides, is restricted to the lowland moist, secondary forest of the provinces of Colón and Darién in Panama. The only species of I. sect. Cassupa with a wide distribution is I. laevis which occurs from Costa Rica south to Bolivia, mostly in the Andes but with significant lowland extensions to the west in moist coastal forests and to the east into upper Amazonia. I have observed I. laevis as a very common tree in roadside, secondary forest in the Province Napo, Ecuador, south of Baeza along the highway to Tena.

The distributions of the eight species of Isertia sect. Isertia are depicted in Maps 5-7. The most common and widespread species of the section, I. hypoleuca, is distributed in terra firme rainforest throughout the Guianas, Venezuela, and the Amazonian regions of Brazil, Colombia, Peru, and Bolivia at elevations of 100-1800 m. The closely related I. coccinea has a distribution in terra firme rainforest of French Guiana, Surinam, and Brazil around the mouth of the Amazon River at elevations of 20-200 m. The occurrences of I. coccinea in the



Maps 6-7. Map 6. Distribution of *Isertia haenkeana* var. *haenkeana*, *I. haenkeana* var. *mirandensis*, *I. parviflora*, and *I. longifolia*. Map 7. Distribution of *I. coccinea*, *I. rosea*, and *I. wilhelminensis*.

Caribbean on St. Vincent and Martinique are probable escapes from cultivation (R. Howard, pers. comm.); although this species tends to occur in secondary or otherwise disturbed forest, it is quite ornamental with its conspicuous panicles of reddish-orange flowers. I have observed I. coccinea in Saül, French Guiana, where it is common in disturbed forest along the road to the airstrip.

Isertia haenkeana has a unique distribution in the section because it is extra-Amazonian/Guayanian. The species is widespread in northern Colombia and throughout Central America as far north as Guatemala. Two disjunctions occur in this species--Caribbean (Pinar del Río, Cuba, and Guadeloupe) and the Cordillera de la Costa, Venezuela. While the Caribbean populations are not in any way distinct from those of the typical variety, the Cordillera de la Costa populations are sufficiently differentiated from the typical variety to be recognized as a separate variety, I. haenkeana var. mirandensis. I. haenkeana var. haenkeana occurs in secondary forests and pastures from sea level to 600 m, while I. haenkeana var. mirandensis occurs in coastal rainforest at 400-1000 m.

Isertia parviflora has a basically Guayanian distribution with scattered occurrences in savanna or white sand habitats of northern Amazonia, frequently in disturbed,

flooded, or riverside locations. Isertia wilhelminensis is restricted to the eastern Guayanan region, being known only from several collections; this species occurs in mossy, probably undisturbed forest at ca 1000 m. I. spiciformis is distributed in two disjunct areas: one area includes Surinam and French Guiana, while the other is to the south in the lower Amazon valley, extending east into Maranhão as far as moist forest occurs. The drier savanna vegetation in Amapá prevents the distribution of I. spiciformis from being continuous. Where I have observed I. spiciformis in Saül, French Guiana, it occurs on rainforest ridgetops at ca 400 m elevation; there, it appears to be a gap species. The species also occurs in disturbed forest vegetation as is the case of at least one collection from Maranhão, Brazil (D. Daly, pers. comm.). Isertia longifolia is restricted to around the mouth of the Amazon River in either várzea or terra firme forest. Although there is a collection of I. longifolia from Rio de Janeiro (Glaziou 9902), this is probably a collection Glaziou pirated from someone else (Wurdack, 1970); Isertia is not known to occur in the Brazilian Atlantic coastal forest. The remaining species, I. rosea, is a plant primarily of the upper Amazon and Orinoco basins, but with scattered occurrences eastward to around the mouth of the Amazon at elevations of 25-300 m. Isertia rosea is primarily a plant of white

sands or savannas, either in terra firme or várzea. It seems to be the ecological equivalent of I. parviflora, distributed to the north in Guayana.

PHYLOGENY

Introduction. The tribe Isertieae (sensu M. Kirkbride, 1979) is comprised of the following genera in the neotropics: Mussaenda L., Isertia Schreb., Gonzalagunia Ruiz & Pav., Raritebe Wernh., Amphidasya Standl., and Sabicea Aubl. Of these, Mussaenda is only cultivated in the New World; it is native to the paleotropics. Sabicea occurs naturally in the neotropics as well as the African tropics, including Madagascar. The remaining genera are restricted to the neotropics.

An important consideration in postulating a phylogeny for Isertia is recognizing the closest relatives of the genus. This is so because of the necessity for using out-group comparison as the basis for polarizing characters. Eldredge & Cracraft (1980) and Watrous & Wheeler (1981) have shown that the application of the time-honored premise of "common = primitive" will always lead to erroneous results when several taxa in a lineage are grouped by advanced characters. Without question, the closest relatives of Isertia are Mussaenda and Gonzalagunia. These three taxa are grouped within the tribe Isertieae in having terminal inflorescences, and large, oval pits in the seed coat walls.

Evidence from wood anatomy supports the close affinity of these genera. Koek-Noorman (1972) found that Isertia

and Mussaenda differ in the percentage of vessels which are arranged in radial multiples (most species of Isertia have vessels that are nearly exclusively solitary, whereas in the species of Mussaenda more than 50 percent of the vessels are arranged in radial multiples). In the other wood characteristics they agree rather well, and she found no reason to doubt the rather close affinity of these genera. She likewise found no reason to dispute the affinity of Gonzalagunia and the other genera.

Kirkbride's (1979) SEM study of seed coats in the Isertieae shows Isertia, Mussaenda, and Gonzalagunia to be most closely related. My own work on fruit morphology suggests that Isertia sect. Cassupa is most closely related to Mussaenda with berry fruits, whereas I. sect. Isertia is closest to Gonzalagunia with pyrenate fruits. So, because it has not been possible to specify either Mussaenda or Gonzalagunia as the sister group, both genera have been used for out-group comparison in the cladistic analysis of Isertia.

Methods. Cladistics may be defined as the concepts and methods for determining branching patterns of evolutionary history. Two major classes of cladistic methods are available: character compatibility analysis and parsimony analysis. Character compatibility analysis, explained in greater detail by Meacham (1980), examines patterns of agreement between characters, and looks for that set of

characters which supports a common evolutionary estimate of relatedness among the organisms under study. The method is not concerned with the final form of the tree, or how long the segments are, or how many steps it takes to get there, but rather the patterns of agreement between the characters. In the other method, parsimony analysis, one assumes the shortest and most feasible pathway for evolving characters. The shape of the final tree and the number of steps it takes to evolve the organisms is important. An example of this method is Wagner's Groundplan-divergence method of cladistics (Wagner, 1980). I have decided to use parsimony analysis because there appears to be more general agreement as to its utility in cladistics than compatibility analysis. Furthermore, and more importantly, I find the visual impact of a tree produced by parsimony methods to be more intellectually satisfying and informative than the type of tree produced by compatibility analysis. Of the parsimony methods available, I have chosen Wagner's Groundplan-divergence method for my Isertia cladistic analysis because the method has stood the test of time in numerous botanical studies, and it is straightforward, and easily explained and comprehended. The major alternative manual parsimony method currently in vogue is the Hennigian methodology. Wiley (1981) has concluded that the Hennig and Wagner methods produce essentially the same results when

appropriate out-group comparisons are used in polarizing character states. I regard the Groundplan-divergence method as the superior of the two in terms of repeatability, straightforwardness, and comprehensibility. While Wagner admits that his method makes no claims for either complete parsimony or complete compatibility, I regard this as a strength of the method (i.e., admitting the limitations). The Hennig adherents are not always so modest in their claims. My decision to do a manual cladistic analysis rather than using a computer program is based on the same reasoning used by Wagner (1980). Manual methods are less expensive, take less time to perform, and are readily understood by any systematist regardless of his mathematical background. More importantly, manual and computer methods usually give the same results.

An outline of the Groundplan-divergence method (Wagner, 1980) is presented in Table 7. Step 1 is the revision of the group under consideration. This is important because "a cladogram is no better than the quality of the taxonomy upon which it is based" (Wagner, 1980). The cladogram produced in this chapter is based on the systematic treatment of the 14 species of Isertia presented in the following chapter. Step 2, the detection and removal of hybrids, is essential if the cladogram is to be correct; confusing hybrid taxa with divergent taxa will cause serious errors. In the case of Isertia, there is one

Table 7. Outline of the Groundplan-divergence method
(Wagner, 1980).

- a. Systematic analysis, based on taxonomy.
 - Step 1. Phenetic classification.
 - Step 2. Detection and removal of hybrid taxa.
 - b. Determination of the common ancestor.
 - Step 3. Analysis of individual character trends.
 - Step 4. Combination of groundplan character states.
 - c. Phylogenetic synthesis based upon divergences.
 - Step 5. Calculation of divergence levels.
 - Step 6. Grouping by shared divergences.
 - Step 7. Insertion of hybrid connections.
-

species of suspected hybrid origin, I. scorpioides. This species is discussed more fully in the next chapter, but for now it is sufficient to say that while it is clearly referable to I. sect. Cassupa due to its 2-3-locular berry fruits, it is intermediate in many respects to I. laevis and I. haenkeana, two sympatric species belonging to different sections of the genus. This is quite interesting for two reasons. First, it occurs in one of the only areas (Panama) where members of both sections are sympatric. And, second, this intersectional hybrid is the best possible evidence for demonstrating the monophyly of the genus. Thus, it supports the recognition of Cassupa as a section of Isertia rather than as a separate genus; interspecific hybrids are known in the Rubiaceae, but I know of no instance of intergeneric hybrids in the family.

Step 3 involves an evaluation of the individual character trends. Because it is obvious that there are two major lines of evolution in the genus, corresponding to the two sections, each trend has been evaluated separately. This is the practice recommended in those cases when there is a very early major divergence of clades. Towards this end, two tables of characters and character states were prepared; Table 8 evaluates ten characters used in constructing the I. sect. Cassupa branches, while Table 9 shows the thirteen characters used in the

Table 8. Characters and character states used in
Isertia sect. Cassupa.

Character	States	
	Plesiomorphic (0)	Apomorphic (1)
A. Leaf tertiary veins	planar	impressed
B. Flowers/infl. 2 \varnothing rachis	7-8	3-5
C. Flower color	red, pink, yellow	white
D. Corolla tube length, mm	<40	>40
E. Infl. rachis vestiture	pubescent	glabrescent
F. Corolla tube surface	smooth	verrucose
G. Corolla tube vestiture	pubescent	glabrescent
H. Leaf lower surface	white canescent	glabrescent
I. Wood pores	radial multiples or clusters	solitary
J. Stigma lobes	2	3-4

Table 9. Characters and character states used in
Isertia sect. Isertia.

Character	States	
	Plesiomorphic (0)	Apomorphic (1)
K. Wood pores	radial multiples or clusters	solitary
L. Fruit type	berry	pyrene
M. Leaf lower side	not floccose	floccose
N. Fruit diam., mm	8-11	4-7
O. Leaf texture	smooth	rugose
P. Corolla tube		
length, mm	>20	<20
Q. Stipules	interpetiolar	intrapetiolar
R. Leaf vein		
vestiture	pubescent	glabrous
S. Infl. type	paniculate- thrysoid	racemose- thrysoid
T. Corolla texture	not fleshy	fleshy
U. Fls./infl. 2♀		
rachis	<20	>20
V. Fls./ultimate		
scorpioid cyme	2-4	4-9
W. Leaf base	cuneately narrowed	obtuse or cordate

I. sect. Isertia line. The characters were polarized by out-group comparison, using Mussaenda, Gonzalagunia, or the entire tribe Isertiaeae. Then the character state manifested by each species was scored in Tables 10 and 11 for either plesiomorphic (0) or apomorphic (1). The nature of each species is denoted by "DV" for divergent species or "HY" for hybrid species; the only hybrid is I. scorpioides. The divergence formula for each species is then listed; this formula is simply made up of those letter designations for characters which show the apomorphic conditions (e.g., I. krausei is apomorphic for three characters, impressed tertiary leaf veins (A), glabrescent inflorescence rachises (E), and wood with solitary pores (I), thus giving the formula of AEI). The divergence level for each species is then calculated; this is simply the count of characters which show the apomorphic condition. Character G, corolla tube vestiture, was found to be of no value in the analysis and was consequently not scored for any of the species.

Once the information in Tables 10 and 11 has been completed, taxa are plotted by divergence level. The dots are connected in such a way as to group taxa with shared apomorphies. The solid dots represent actual taxa; the empty dots represent hypothetical taxa. The apomorphies represented at each point on the diagram are indicated by letters corresponding to the characters

Table 10. Character states, taxon types, divergence formulae and divergence levels for Isertia sect. Cassupa.

Taxon	Character States										Taxon Type	Divergence Formula	Divergence Level
	A	B	C	D	E	F	G	H	I	J			
1. <u>I. krausei</u>	1	0	0	0	1	0	-	0	1	0	DV	AEI	3
2. <u>I. reticulata</u>	1	0	0	0	0	0	-	0	1	1	DV	AIJ	3
3. <u>I. verrucosa</u>	0	1	0	1	1	1	-	0	1	0	DV	BDEFI	5
4. <u>I. laevis</u>	0	1	1	1	0	0	-	0	1	0	DV	BCDI	4
5. <u>I. scorpioides</u>	0	0	0	0	0	0	-	1	1	0	HY	HI	2
6. <u>I. pittieri</u>	0	1	1	1	0	0	-	1	1	0	DV	BCDHI	5

Table 11. Character states, taxon types, divergence formulae, and divergence levels for Isertia sect. Isertia.

Taxon	Character States													Taxon Type	Diverg. Formula	Diverg. Level
	K	L	M	N	O	P	Q	R	S	T	U	V	W			
7. <u>I. hypoleuca</u>	1	1	0	0	0	0	0	0	0	0	1	0	0	DV	KLT	3
8. <u>I. coccinea</u>	1	1	1	0	0	0	0	0	0	0	1	0	0	DV	KLMT	4
9. <u>I. haenkeana</u>	1	1	0	1	0	0	0	0	0	0	0	1	0	DV	KLNV	4
10. <u>I. parviflora</u>	1	1	0	1	0	1	0	0	0	0	1	0	1	DV	KLNPW	6
11. <u>I. wilhelminen.</u>	1	1	0	1	1	0	0	0	0	0	0	0	1	DV	KLNOW	5
12. <u>I. longifolia</u>	1	1	0	1	0	1	1	1	1	0	0	0	0	DV	KLNPQRS	7
13. <u>I. spiciformis</u>	1	1	0	1	0	0	1	0	1	0	0	0	0	DV	KLNQS	5
14. <u>I. rosea</u>	1	1	0	1	0	0	1	1	0	0	0	0	0	DV	KLNQR	5

listed in Tables 8 and 9. The final step is to place the hybrid taxa on the diagram at the appropriate divergence level and to connect them with dashed lines to the putative parents.

Discussion. The cladogram presented in Fig. 30 conforms quite well with my ideas on the phylogeny of the group which I developed in the course of completing the taxonomic revision. From the hypothetical common ancestor two major lines are shown to diverge. To the left branches the clade representing Isertia sect. Cassupa, species 1-6. To the right branches the clade representing Isertia sect. Isertia, species 7-14. The putative hybrid origin of I. scorpioides, species 5, is depicted by dashed lines connecting it to the parent species, I. haenkeana, species 9, and I. laevis, species 4. Each species will now be discussed individually, incorporating geographical distributional data. References to forest refuges refer to those of Prance (1982).

Isertia sect. Cassupa diverges from the common ancestor to divergence level 1 with the acquisition of solitary vessels in the wood. From this hypothetical taxon two lines diverge, one manifesting impressed tertiary leaf veins and the other marked by a reduction in the number of flowers/secondary inflorescence rachis and the increase in corolla tube length. The first of these two

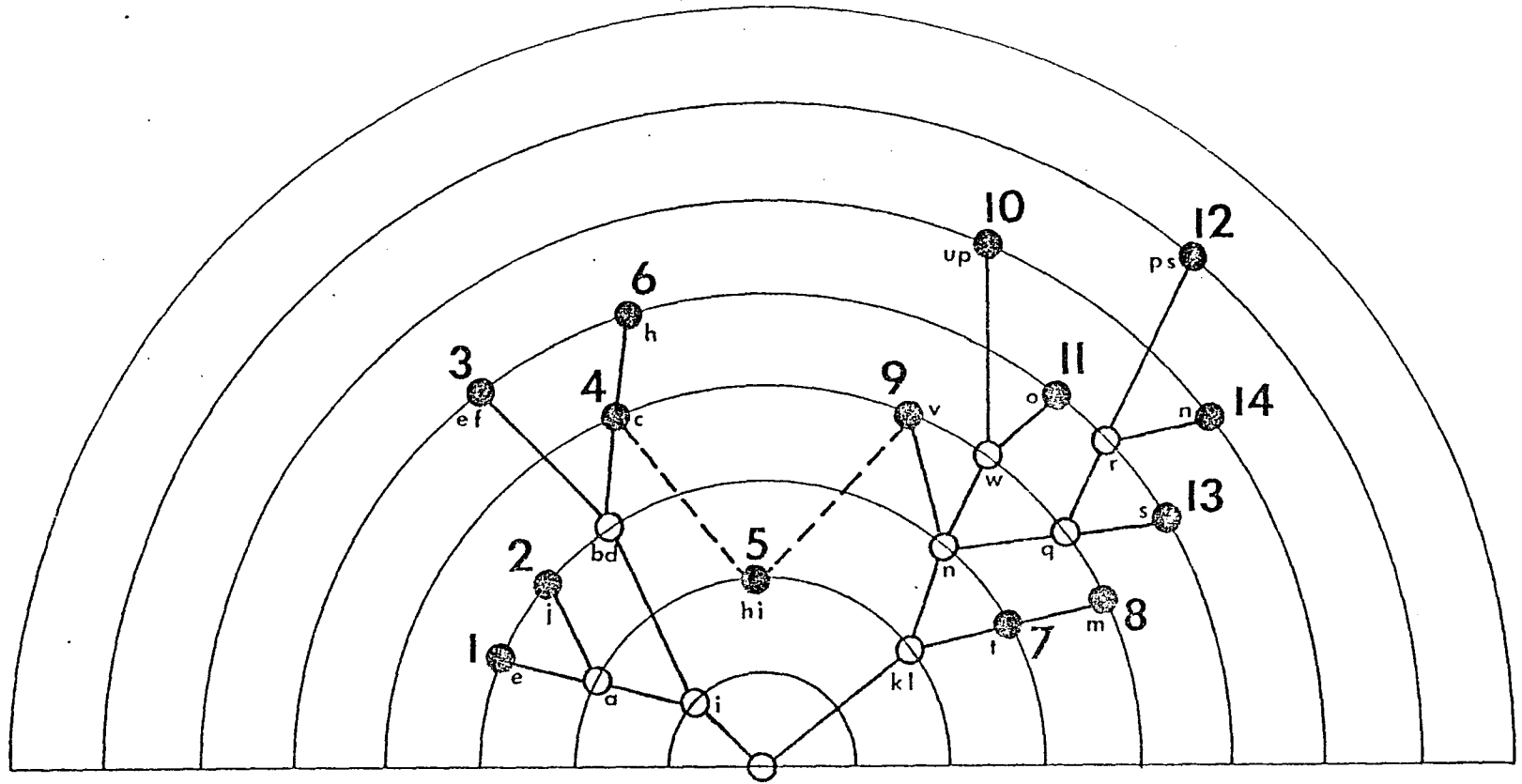


Fig. 30. Groundplan-divergence cladogram for Isertia. 1. I. krausei; 2. I. reticulata; 3. I. verrucosa; 4. I. laevis; 5. I. scorpioides; 6. I. pittieri; 7. I. hypoleuca; 8. I. coccinea; 9. I. haenkeana; 10. I. parviflora; 11. I. wilhelminensis; 12. I. longifolia; 13. I. spiciformis; 14. I. rosea. Letter designations correspond to characters listed in Tables 8 and 9.

lines terminates at divergence level 3 in species 1, I. krausei, characterized by its glabrescent inflorescence rachises, and species 2, I. reticulata, characterized by a style with 3-4 stigmatic lobes. Each of these species is endemic to different regions of the Andes, I. krausei in Peru and I. reticulata in Bolivia. Isertia krausei is known from one collection made just to the west of the the East Peru-Acre refuge. Isertia reticulata has a distribution more or less coincident with the Beni refuge.

The second of these two lines in I. sect. Cassupa terminates in three taxa. Species 3, I. verrucosa, at divergence level 5, is characterized by a verrucose corolla tube and glabrescent inflorescence rachises (a parallel character, developed also in I. krausei discussed above). Isertia verrucosa is restricted to the Imerí refuge. The second branch leads to two taxa with the shared apomorphy of white flowers, I. laevis, species 4, at divergence level 4, and I. pittieri, species 6, at divergence level 5. Isertia pittieri appears quite clearly to have been derived from I. laevis and is specialized in the loss of white canescent vestiture from the leaf undersurfaces. Isertia laevis is widespread throughout the Andes and up into Central America to Costa Rica. Isertia pittieri is essentially restricted to the Chocó refuge. The species of hybrid origin, I. scorpioides, species 5, is restricted to Panama and was

discussed previously.

The more diverse and advanced Isertia sect. Isertia diverges to the right in Fig. 30 from the common ancestor in having pyrenate fruits and wood with solitary vessels. From this hypothetical ancestor two lines diverge. The first line terminates in two taxa characterized by fleshy corollas, I. hypoleuca, species 7, at level 3, and I. coccinea, species 8, at level 4. Isertia coccinea is quite clearly derived from I. hypoleuca, but it is just as clearly distinct from it in its unique floccose vestiture on the leaf blade undersurfaces. While I. hypoleuca is widespread throughout Amazonia and the Guianas, I. coccinea is allopatrically distributed to it and is restricted to Surinam, French Guiana, and in Brazil around the mouth of the Amazon River, occurring essentially in the East Guiana and Belém refuges.

The second major line in I. sect. Isertia trifurcates at divergence level 3. All the taxa in this line are specialized in their reduced fruit diameter (except I. rosea which is specialized in its larger fruit size; the character reverses). The cladogram is not fully resolved at this point due to the lack of data points; the result is a trichotomy. One branch terminates at level 4 in I. haenkeana, species 9, which is specialized in its extensively branched scorpioid cymes as the ultimate branches in the secondary rachises of the inflorescence.

Isertia haenkeana is distributed in northern Colombia, Venezuela, Central America and the Caribbean, and, as mentioned above, it is postulated that it is involved in the formation of the hybrid I. scorpioides. A second branch of this line, specialized in having an obtuse or cordate leaf base, terminates in two species, I. parviflora, species 10, at level 6, and I. wilhelminensis, species 11, at level 5. Isertia parviflora is characterized by the automorphies of corolla tube length reduction and increase in the number of flowers/secondary inflorescence rachis; it is distributed widely through the Guyanas, Venezuela, and northern Brazil. Isertia wilhelminensis is specialized by its rugose leaf blade surface; it is endemic to the Guayana Highlands in Surinam, French Guiana, and Brazil.

The most advanced line in the genus is characterized by intrapetiolar stipules. From the hypothetical ancestor at level 4, two lines diverge. One line terminates at level 5 with I. spiciformis, species 13. Isertia spiciformis, characterized by a lax, racemose-thyrsoid inflorescence, is distributed in French Guiana, Surinam, and the lower Amazon River region of Brazil. The other line goes to a hypothetical taxon at level 5 which is characterized by glabrous leaf veins. From this point two taxa diverge, one at level 6, I. rosea, species 14, and the other at level 7, I. longifolia, species 12.

The automorphy of I. rosea is a reversal of the trend for fruit diameter reduction; I. rosea is widely distributed in the upper Amazon River basin. The two automorphies of I. longifolia are reduction in corolla tube length (parallel with such a reduction in I. parviflora) and the racemose-thyrsoid inflorescence (parallel with this inflorescence type in I. spiciformis). Isertia longifolia is restricted to around the mouth of the Amazon River, mostly in the Belém refuge. It is the most advanced species in the genus.

It may be observed that the distributions of several species are more or less coincident with forest refuges proposed by Prance (1982). It seems reasonable to postulate that diversification at the species level in Isertia took place as a result of climatic fluctuations during the Pleistocene as predicted by the Refuge Theory (Haffer, 1982). It may also be observed that the major uplift of the Andes during the Pliocene was probably responsible for diversification of Isertia at the sectional level, creating the present situation in South America with I. sect. Cassupa primarily of the Andes and I. sect. Isertia primarily of Amazonia and the Guianas. Distributions of both sections into Central America or the West Indies appear to be of a secondary nature and to have taken place subsequent to an origin and diversification in northern South America.

SYSTEMATIC TREATMENT

ISERTIA Schreber

Isertia Schreber, Gen. Pl. 1: 234. 1789. TYPE: Isertia coccinea (Aubl.) J. F. Gmelin, non Vahl, 1798, based on Guettarda coccinea Aubl.

Cassupa Humb. & Bonpl., Pl. Aequin. 1: 43, pl. 12. 1806. TYPE: Cassupa verrucosa Humb. & Bonpl.

Phosanthus Raf., Ann. Gén. Sci. Phys. 6: 82. 1820. TYPE: Phosanthus coccinea (Aubl.) Raf., based on Guettarda coccinea Aubl. [= Isertia coccinea (Aubl.) J. F. Gmelin].

Brignolia DC., Prodr. 4: 444. 1830. TYPE: Brignolia acuminata DC. [= I. parviflora Vahl].

Bruinsmania Miq., Linnaea 17: 72. 1843. TYPE: Bruinsmania isertioides Miq. [= Isertia parviflora Vahl].

Creatantha Standley, Publ. Field Columbian Mus., Bot. Ser. 8(5): 344. 1931. TYPE: Creatantha peruviana Standley [= Isertia laevis (Triana) B. M. Boom].

Shrubs or trees, glabrous or pubescent, with slender subrotund or thick quadrangular branchlets; leaves opposite, petiolate, membranaceous or coriaceous; stipules 4 and interpetiolar or 2 and intrapetiolar. Inflorescence terminal, thyrsiform-paniculate or thyrsiform-racemose with secondary rachises terminating in dichasia or scorpioid cymes of sessile or pedicellate flowers. Flowers:

calyx 4-6-lobate, the lobes small, often indistinct, equal or unequal, persistent; corolla tube cylindrical, short or elongate, the throat villous inside, the lobes 5-6 (7), short and spreading, valvate or imbricate in bud; stamens 4-7, inserted in corolla tube near mouth, the anthers dorsifixed, loculate, included or slightly exserted; ovary 2-6 (7)-celled, the style linear, the stigma with 2-6 (7) narrowly oblong lobes, included or slightly exserted, ovules numerous; ovarian disc prominent and padlike. Fruit a berry or pyrene, globose, 2-6 (7)-celled, many seeded; seeds minute, brownish, angular, the testa deeply foveolate.

Key to the sections and species of Isertia

- 1 Fruit a berry, endocarp fleshy; ovary with 2-3 (4) locules, stigma 2-3 (4)-lobed (sect. Cassupa).
- 2 Lower surface of leaf blade with white canescent vestiture.
- 3 Upper surface of leaf blade with impressed tertiary venation.
- 4 Inflorescence glabrous; leaf blade oblanceolate; Peruvian Andes 1. I. krausei
- 4 Inflorescence pubescent; leaf blade elliptic to obovate; Bolivian Andes 2. I. reticulata
- 3 Upper surface of leaf blade with planar tertiary venation.

- 5 Leaf blade coriaceous; corolla tube red and yellow, with tubercles just below lobes; restricted to upper Río Negro drainage in Venezuela and Brazil 3. I. verrucosa
- 5 Leaf blade membranaceous to subcoriaceous; corolla tube white, without tubercles below lobes; widespread in the Andes, extending north to Costa Rica and east to western Amazonia 4. I. laevis
- 2 Lower surface of leaf blade glabrescent or pubescent, but never with white canescent vestiture.
- 6 Corolla pink or red, tube 35-40 mm long, lobes 13-14 mm long; inflorescence secondary rachises of a simple 9-flowered dichasium, the ultimate branched of which having 4-flowered scorpioid cymes; fruit ca 5 mm diam.; Panama 5. I. scorpioides
- 6 Corolla white, tube 60-70 mm long, lobes 11-20 mm long; inflorescence secondary rachises of a simple 5-flowered dichasium, the ultimate branches of which having 2-flowered scorpioid cymes; fruit ca 10 mm diam.; Pacific slope of Colombia and Ecuador 6. I. pittieri
- 1 Fruit a pyrene, endocarp bony; ovary with (4) 5-6 (7) locules, stigma 4-6-lobed (sect. Isertia).
- 7 Stipules 4 per node, interpetiolar.

- 8 Corolla tube 50-70 mm long; fruit ca 10 cm diam.
- 9 Lower surface of leaf blade with white-
 canescent vestiture; inflorescence
 secondary rachises of a simple 7-flowered
 dichasium, the ultimate branches having
 3-flowered scorpioid cymes; widespread in
 Amazonia and Guayana 7. I. hypoleuca
- 9 Lower surface of leaf blade with floccose
 vestiture; inflorescence secondary rachises
 of a simple 3-flowered dichasium or a
 compound 7-flowered dichasium, the
 ultimate branches having 2-flowered
 scorpioid cymes; restricted to Surinam,
 French Guiana, and around the mouth of the
 Amazon River 8. I. coccinea
- 8 Corolla tube 5-30 mm long; fruit 4-8 mm diam.
- 10 Corolla tube 5-13 mm long, pink; inflores-
 cence secondary rachises of a compound
 dichasium of ca 31 flowers
 10. I. parviflora
- 10 Corolla tube 24-30 mm long, red, orange, or
 yellow; inflorescence secondary rachises
 of a simple or compound dichasium of ca
 8-18 flowers.

11 Leaf blades neither rugose nor with prominent tertiary venation; leaf blade base decurrent on petiole; inflorescence secondary rachies of a simple 8-18-flowered dichasium, the ultimate branches having scorpioid cymes of 4-9 flowers; widespread in Central America, northern Colombia, Cuba, coastal Venezuela

..... 9. I. haenkeana

11 Leaf blade rugose with prominent tertiary venation on upper and lower surfaces; leaf blade base obtuse to rounded, not decurrent on petiole; inflorescence secondary rachises of a compound 11-flowered dichasium, the ultimate branches of which having 2-flowered scorpioid cymes; restricted to sandstone table mountains in Surinam and adjacent Brazil. 11. I. wilhelminensis

7 Stipules 2 per node, intrapetiolar.

12 Leaf veins and blade pubescent to papillose-glandular beneath; stipules 8-9 mm long; inflorescence secondary rachises of a single flower or of a simple 3-flowered dichasium or of a simple 5-flowered dichasium, the

- ultimate branches having 2-flowered
 scorpioid cymes; calyx and corolla tube
 pubescent or papillate outside, tube
 orange-red, corolla lobes yellow; Surinam,
 French Guiana, and the lower Amazon River
 basin in Brazil 13. I. spiciformis
- 12 Leaf veins and blade glabrous or glabrescent
 beneath; stipules 3-5 mm long; inflorescence
 secondary rachises of a compound 7-11-
 flowered dichasium; calyx and corolla tube
 glabrous or glabrescent outside, tube pink
 or reddish-violet, corolla lobes pink or
 white; Amazonia.
- 13 Corolla tube 9-13 mm long, pink; corolla
 lobes white; inflorescence slightly
 pyramidal or more commonly cylindrical;
 inflorescence secondary rachises of a
 compound 7-flowered dichasium, the
 ultimate branches having a simple 3-
 flowered dichasium; restricted to lower
 Amazonia 12. I. longifolia
- 13 Corolla tube 35-50 mm long, reddish-violet;
 corolla lobes pink; inflorescence ovoid
 to ellipsoid; inflorescence secondary
 rachises of a compound 11-flowered
 dichasium, the ultimate branches having

2-flowered scorpioid cymes; widespread throughout Amazonia, but principally distributed in western portions
..... 14. I. rosea

Isertia sect. Cassupa (Humb. & Bonpl.) B. M. Boom,
stat. nov.

Cassupa Humb. & Bonpl., Pl. Aequin. 1: 43, pl. 12. 1806.

TYPE: Cassupa verrucosa Humb. & Bonpl. [= Isertia
verrucosa (Humb. & Bonpl.) Standley].

This new section is based on Humboldt and Bonpland's genus Cassupa. Isertia section Cassupa is distinguished from section Isertia by fruits with fleshy endocarp, stigmas 2-3-lobed, and ovaries 2-3 (4)-locular. While the characters, particularly fruit type, are always distinct, they are not substantial enough to warrant segregating Cassupa at the generic level. I agree with Standley (1931a) that the identical general appearance of species in Isertia and Cassupa makes it practical to recognize all taxa concerned under one genus, Isertia. by recognizing Cassupa at the sectional level, however, the two major lines of evolution in these taxa are emphasized, but not at the expense of a realistic generic concept. The geographic distribution of Isertia sect. Cassupa is primarily Andean and southern Central American with some elements extending into western Amazonia (Map 1).

1. Isertia krausei Standley

Isertia krausei Standley, Publ. Field Mus. Nat. Hist.,

Bot. Ser. 11(5): 216. 1936. TYPE: PERU. LIBERTAD:

Prov. Pataz, valley of the Mishiollo, tributary of

the Huallaga, 1700 m, Aug 1914, Weberbauer 7066

(HOLOTYPE: F!; ISOTYPE: GH!).

Shrub 5 m tall, the branchlets quadrangular, glabrous. Leaves with blades coriaceous, oblanceolate, 28-33 x 7-10 cm, acute or acuminate at apex, acute to attenuate at base, glabrous above with white tomentum beneath confined to the bottom of the areoles; midrib glabrous above and beneath; primary veins ca 25 pairs, impressed and glabrous above, prominulous and ciliolate beneath; petiole 25-40 x 2-4 mm, glabrous; stipules 4, interpetiolar, deeply bifid, ca 1 cm long with obtuse apices, glabrous. Inflorescence ellipsoidal, ca 22 x 7 cm, with secondary rachises of a compound 7-flowered dichasium, the ultimate branches having a simple dichasium of 3 flowers, the secondary rachises spreading at ca 45 degree angles from primary rachis, glabrous, ca 30 x 3 mm, subtended by triangular cymbriform bracteoles, glabrous, 2-3 mm long. Flowers: calyx ca 7 x 5 mm, glabrous outside with conspicuous patches of red squamose cells inside, with acute lobes ca 2 mm long; corolla "brownish red with yellow border" (Weberbauer 7066), the tube ca 35 mm long, glabrous outside with villous pubescence inside around mouth and on

inside of lobes, the lobes 5, ca 10 mm long, with obtuse apices; stamens 6, the anthers narrowly oblong, ca 8 mm long, the filaments ca 3 mm long; ovary 2-celled; style ca 35 mm long, the stigma 2-lobed, the lobes clavate, ca 6 mm long. Fruit unknown.

Distribution: known only from the type collection in Peru (Map 4).

2. Isertia reticulata Britton ex Rusby

Isertia reticulata Britton ex Rusby, Mem. Torrey Bot.

Club 6(1): 46. 1896. TYPE: BOLIVIA. PA PAZ: between Guanai and Tipuani, Apr-Jun 1892, Bang 1358

(LECTOTYPE: NY!, herein designated; ISOLECTOTYPES: F!, GH!, M!, MO!, NY!, US!).

Shrub or small tree to 8 m tall, 13 cm diam., the branchlets quadrangular to subrotund, strigose to tomentose. Leaves with blades coriaceous, obovate to elliptic 22-42 x 8-15 cm, slightly cuspidate at apex, the cusp 0.5 -1 cm long, acute to acuminate at base, glabrescent above, tomentose and prominent beneath; midrib strigulose and impressed above, tomentose and prominent beneath; primary veins 20-30 pairs, impressed and sparingly strigulose above, prominent and tomentose beneath; petiole (15) 25-45 x 2-6 mm, strigose to tomentose; stipules 4, interpetiolar, triangular, 8-15 (20) mm long, strigulose with ciliolate margins. Inflorescence narrowly ellipsoid

to ellipsoid, 10-34 x 7-12 cm, with secondary rachises of a simple 8-9-flowered dichasium, the ultimate branches having scorpioid cymes of 3-4 flowers, the secondary rachises spreading at ca 45 degrees from primary rachis, strigose, 15-35 x 1.5-3 mm, subtended by ovate to lanceolate cymbriform bracteoles, these strigulose and ciliate, 3-10 mm long, apex acuminate. Flowers: calyx cup-shaped, 7-8 x 4-5 mm, flaring at apex, sparingly strigose inside, more so outside, irregularly 4-lobed, the lobes broadly rounded, ciliate, ca 2 mm long; corolla yellow or orange, the tube 35-40 mm long, tomentose outside with copious golden-villous pubescence inside restricted to around mouth, the lobes 5-6, ovate, 4-7 mm long, acute at apices; stamens 6-8, the anthers narrowly oblong, 8-9 mm long, the filaments ca 3 mm long; ovary (2) 3-4-celled; style 38-40 mm long, the stigma 3-4-lobed, the lobes narrowly oblong, ca 3.5 mm long. Fruit a berry, broadly ellipsoid, 6-8 mm diam., scabridulous, strigose; seeds 0.9-1 mm long.

Distribution: restricted to the Bolivian Andes at elevations from ca 750-1800 m (Map 4).

Representative specimens examined: BOLIVIA. COCHABAMBA: Prov. Chapare, on new road to Todos Santos, 125 km NE of Cochabamba near Chimore, on S bank of Río San Mateo, Eyerdam 24732 (F). LA PAZ: San Carlos, Mapiiri region, Buchtien 64 (F, GH, NY); Mapiiri, May 1886, Rusby s.n.

(F, GH, NY); near Apolo, Williams 1563 (F, NY, US).

Isertia reticulata is a seldom collected and imperfectly known species. It is, however, easily distinguished by its strongly impressed tertiary leaf venation, coriaceous leaves, and inflorescence branching pattern. A photograph of a specimen at B (F neg. no. 276) is either referable to this species or else is very closely related to it. The only label data are "Colombia, Sonndulj," and therefore this species may occur in Colombia.

3. Isertia verrucosa (Humb. & Bonpl.) Standley

Cassupa verrucosa Humb. & Bonpl., Pl. Aequin. 1: 43,

pl. 12. 1806. Isertia verrucosa Standley, Publ.

Field Columbian Mus., Bot. Ser. 8(5): 346. 1931.

TYPE: VENEZUELA. AMAZONAS: San Carlos de Río Negro,

Humboldt & Bonpland 998 (HOLOTYPE: P!).

Small tree to 16 m tall, 40 cm diam., the branchlets quadrangular, glabrescent to minutely strigulose. Leaves with blades coriaceous, obovate, 26-40 (80) x 12-20 (35) cm, acute to cuspidate at apex, the cusp 0.5-1 cm long, acute to acuminate at base, glabrous above, silvery white canescent beneath; midrib glabrous and prominulous above, glabrescent to sparingly strigulose and prominent beneath; primary veins 19-24 pairs, planar and glabrous above, prominulous and puberulent beneath; petiole 30-65 (90) x 3-4 mm, glabrescent; stipules 4, interpetiolar, lanceolate,

15-35 mm long, glabrous. Inflorescence narrowly ellipsoidal, 10-24 x 4-11 cm, with secondary rachises of a single flower or a simple 3-flowered dichasium or 2-flowered scorpioid cymes, the secondary rachises spreading at ca 45 degree angles from primary rachis, glabrescent to puberulent, 20-30 x 2-3 mm, subtended by triangular bracteoles ca 2 mm long, margins ciliolate, apex acute. Flowers: calyx pale green to salmon-red, shallow cup-shaped, 5-6 x 4-8 mm, glabrous but with patches of red squamose cells inside, glabrescent outside, indistinctly 5-6-lobed, the lobes broadly rounded, ciliolate, ca 1 mm long; corolla tube red proximally grading to yellow distally, 40-55 mm long, white- or yellow-villous pubescent inside around mouth, glabrous outside with prominent tubercles distally, the lobes 6, with dense villous pubescence inside, glabrous outside, cucullate, 9-14 mm long, acute at apices; stamens 6, the anthers narrowly oblong, 8-9 mm long; ovary 2-celled; style 51-60 mm long, the stigma 2-lobed, the lobes narrowly oblong, 2-3 mm long. Fruit a berry, ellipsoidal, slightly asymmetrical, ca 9 mm diam., glabrous and smooth outside; seeds ca 1.5 mm long.

Distribution: watershed of the upper Río Negro in Venezuela and adjacent Brazil at elevations of 100-140 m (Map 4).

Representative specimens examined: BRAZIL. AMAZONAS:

São Gabriel, Rio Negro, Ducke 24375 (US). VENEZUELA.
AMAZONAS: 2 km E of San Carlos de Río Negro, Liesner
3435 (MO); along Yavita-Pimichin trail near Pimichin,
Maguire et al. 36312 (NY, VEN); San Carlos de Río Negro,
Steyermark & Bunting 102693 (NY, US, VEN).

4. Isertia laevis (Triana) B. M. Boom, comb. nov.

Cassupa laevis Triana, Ann. Sci. Nat. (Paris) Ser. IV.
9: 44. 1858. TYPE: COLOMBIA. CUNDINAMARCA: La Mesa,
Bogotá, alt. 1400 m, Triana 1838 (3311.1) (Kirkbride,
1982) (LECTOTYPE: P!, herein designated; ISOLECTO-
TYPES: BR!, COL, K!, P!, US!).

Cassupa alba K. Schum. in Engl. & Prantl, Nat. Pflanzenf.
4, Abt. 4: 63. 1891, nomen nudum.

Isertia alba Sprague, Trans. & Proc. Bot. Soc. Edinburgh
22: 434. 1905. TYPE: PERU. LORETO: Yurimaguas,
Huallaga River, in secondary forest, May 1855, Spruce
3878 (HOLOTYPE: K!; ISOTYPE: BR!).

Isertia purdiei Sprague, Trans. & Proc. Bot. Soc.
Edinburgh 22: 434. 1905. TYPE: COLOMBIA. BOYACA:
Muzo, Purdie s.n. (HOLOTYPE: K!).

Cassupa juruana K. Schum., Bot. Jahrb. Syst. 40: 148.
1907, nomen nudum.

Cassupa juruana K. Schum. & K. Krause, Verh. Bot.
Vereins Prov. Brandenburg 50: 97. 1908. Isertia
juruana Standley, Publ. Field Columbian Mus., Bot.

Ser. 8(5): 346. 1931. TYPE: BRAZIL. AMAZONAS: prope
Juruá Miry, May 1901, Ule 5488 (HOLOTYPE: B; ISOTYPES:
K!, fragment F!, L!).

Cassupa alba K. Schum. & K. Krause, Bot. Jahrb. Syst.
40: 322. 1908. Isertia alba Standley, Publ. Field
Mus., Bot. Ser. 8(5): 346. 1931. TYPE: COLOMBIA.
CUNDINAMARCA: Cundai, alt. 1200 m, Lehmann 2590
(LECTOTYPE: Standley, 1930a).

Isertia spraguei Wernham, Bull. Misc. Inform., p. 65.
1914. TYPE: COLOMBIA. HUILA-CAUCA: eastern cor-
dilleras between Pitalito and Mocoa, 1898-99,
Sprague s.n. (HOLOTYPE: K!; ISOTYPE: K!).

Cassupa panamensis Standley, Contr. U.S. Natl. Herb.
18: 135. 1916. Isertia panamensis Standley, Publ.
Field Columbian Mus., Bot. Ser. 8(5): 346. 1931.
TYPE: PANAMA. COLON: along Río Fato, alt. 10-100 m,
8 Jul 1911, Pittier 3889 (HOLOTYPE: US!; ISOTYPE:
US!).

Isertia weberbaueri Standley, Publ. Field Columbian
Mus., Bot. Ser. 4(8): 277. 1929. TYPE: PERU.
LIBERTAD: Pataz, valley of the Río Mixiollo, alt.
1400 m, Aug 1400, Aug 1914, Weberbauer 7054 (HOLO-
TYPE: F!; ISOTYPES: F!, US!).

Isertia parvifolia Standley, Publ. Field Columbian Mus.,
Bot. Ser. 4(8): 277. 1929. TYPE: PERU. JUNIN:
Chanchamayo Valley, alt. 1500 m, Apr 1924-27,

Schunke 393 (HOLOTYPE: F!).

Creatantha peruviana Standley, Publ. Field Columbian
Mus., Bot. Ser. 8(5): 344. 1931. TYPE: PERU. JUNIN:
Puerto Yessup, alt. 400 m, 10-12 Jul 1929, Killip &
Smith 26331 (HOLOTYPE: F!; ISOTYPE: US!).

Shrub or small tree to 12 m tall, the branchlets
quadrangular, strigulose. Leaves with blades membra-
ceous to subcoriaceous, elliptic, 29-43 (68) x 14-20 (36)
cm, acute to cuspidate at apex, the cusp 1-2 cm long,
acute to rounded at base, glabrous above, white canescent
beneath; midrib glabrescent or ciliolate and prominulous
above, strigulose and prominent beneath; primary veins
19-25 pairs, planar and glabrescent to ciliolate above,
prominulous and strigulose to canescent beneath; petiole
(20) 40-120 x 2-5 mm, strigulose; stipules 4, inter-
petiolar, triangular, 5-13 (45) mm long, sometimes
foliaceous. Inflorescence ovoid to ellipsoid, 16-34 x
7-9 cm, with secondary rachises of a simple 5-flowered
dichasium, the ultimate branches having scorpioid cymes
of 2 flowers, the secondary rachises spreading at ca 45
degree angles from primary rachis, strigulose to tomen-
tose especially in axes, 25-45 x 2-4 mm, subtended by
widely ovate cymbriform bracteoles, these strigulose
with ciliolate margin, ca 4 mm long. Flowers: calyx
cup-shaped, 5-6 x 3-4 mm, glabrous or ciliolate inside,
strigulose and scabridulous outside, indistinctly

5-6-lobed; corolla white, the tube 32-53 (60) mm long, with copious villous pubescence inside restricted to around the mouth, puberulent outside, the lobes 5-6, cucullate at apex, 10-14 mm long; stamens 6-7, the anthers narrowly oblong, 7-9 mm long, the filaments laminar, ca 3 mm long; ovary 2-3-celled; style ciliolate, 32-47 (57) mm long, the stigma 2-lobed, the lobes narrowly oblong, 3-5 mm long. Fruit a berry, ellipsoidal, 8-11 mm diam., smooth, glabrescent or sometimes puberulent; seeds 0.7-1 mm long.

Distribution: at elevations from 100-2000 m, primarily in the Andes, but extending north to Costa Rica and east to western Amazonia (Map 4).

Representative specimens examined: BOLIVIA. LA PAZ: Prov. Larecaja, Tuiriri, near Mapiiri, on left bank of Río Mapiiri, Krukoff 10933 (F, GH, NY, U). BRAZIL. ACRE: Rio Moa at Cachoeira Grande, Prance et al. 12527 (MO, NY); between Lucania and Porangaba, Rio Juruá-Mirim, Steward et al. P12942 (MO, NY, US). AMAZONAS: Rio Javari, fields around Palmeiras Army Post, Lleras P17048 (NY, US). COLOMBIA. BOYACA: Tauramena, a orilla de la quebrada Agua blanca, Uribe 3763 (F, NY). CHOCO: small plateau above Río Dubasa, 1 km upstream of Catru, White & White 67 (GH, MO). META: Villavicencio, near town along hwy. to Bogotá, Zarucchi et al. 1088 (F, GH). COSTA RICA. PUNTARENAS: steep forested slopes above Golfito along

trail to the television tower, Burger & Matta 4747 (F); Osa Peninsula, along the Camino de Altura, 2-5 mi W of Rincon de Osa, Raven 21483 (F, NY); on road to radio and telecommunications tower 6 km N of Golfito, Utley & Utley 4895 (F, MO, NY). ECUADOR. AZUAY: 20-25 km E of Jesus María, Gentry et al. 28503 (MO). NAPO: 46 km S of Baeza along hwy. to Tena, Boom & Luteyn 1386 (COL, F, GH, K, MO, NY, QCA, US). PASTAZA: Mera, Río Pastaza, Harling 11062 (US). PANAMA. BOCAS DEL TORO: Chiriquicito to 5 mi S along Río Guarumo, Dwyer 2054 (GH, MO, US). COLON: Santa Rita Ridge, 2-3 mi from Transisthmian Hwy., Gentry 1856 (F, NY). DARIEN: Río Paya, Duke & Kirkbride 14069 (MO). PERU. LORETO: on route 16, near km 96, NE of Tingo María on the way to Pucallpa, Davidson 3495 (F, MO, NY); Maynas, Río Amiyacu, Pebas and vicinity, Plowman et al. 6593 (F, K). SAN MARTIN: Mariscal Caceres, Malpaso de Balsa Probana, 1 km abajo de la desembocadura del Río Mishollo, Schunke 4731 (F, GH, MO, NY, US). VENEZUELA. BARINAS: La Soledad, antes de llegar a Barinitas, Berti & Bautista 1516 (VEN); along hwy. 1, 12 km NW of Barinitas on road to Santo Domingo, Nee & Whalen 16931 (F). TACHIRA: Cerro Las Minas, bordering Quebrada Las Minas, 18-20 km SE of Santa Ana, Steyermark & Liesner 119026 (VEN).

Mexia 6086 reports that in Peru the wood of I. laevis is used in hut construction and is known as "asaquíro."

Other common names have been recorded for this species in Peru: "caaynum"(Berlin 590), "tsagnum"(Kayap 732), and "cagnum"(Kayap 998).

This new combination was necessitated by the discovery of an earlier available name for this species. When Triana described Cassupa laevis he did not specify a holotype, so lectotypification was also necessary. Interestingly, Triana 1838 was cited by Krause (1908) as a syntype of I. alba K. Schum. & K. Krause. Clearly, they must have been unaware of Triana's publication, as have been more recent authors.

5. Isertia scorpioides B. M. Boom, sp. nov.

Species nova ab speciebus ceteris sectionis Cassupa (Humb. & Bonpl.) B. M. Boom inflorescentiae rhachidibus secundariis dichotomes cymosis, cymae ramis scorpioides, fructibus pro sectionis minimas differt.

Shrub or small tree to 10 m tall, the branchlets quadrangular, covered with grayish-brown strigose tomentum. Leaves with blades membranaceous, elliptic to obovate, 22-44 x 13-27 cm, cuspidate at apex, the cusp 1.5-2 cm long, acuminate to attenuate at base, glabrous above, sparingly setose beneath; midrib strigulose above and beneath, planar to prominulous above, prominent beneath; primary veins 18-24 pairs, glabrous and planar above, strigulose and prominulous beneath; petiole 50-55 x 2.5-

4 mm, vestiture strigulose; stipules 4, interpetiolar, narrowly triangular and somewhat falcate, 10-12 mm long, strigulose with ciliate margins. Inflorescence shallowly deltoid to ovoid, 20-25 x 10-15 cm, with secondary rachises of a simple 9-flowered dichasium, the ultimate branches having scorpioid cymes of 4 flowers, the secondary rachises spreading at 45-60 degree angles from primary rachis, strigose, 25-40 x 2-3 mm, subtended by triangular cymbriform bracteoles, these strigulose and ciliate, 4-18 mm long, sometimes aristate. Flowers: calyx green cup-shaped, ca 4 x 3 mm, essentially glabrous inside with occasional small patches of squamose cells near mouth, strigulose to glabrescent outside, indistinctly 4-6-lobed; corolla first white or yellow turning pink (or red?) with purple throat, the tube 35-40 mm long, strigulose and rugose outside, glabrous inside, the lobes 6, somewhat spatulate apically, ca 13-14 mm long, with dense (whitish?) villous pubescence inside; stamens 6, the anthers narrowly oblong, 6-6.5 mm long, the filaments ca 3 mm long; ovary (2) 3 (4)-celled; style ciliolate, ca 35 mm long, the stigma (2) 3 (4)-lobed, the lobes narrowly oblong, ca 3 mm long. Fruit a berry, broadly ellipsoid to spheroid, 5-6 mm diam., rugulose and sparingly strigose to glabrescent; seeds 0.9-1.1 mm long.

TYPE: PANAMA. COLON: Atlantic side of Isthmus on road

to Piña, 25 Aug 1967, Kirkbride & Hayden 316 (HOLOTYPE: NY!; ISOTYPES: MO!, NY!).

Paratypes: PANAMA. COLON: vicinity Nuevo Limon, Allen 5141 (F, NY); Cocle Del Norte, Hammel 4505 (MO, NY); along road between Piña and Gatun, Luteyn 1309 (MO). DARIEN: Peñas Bay near hotel, Tyson 5537 (MO).

Distribution: Panama in the provinces of Colón and Darién at elevations of less than 100 m (Map 4).

Isertia scorpioides is similar vegetatively, in inflorescence branching, and in fruit size to I. haenkeana DC. from which it differs in having a somewhat strigulose midrib on upper leaf blade, green colored calyx with patches of squamose cells inside near mouth, ciliolate style, larger (35-40 vs. 24-28 mm long) pinkish flowers, (2) 3 (4) locules in ovary, and fleshy fruits with seeds not contained in pyrenes. Isertia scorpioides is distinct from other members of Isertia sect. Cassupa in its extensively branched inflorescence and in its small fruit size (ca 5 vs. 10 mm). Within the section it is most similar to I. laevis. Isertia scorpioides possesses several characters that appear intermediate between I. haenkeana and I. laevis. It seems probable that I. scorpioides originated as a hybrid between these species. It may be significant that I. scorpioides occasionally produces 4-locular fruits, for this represents a condition which, numerically, is

intermediate between that characteristic of Isertia sect. Cassupa and Isertia sect. Isertia.

6. Isertia pittieri (Standley) Standley

Cassupa laevis Triana var. chocoensis Triana, Ann.

Sci. Nat. (Paris) Ser. IV. 9: 44. 1858. TYPE:

COLOMBIA. CHOCO: prope Novita et Quibdó, Triana 1839

(3311.2) (HOLOTYPE: P, photo F! neg. no. 37299, holotype fragment F!; ISOTYPE: COL).

Cassupa pittieri Standley, Contr. U.S. Natl. Herb.

17(5): 445. 1914. Isertia pittieri Standley, Publ.

Field Columbian Mus., Bot. Ser. 8(5): 346. 1931.

TYPE: COLOMBIA. VALLE DEL CAUCA: Cauca near Córdoba, Dagua Valley, in the Pacific coastal zone, alt. 30-100 m, Dec 1905, Pittier 514 (HOLOTYPE: US!).

Shrub or large tree to 25 m tall, the branchlets quadrangular, viscid-strigulose to tomentose. Leaves with blades membranaceous, obovate to elliptic, 29-45 x 8-25 cm, cuspidate at apex, the cusp ca 2 cm long, acute, acuminate or rounded at base, glabrous above, glabrescent to tomentose beneath; midrib ciliolate and prominulous above, puberulent to tomentose and prominent beneath; primary veins, prominulous above and beneath; petiole 50-100 x 2-4 mm, puberulent to tomentose; stipules 4, interpetiolar, lanceolate, 15-30 mm long, the margins ciliolate. Inflorescence ellipsoid to broadly ellipsoid,

10-30 x 10-15 cm, with secondary rachises of a simple 5-flowered dichasium, the ultimate branches having scorpioid cymes of 2 flowers, the secondary rachises spreading at ca 45 degree angles from primary rachis, strigulose to tomentose, 20-50 x 2-5 mm, subtended by lanceolate cymbriform bracteoles, these ciliolate, 10-20 mm long. Flowers: calyx 6-7 x 4-5 mm, glabrous inside but with scattered patches of red squamose cells, glabrescent and smooth outside, indistinctly 5-6-lobed; corolla white, the tube 60-75 mm long, with copious villous pubescence inside around mouth, pubescent outside grading to glabrous and rugulose distally, the lobes 6, oblong, 11-20 mm long, acute and cucullate at apices; stamens 6, the anthers narrowly oblong, ca 12 mm long, the filaments laminar, ca 3 mm long; ovary 2-celled; style 50-70 cm long, ciliolate, the stigma 2-lobed, the lobes narrowly oblong, 5-7 mm long. Fruit a berry, ellipsoid, ca 10 mm diam., smooth, glabrous; seeds 1-1.2 mm long.

Distribution: Pacific slope of Colombia and Ecuador from mangroves to wet montane forests at elevations from sea level to 1500 m (Map 4).

Representative specimens examined: COLOMBIA. CHOCO: Quibdó, Río Atrato, Archer 1776 (F, US); ca 10 km E of San Pablo on Río Quito on new Pan American Hwy., ca 8 km W of Quibdó-Istmina road N of Istmina, Gentry & Renteria

23845 (MO, NY). NARINO: 2 km E of Barbacoas, just S of Río Telembí, Fosberg 21237 (NY, US). ECUADOR. CARCHI: Alrededores de Maldonado, 90 km al oeste de Tulcan, Balslev 1983 (NY). ESMERALDAS: San José, km 321 along railroad from Ibarra to San Lorenzo, Boom 1385 (COL, F, GH, K, MG, MO, NY, QCA, US, VEN). IMBABURA: region of junction of Río Meta and Río Lita, Steere 8221 (F, US).

Isertia pittieri is a very common second growth species within its rather limited geographic range. Archer 1776 reports that the flowers have a strong musky odor and are used for funeral wreaths, and that the leaves are a good substitute for soap, hence the common name in Colombia, "jaboncillo." Solís 12007 reports the common name "masamorro" from Ecuador. Although I. pittieri is surely closely related to I. laevis, it is sufficiently distinct from that species to be recognized itself at the species level. Isertia pittieri is distinguished immediately from I. laevis by its glabrescent leaf blade undersurface and long (60-70 mm), fleshy corolla.

Isertia sect. Isertia

Isertia section Isertia is distinguished from section Cassupa by fruits with bony endocarp, stigmas 4-6 (7)-lobed, and ovaries with (4) 5-6 (7) locules. The geographic distribution of section Isertia is primarily northern South American and Amazonian with elements

extending into Central America and the West Indies
(Map 3).

7. Isertia hypoleuca Benth.

Isertia breviflora Mart. ex Steudel, Nom. Bot. ed. 2.

1: 825. 1840, nomen nudum.

Isertia hypoleuca Benth., J. Bot. (Hooker) 3: 220.

1841. Isertia coccinea Vahl var. hypoleuca K. Schum.

in Mart. Fl. bras. 6(6): 286. 1889. TYPE: GUYANA.

Schomburgk 281 (HOLOTYPE: BM; ISOTYPES: F!, GH!, L!,
US!).

Cassupa scarlatina K. Schum., Bot. Jahrb. Syst. 40: 148.

1907, nomen nudum.

Cassupa scarlatina K. Schum. & K. Krause, Verh. Bot.

Vereins Prov. Brandenburg 50: 98. 1908. TYPE: BRAZIL.

AMAZONAS: ad Juruá Miry, Ule 5846 (HOLOTYPE: B, photo
F! neg. no. 275; ISOTYPES: K!, fragment F!, L!).

Isertia hoehnei K. Krause, Archiv. Bot. Estado São

Paulo 1: 115. 1925. TYPE: BRAZIL. AMAZONAS: S. Manuel,

Rio Tapajós, em Fev. de 1915, Kuhlmann 1474 (LECTO-

TYPE: R, herein designated; ISOLECTOTYPE F!, fragment).

Shrub or small tree to 15 m tall, 35 cm diam., the
branchlets subrotund to quadrangular, glabrescent or
pulverulent. Leaves with blades membranaceous, elliptic
to obovate, 18-65 x 9-18 cm, cuspidate at apex, the cusp
0.5-1.5 cm long, acute at base, glabrous above, white-

canescent beneath; midrib glabrous and prominulous above, glabrescent or puberulent and prominent beneath especially proximally; primary veins 16-28 pairs, planar and glabrous above, prominulous and puberulent beneath; petiole 35-75 x 2.5-3 mm, glabrescent; stipules 4, interpetiolar, narrowly triangular, ca 9 mm long. Inflorescence ovoid to broadly ovoid, 8-22 x 6-18 cm, with secondary rachises of a simple 7-flowered dichasium, the ultimate branches having scorpioid cymes of 3 flowers, the secondary rachises spreading at ca 45 degree angles from primary rachis, glabrescent to strigulose especially in axes, 25-35 x 2.5-3 mm, subtended by widely ovate cymbriform bracteoles, these strigulose with ciliolate margin, 3-4 mm long. Flowers: calyx pinkish-green, cup-shaped, 4-6 x 5 mm, glabrous inside but with small patches of red squamose cells near mouth, glabrescent and scabridulous outside, indistinctly 4-5-lobed; corolla reddish-orange, the tube 43-65 mm long, puberulent outside, with copious yellow-villous pubescence inside restricted to around mouth, the lobes 6-7, spatulate, 8-10 (13) mm long with tubercules protruding externally 0.5-1 mm at jct. of lobes and tube; stamens 6-7, the anthers narrowly oblong, 7-10 mm long, the filaments laminar, ca 2 mm long; ovary 5-6-celled; style glabrous, 41-53 mm long, the stigma 5-6-lobed, the lobes narrowly oblong, ca 2 mm long. Fruit a pyrene, very broadly ovoid, ca 10 mm diam., smooth

or scabridulous, occasionally puberulent; seeds 0.8-1.1 mm long.

Distribution: throughout the Guianas, Venezuela, and Amazonian regions of Brazil, Colombia, Peru, and Bolivia at elevations of ca 100-1400 m (Map 5).

Representative specimens examined: BOLIVIA. PANDO: W bank of Río Madeira, 3 km above Abuña, Prance et al. 8366 (F, L, NY, U). BRAZIL. AMAZONAS: São Paulo de Olivença, Ducke 638 (F, MO, US); Manaus-Porto Velho Hwy. (BR319), km 268, 28 km S of Igapó Açu, Prance et al. 20647 (K, MO, NY, U). RONDONIA: between Jaciparana and Rio Madeira, Prance et al. 5219 (F, NY, U). COLOMBIA. AMAZONAS: Río Iagara-Parana (affl. Río Putumayo), Gasche & Desplats 139 (US, VEN); Leticia, near outskirts of town on Brazilian border, Gentry 12725 (MO, NY); Peru-Colombia boundary, Río Putumayo, Klug 1627 (F, GH, MO, NY, US). FRENCH GUIANA: Mélinon 262 (F, P, US); Wachenheim 24 (NY, P). GUIANA. MAZARUNI-POTARO: Kaieteur Plateau, Maguire & Fanshawe 23132 (F, MO, NY, U, US, VEN). RUPUNUNI: Kurupukari, Essequibo River, Smith 2160 (F, MO, NY, U). PERU. LORETO: near mouth of Río Napo, Croat 20124 (F, GH, MO, NY, L); Prov. Maynas, Río Ampiyacu, Puca Urquillo and vicinity, Plowman et al. 6618 (F, GH); Prov. Maynas, Río Nanay below Bellavista, Carretera de Picuruyacu, Rimachi 2179 (F, MO). SURINAM. BROKOPONDO: Saramacca River near Posoegronoe, Maguire 24020 (F, MO, NY, U, VEN). SARACACCA:

Coppename River above Tonkens Falls, Geijskes 987 (U, VEN); upper Coppename River near Raleigh Falls, Schulz 7817 (NY, U). VENEZUELA. BOLIVAR: Alto Paragua, Playa del Raudal Guaiquinima, Cardona 871 (F, GH, NY, US, VEN); Uaipan-tepui, plateau at SE foot of the peaks of Uaipan, Koyama & Agostini 7324 (NY, VEN); Alto Río Cuyuni, La Escalera, Maguire et al. 46956 (NY, VEN).

Isertia hypoleuca has numerous common names throughout its extensive range: Venezuela, "manáse-yek," (Steyermark 60604); Colombia, "erilloquei," (Gasche & Desplats 139); Peru, "sacha rifari," (Plowman 2520); Brazil, "Jambo de Mata," (Prance 18234); Surinam, "panga panga," (Mennega 513).

Dwyer (1980) misattributed I. hypoleuca to Panama by confusing it with I. laevis (as I. alba Sprague). The two species are superficially similar, especially in terms of the white canescent pubescence on the leaf undersurfaces of both species. But even this pubescence is of a different nature in each species, and the list of other differences is quite long, including flower color, number of stigmatic lobes, style pubescence, number of locules in the ovary, and fruit type (berry vs. pyrene). The two species are in different sections of the genus and are not sympatric.

8. Isertia coccinea (Aubl.) J. F. Gmelin

Guettarda coccinea Aubl., Hist. Pl. Guiane 1: 317, pl.

123. 1775. Isertia coccinea J. F. Gmelin, Syst. Nat.

2: 567. 1791, non Vahl, 1798. Isertia coccinea Vahl,

Eclogae Americanae 2: 27. 1798, misattributed by Index

Kewensis. Phosanthus coccinea Raf., Ann. Gén. Sci.

Phys. 6: 82. 1820. TYPE: FRENCH GUIANA: Aublet s.n.

(HOLOTYPE: P!).

Isertia flava Miq., Linnaea 18: 613. 1844. TYPE:

Focke 939 (LECTOTYPE: U!, herein designated).

Isertia coccinea var. pentamera Bremek., Recueil Trav.

Néerl. 31: 263. 1934. TYPE: SURINAM. MAROWIJNE:

Marowyne River, Joeba Creek, Gonggriyp 3745

(HOLOTYPE: U!; ISOTYPE: U!).

Shrub or small tree to 18 m tall, 20 cm diam., the branchlets quadrangular to subrotund, covered with brownish strigulose tomentum. Leaves with blades membranaceous, obovate to elliptic, 12-25 (45) x (6) 9-13 (17) cm, cuspidate at apex, the cusp 1.5-2.5 cm long, obtuse to acuminate at base, glabrous above, floccose beneath; midrib strigulose and planar above, strigulose to short floccose and prominulous distally to prominent proximally beneath; primary veins 15-24 pairs, planar and sparingly strigose above, prominulous and mostly floccose beneath; petiole 25-40 (50) x 2-3 mm, vestiture strigulose; stipules 4, interpetiolar, cymbriform and

narrowly triangular, 5-15 (25) mm long, strigulose with ciliate margins. Inflorescence broadly ovoid to spherical 8-13 (20) x 5-11 cm, with secondary rachises of a simple 3-flowered dichasium or a compound 7-flowered dichasium, the ultimate branches having scorpioid cymes of 2 flowers, the secondary rachises spreading at ca 45 degree angles from primary rachis, strigose, 15-42 x 1.5-2 mm, subtended by ovate to lanceolate cymbriform bracteoles, these strigulose and ciliate, 5-7 (25) mm long, apex long-caudate especially beneath more proximal branches. Flowers: calyx red, cup-shaped, 6-7 x 5-6 mm, glabrescent inside, tomentose or strigose outside, 4-lobed, occasionally with one or several lobes elongated to 1.5 cm; corolla reddish-orange proximally, grading to yellow distally or rarely entirely white, the tube 50-70 mm long, densely tomentose outside, with copious yellow-villous pubescence inside restricted to around mouth, the lobes (5) 6, lanceolate, 6-8 mm long, cucullate at apices; stamens (4) 5-6, the anthers narrowly oblong, 8-10 mm long, the filaments ca as long as anthers; ovary (4) 5-6-celled; style 60-65 mm long, the stigma (4) 5-6-lobed, the lobes narrowly oblong, ca 2 mm long. Fruit a pyrene, broadly ovoid, ca 10 mm diam., scabridulous, pubescent; seeds 0.9-1 mm long.

Distribution: French Guiana, Surinam, Brazil (around mouth of the Amazon River), and naturalized on St. Vincent

and Martinique in the Lesser Antillies. Elevations range from 50-500 m (Map 7).

Representative specimens examined: BRAZIL. AMAPA: Oiapoque, campo de aviação, Black 49-8173 (U); Rio Araguari, Frões & Black 27588 (U, VEN); middle slopes of Mt. Tipac, Irwin 48706 (F, MO, NY, U); along road between Oiapoque and Clevelândia, Maguire et al. 47069 (NY, U); ca 6 km from Porto Platon, Pires et al. 51135 (F, NY, U); along roadside between Rios Cujubim and Flechal, Pires et al. 52612 (NY); Cupixi, Ribeiro 1541 (NY); margem do Rio Cachorrinho, afluente do Cupixi, Rosa 1030 (NY). PARA: Rio Piriá, Frões 34584 (U); Viseu, Pires et al. 13870 (NY); vicinity of Cachoeira, km 96 along BR22, Prance et al. 1693 (F, NY, U); km 60 along BR22, Capanema to Maranhão, Prance et al. 58711 (NY, others to be distributed). FRENCH GUIANA: Saül, Boom & Mori 1868 (CAY, F, K, MO, NY, P, U, US); région de Cayenne, route Cayenne le Gallion à km avant le camp militaire du Gallion, Descoings et al. 20256 (P); haut Oyapock, Takawana, de Granville B-5205 (CAY, US); fleuve Approuague, 1 km en amont de la crique Sapokaye, Oldeman B-1707 (U); 14 km WSW de Sinnamary, Raynal 19711 (CAY); haut Oyapock, Trois Sautes, près du village Zidock, Sastre 4678 (US). SURINAM. BROKOPONDO: bank of Sara Creek, Donselaar 1116 (U); road Afobaka-Brownsweeg, N of Brokopondo Lake, along lumber trail, Maas et al. 2337 (U). MAROWIJNE: along bank

of Oelemari River, Wessels Boer 1140 (MO, U); Nassau Mountains, Marowijne River, Cowan et al. 39083 (NY); fluv. Litani, propre Jamaiké, Rombouts 777 (U, US). SARAMACCA: Joden savanne, Mapanecreek area, Hekking 1221 (U, VEN). SURINAME: surroundings of Blakawatra, camp 8, 60 km SE of Paramaribo, Outer 851 (U). LESSER ANTILLIES. MARTINIQUE: Bèlanger 149 (P). ST. VINCENT: 1882, Guilding s.n. (K, NY).

Isertia coccinea is a common lowland pioneer species in terra firme forests and savannas. Local names include the following: French Guiana, "bois pian," (BAFOG, Service Forestier 1087); French Guiana, "aieato," (Bena 1127); Surinam, "pin-pin," (Lanjouw et al. 2781); Surinam, "kandrahoedoe," (Lanjouw et al. 2860).

Regarding the wood and bark of Isertia coccinea, Outer et al. 851 notes that "bole smooth, spotted with grey-brown; slash white with orange spots, turning brown-black on exposure; sapwood white-yellow." Oldeman 2974 and B-2406 add that the bark is green with maroon spots and note that the species has red latex and white wood. The wood is sometimes described as reddish which is doubtlessly due to the red resin ducts.

Mori (pers. comm.) has observed the Crimson Topaz hummingbird (Topaza pella) visiting the flowers of I. coccinea in Saül, French Guiana. Both the male and female were observed in the same tree. The male was actually seen to stick its beak in flowers and then to make foraging flights only to return to the same branch

to rest for long periods. Mori also observed a Bombus sp. and the Long-tailed Hermit (Phaethornis superciliosus) to visit I. coccinea. The bees and birds were seen to engage in antagonistic behavior towards one another; this may be an important means of insuring cross-pollination.

Many more trees of I. coccinea in Saül were in flower in April, 1983 (wet season) than in September, 1982 (dry season), but, as always, only a few flowers on each tree were open at any one time.

9. Isertia haenkeana DC.

Shrub or small tree to 20 m tall, the branchlets quadrangular to subrotund, covered with grayish-brown strigose tomentum. Leaves with blades chartaceous, ovate, elliptic or obovate, 29-64 x 10-30 cm, cuspidate at apex, the cusp 1.5-2 cm long, acuminate to attenuate or decurrent at base, glabrous above, sparingly setose beneath; midrib glabrous and planar to prominulous above, strigulose and prominent beneath; primary veins 16-23 pairs, glabrous and planar above, strigulose and prominulous beneath; petiole 5-50 x 2.5-5 (7) mm, vestiture strigulose; stipules 4, interpetiolar, lanceolate and somewhat falcate, 8-45 mm long, strigulose with ciliolate margins. Inflorescence shallowly deltoid to ovoid, 10-21 x 9-17 cm, with secondary rachises of a simple 8-18-flowered dichasium, the ultimate branches having scorpioid

cymes of 4-9 flowers, the secondary rachises reddish-orange, spreading at 45-60 degree angles from primary rachis, strigose, 14-32 (45) x 1.5-2.5 (3) mm, subtended by triangular cymbriform bracteoles, these strigose and ciliate, 3-11 mm long. Flowers: calyx reddish-orange, cup-shaped, 2.5-3 x 3 mm, glabrous inside, strigulose outside, indistinctly 4-lobed; corolla bright yellow, turning brilliant orange or reddish, the tube 24-28 mm long, strigulose to hispid outside, glabrous inside, the lobes 6, lanceolate, 8-9 mm long, with dense yellow-villous pubescence inside, usually with a tubercule protruding ca 1 mm on the outer surface; stamens 6, the anthers narrowly oblong, 4-6 mm long, the filaments ca as anthers; ovary (5) 6 (7)-celled; style glabrous, 20-28 mm long, the stigma (5) 6-lobed, the lobes narrowly oblong, 3.5-5 mm long. Fruit a pyrene, 6-8 mm diam., smooth, strigulose; seeds 0.6-0.9 mm long.

Key to the varieties of Isertia haenkeana

- 1 Stipules 8-13 mm long; corolla tube strigulose to glabrate, the lobes usually with a tubercule at point of junction with the tube in bud; widespread in Central America, NW South America, and Cuba 9a. var. haenkeana
- 1 Stipules 20-45 mm long; corolla tube hispid, the lobes without a tubercule at point of junction with the tube in bud; restricted to the Cordillera de la

- Costa, Venezuela 9b. var. mirandensis
- 9a. Isertia haenkeana DC. var. haenkeana
- Isertia haenkeana DC, Prodr. 4: 437. 1830. TYPE:
MEXICO: Haenke s.n. (HOLOTYPE: PR).
- Isertia coccinea Bartlett ex DC., Prodr. 4: 437. 1830,
non J. F. Gmelin, 1791, non Vahl, 1798, misattributed
by Index Kewensis.
- Isertia deamii Bartlett, Proc. Amer. Acad. 33: 59.
1907. TYPE: GUATEMALA. IZABAL: Puerto Barrios, 24 Feb
1905, Deam 48 (HOLOTYPE: GH!).
- Isertia humboldtiana K. Schum. & K. Krause, Bot. Jahrb.
Syst. 40: 321. 1908. TYPE: COLOMBIA: Lehmann 198
(HOLOTYPE: B, photo F!, neg. no. 279).
- Isertia deamii var. stenophylla J. D. Smith, Bot. Gaz.
61: 374. 1916. TYPE: COSTA RICA. PUNTARENAS: prope
Boca Culebra, Comarca de Puntarenas, Jan 1898,
Pittier 11989 (HOLOTYPE: US!; ISOTYPES: F!, P!).
- Isertia leiantha Standley, Publ. Field Columbian Mus.,
Bot. Ser. 8(3): 163. 1930. TYPE: COLOMBIA. ANTIOQUIA:
Peñas Blancas, Juzepczuk 4478 (HOLOTYPE: F!; ISOTYPE:
LE).

Distribution: Cuba, throughout Central America,
northern Colombia, and northwestern Venezuela at eleva-
tions from sea level to 2300 m. The type (Haenke s.n.)
purportedly came from Mexico, but I have seen no collec-
tions made north of Guatemala. Grisebach (1864) reported

the species from Guadeloupe (Map 6).

Representative specimens examined: COLOMBIA. AMAZONAS: Río Putumayo, carretera entre Caucaya (Puerto Leguizamo) y La Tagua, Schultes 3786 (VEN). ANTIOQUIA: banks of the Río Valdivia, Metcalf & Cuatrecasas 30078 (F, GH, MO, US). BOLIVAR: Frasuquillo on Río Sinu, Pennell 4600 (F, NY, US). COSTA RICA. SAN JOSE: ca 17-25 km S of La Palma on road to Dominical, Alemeda et al. 3318 (F, NY); 1.5 km E of Puntarenas Prov., boundary along San Isidro-Dominical Road, ca 12 km W of San Cristobal, Whitmore 56 (F, MO, NY). CUBA. PINAR DEL RIO: Sierra de Cabra on Guane Road, Britton et al. 7212 (F, NY, US); Arroyo del Sumidero, Shafer & León 13577 (F, NY, US). GUATEMALA. IZABAL: ca 7 mi S of Puerto Barrios, Croat 41784 (MO); along RR, ca 1 mi E of Puerto Barrios, Deam 60616 (F, GH, MO, NY, US); along road between Puerto Barrios and Santo Tomas, Steyermark 42040 (F). HONDURAS. COLON: near mouth of Río Platano, vicinity of Ras, Gentry et al. 7479 (MO). SAN PEDRO SULA: Aldea de Corinto y alrededores frontera con Guatemala, 55 km al O de Puerto Cortes, Nelson et al. 2830 (MO). NICARAGUA. ZELAYA: Bluefields, Marshall & Neill 6496 (GH, NY); Finca Santa Rosa, ca 2.5 km ENE of Rama, Proctor et al. 27373 (F, NY); Comarca del Cabo, France ya Sirpi, Robbins 5629 (F, GH, NY). PANAMA. CANAL ZONE: along roads K-10 and K-15 surrounding the U.S. Naval Ammunition Depot, Luteyn 1584 (F, MO); at end of

Pipeline Road, 15-20 mi NW of Gamboa, Mori & Kallunki
1741 (MO). SAN BLAS: Isla de Pinus, Kirkbride 214 (MO,
NY). VENEZUELA. BARINAS: Ticoporo Forest Reserve near Río
Socopo, Bretler 3731 (NY, US, VEN); between La Esmeralda
and El Curito, Steyermark & Rabe 96524 (NY, VEN). MERIDA:
between Caja Seca and Torondoy, 3-5 km SE of Caja Seca,
Steyermark & Wiehler 106577 (MO, US, VEN).

Steyermark (1974) reports that the common name for I.
haenkeana is "coralito." This is the most common species
of the genus in Central America where it is usually
found in secondary growth or weedy situations. Croat
(1978) reports that on Barro Colorado Island, Panama,
I. haenkeana flowers throughout, but mostly early, in
the rainy season to the early dry season. Croat gives
the common name "canelito."

9b. Isertia haenkeana var. mirandensis Steyerm.

Isertia haenkeana var. mirandensis Steyerm., Mem. New
York Bot. Gard. 17(1): 298. 1967. TYPE: VENEZUELA.
MIRANDA: Parque Nacional de Guatopo, alt. 500 m, 11
Sep 1960, Steyermark 87079 (HOLOTYPE: VEN!; ISOTYPE:
NY!).

Distribution: restricted to the Cordillera de la Costa
of north-central Venezuela at elevations from 35-1000 m
(Map 6).

Representative specimens examined: VENEZUELA. DISTRITO
FEDERAL: Cerro Naignuata, laderas pendientes que miran al

norte, entre Las Delicias y La Toma de Quebrada de Mata de Platano, 12 km oeste de Hacienda Cocuizal de la Electricidad de Caracas, Steyermark 97527 (F, NY, VEN).
MIRANDA: Parque Nacional Guatopo, near park headquarters at south entrance, Croat 21764 (MO); 3 km SW of Araguaita along road between Caucagua and Altigracia de Orituco, Davidse 4131 (MO, VEN).

10. Isertia parviflora Vahl

Isertia parviflora Vahl, *Eclogae Americanae* 2: 28, t.

15. 1798. TYPE: Trinidad: Ryan s.n. (HOLOTYPE: C).

Brignolia acuminata DC., *Prodr.* 4: 444. 1830. TYPE:

TRINIDAD: Lockhart s.n. (HOLOTYPE: G-DEL, photo F!

neg. no. 33527; ISOTYPES: GH!, K!, NY!).

Brignolia pubigera Benth., *J. Bot. (Hooker)* 3: 219.

1841. TYPE: GUYANA: Schomburgk s.n. (HOLOTYPE: K!, photos NY! neg. nos. 3254 & 6255).

Bruinsmania isertioides Miq., *Linnaea* 17: 73. 1843.

TYPE: SURINAM. PARA: *crescit in sylvis ad Para,*

Focke 155 (HOLOTYPE: U!).

Isertia glabra Ducke, *Arch. Jard. Bot. Rio de Janeiro*

4: 179. 1925. TYPE: BRAZIL: 6/3/1923, Ducke s.n., RB accession no. 17373 (LECTOTYPE: US!; ISOLECTOTYPES: K!, P!, U!).

Isertia parviflora var. hirta Steyerm., *Mem. New York*

Bot. Gard. 17(1): 295. 1967. TYPE: GUYANA. RUPUNUNI:

Wabuwak, Kanuku Mts., alt. 605 m, Oct 1948, Forest
Dept. Field No. WB388 (HOLOTYPE: NY!; ISOTYPE: NY!).

Shrub or small tree to 12 m tall, 10 cm diam., the branchlets quadrangular to subrotund, strigulose to glabrescent. Leaves with blades coriaceous, ovate, 13-39 x 6-17 cm, cuspidate at apex, the cusp 1-2 cm long, cordate to obtuse or rounded at base, glabrous above, sparsely to densely pubescent beneath; midrib glabrous to sparingly strigulose and prominulous above, strigulose and proximally prominent beneath; primary veins 16-21 pairs, planar and glabrous above, prominulous and strigulose beneath; petiole 20-25 x 2-3 mm, strigulose; stipules 4, interpetiolar, lanceolate, 15-25 mm long, margin entire. Inflorescence very broadly ovoid, 9-12 x 8-13 cm, with secondary rachises of a compound 31-flowered dichasium, the ultimate branches having scorpioid cymes of 3-4 flowers, the secondary rachises spreading at ca 45-60 degree angles from primary rachis, sparsely to densely strigulose, 25-30 x 1-2 mm, subtended by widely ovate cymbriform bracteoles, these pubescent, 4-5 mm long. Flowers: calyx pink, cup-shaped, ca 4 x 3 mm, glabrous inside, sparingly to densely pubescent outside, 4-6-lobed; corolla tube pink, 5-13 mm long, with copious villous pubescence inside around mouth, glabrous outside, the lobes 6, oblong, white with purple markings at base within, 4-7 mm long, acute and cucullate

at apices; stamens 6, the anthers narrowly oblong, 4-5.5 mm long, the filaments 3 mm long; ovary 4-6-celled; style 9-14 mm long, minutely tuberculate, the stigma 4-6-lobed, the lobes narrowly oblong, 1-1.5 mm long. Fruit a pyrene, broadly ovoid, ca 5 mm diam., strigulose, rugulose; seeds ca 1 mm long.

Distribution: Trinidad, the Orinoco and northern Amazon River drainages of Venezuela, the Guianas, and Brazil at elevations of 100-750 m (Map 6).

Representative specimens examined: BRAZIL. PARA: Alenquer, Colonia Lauro Sodré, estrada para o igarapé do Cipoal, Frões & Filho 29370 (U). RORAIMA: banks of Rio Apiau, 30 km from mouth, Prance et al. 4148 (NY); base of Serra Tepequem, Boca da Mata, Prance et al. 4307 (F, MO, NY, U). FRENCH GUIANA: Charvein, Benoist 586 (P); bord de l'Orénoque, 4 Aug 1887, Gaillard s.n. (P); Maroni, Mélinon 406 (F, NY, P). GUYANA. RUPUNUNI: Turuk Wau, Cook 161 (K, NY, U); watershed between Rupununi and Kuyuwini Rivers, Parabarú Savanna, Smith 3068 (F, MO, NY, U); western extremity of Kanuku Mts. in drainage of Takutu River, Smith 3201 (F, MO, NY, U). SURINAM. BROKOPONDO: banks of Saramacca River below rapids Jacob kondre, Maguire 23825 (F, MO, NY, U, US); along railway near Brownsveg, km 116, Wessels Boer 671 (GH, MO). TRINIDAD: Waller Field, ca 10 km E of Arima, Feinsinger 105 (F, MO, U,); Aripo Savanna at Waller Field, Howard 10302 (NY);

Aripa Savanna, Long Stretch Forest Reserve, 4-5 mi NE of Comuto village, Steyermark 90918 (NY, VEN). VENEZUELA. AMACURO: Río Cuyubini, Cerro La Paloma, Sierra Imataca, Steyermark 87612 (NY, VEN). BOLIVAR: Igarape Vista Geral, Río Cotinga, Maguire & Maguire 40257 (NY, VEN); Río Parguaza, 3-5 km below El Carmen, ca 50 river km from mouth, Wurdack & Monachino 40936 (NY).

Williams 13331 reports the common name "café negro" from Venezuela. Steyermark has annotated several specimens of I. parviflora as showing signs of introgression with I. rosea. His primary criterion for these annotations appears to be a reduction in pubescence in I. parviflora; in all other aspects the specimens appear to typical I. parviflora. Actually, there appears to be a great deal of variation in pubescence in this species, and Steyermark's variety hirta appears to be nothing more than one end of this pubescence gradient. Furthermore, the degree of pubescence cannot be correlated with geographic distribution or any other other morphological characters.

More ecological work has been done with I. parviflora than any other species in the genus. Bolten and Feinsinger (1978) studied the pollination ecology and phenology of the species in Trinidad. They found that the light pink flowers of I. parviflora emit a sweet odor and attract foraging bees as well as short-billed

hummingbirds. Feinsinger (pers. comm.) has provided additional information on the two populations of I. parviflora they studied. For the Arima Valley population flowering is from April to October (very low flowering until Aug, then a sudden peak, followed by rapid decline). The lower elevation population at Waller Field has some plants (larger, older ones) in flower all year, but there is a definite lull from Oct through Jan (peaks Apr-May and Jul).

Regarding nectar production, Feinsinger commented that the flowers last a single day only, opening just before dawn. Most nectar to be secreted is apparently in them at anthesis; relatively little secretion after dawn, and that concentrated into the first two hours after dawn. Secretion ceases by noon in all flowers examined. Many bees (solitary and social), wasps, and lepidopterans were sighted at the flowers and are probably important pollinators. Spingid pollination possibly occurs before dawn. Feinsinger further suggests that hummingbirds may be the most important pollinators simply because they were the most common early morning visitors and thus the pollen they carried might have been the successfully fertilizing grains. At the Waller Field site, hummingbirds are Chrysolampsis mosquitus (primarily), Anthracothorax nigrocollis, and very occasionally other species. At the Arima Valley site, hummingbirds are Amazilia tobaci,

Chlorestes notatus, and Amazilia chionopectus (very occasionally others).

11. Isertia wilhelminensis Steyerm.

Isertia wilhelminensis Steyerm., Mem. New York Bot.

Gard. 17(1): 296. 1967. TYPE: SURINAM. SARAMACCA:

Wilhelmina Gebergte, on summit of Frederik Top, 3 km

SE of Juliana Top, alt. 1050 m, 22 Aug 1963, H. S.

Irwin, G. T. Prance, T. R. Soderstrom & N. Holmgren

54949 (HOLOTYPE: NY!; ISOTYPES: NY!, VEN!).

Small tree to 10 m tall, the branchlets subrotund or quadrangular, hirtellous to glabrescent. Leaves with blades subcoriaceous, elliptic to ovate, 24-47 x 12-21 cm, cuspidate at apex, the cusp to 5 cm long, rounded or acute at base, glabrous above, hirtellous beneath; midrib strigulose and prominulous above, hirtellous and prominent beneath; primary vein 12-22 pairs, impressed and strigulose above, prominulous and hirtellous beneath; petiole 20-55 x 2-3 mm, tomentose; stipules 4, interpetiolar, lanceolate, ca 20 mm long, ciliolate.

Inflorescence ovoid, 6-15 x 4-6 cm, with secondary rachises of compound 11-flowered dichasium, the ultimate branches having scorpioid cymes of 2 flowers, the secondary rachises spreading at ca 45 degree angles from primary rachis, subtended by lanceolate cymbriform bracteoles, these strigulose with ciliolate margins.

Flowers: calyx cup-shaped, 4-6 x 4-5 mm, glabrous inside but with patches of red squamose cells near mouth, stri-gulose outside, indistinctly 4-lobed, the lobes with apices truncate or subtruncate; corolla tube ca 27 mm long (immature), glabrescent outside, villous inside around mouth, red, orange, or yellow, the lobes ovate to subovate, 3 x 1 mm; stamens unknown; ovary 5-celled; style unknown. Fruit a pyrene, subglobose, 5-5.5 mm diam., smooth and glabrous; seeds ca 1.1 mm long.

Distribution: Wilhelmina Gebergte in Surinam and in Brazil near the frontier with French Guiana and Surinam (Map 7).

Representative specimens examined: BRAZIL. PARA: Point de Trijonction-Mitaraka, km 6.5, Sastre 1600 (P, VEN). SURINAM. SARAMACCA: Wilhelminagebergte, Stahel 410 (U).

12. Isertia longifolia (Hoffsgg. ex Roemer & Schultes)

K. Schum.

Psychotria longifolia Hoffsgg. ex Roemer & Schultes,

Syst. Veg. 5: 190. 1819. Isertia longifolia K. Schum.,
Mart. Fl. bras. 6(6): 288. 1889. TYPE: BRAZIL. PARA:
Herb. Kunth ex Willd. no. 4072 (HOLOTYPE: B, photo F!,
neg. no. 281).

Allemaõa longifolia Hoffsgg. ex Schldl., Linnaea 28:

511. 1856, in synon.

Shrub or small tree to 12 m tall, 15 cm diam., the branchlets quadrangular, glabrous. Leaves with blades subcoriaceous, oblanceolate, 17-45 x 7-16 cm, cuspidate at apex, the cusp 0.5-3.5 cm long, acuminate to attenuate at base, glabrous on both surfaces; midrib glabrous, prominulous above, prominent beneath, especially proximally; primary veins 15-20 pairs, prominulous above and beneath, generally glabrous but occasionally sparingly setose to short tomentose in small patches at juncture of midrib and primary veins beneath; petiole 35-70 x 2-4 mm, glabrescent; stipules 2, intrapetiolar, ca 5 mm long, widely ovate or triangular, glabrous with ciliolate margins. Inflorescence slightly pyramidal or more commonly cylindrical, 5-16 (25) x 3-5 (7) cm, with secondary rachises of a compound 7-flowered dichasium, the ultimate branches having a simple dichasium of 3 flowers, the secondary rachises spreading at ca 90 degree angles from primary rachis, glabrous or with small patches of tomentum, 10-15 x 1-2 mm, subtended by very widely ovate, cymbriiform, ciliate bracteoles ca 1 m long. Flowers: calyx red, shallow cup-shaped, 3-5 x 4-5 mm, glabrous inside but with small patches of red squamose cells near mouth, glabrescent outside, indistinctly 4-5-lobed with short, scattered cilia on margin; corolla tube pink, 9-13 mm long, glabrous outside, with copious yellow-villous pubescence down to within 1-2 mm from

base within, the lobes 5-6, white, lanceolate to ovate, cucullate at apices; stamens 5-6, the anthers narrowly oblong, 4.5-6.5 mm long, acuminate at apex, the filaments ca as long as anthers; ovary (5) 6 (7)-celled; style 7-8 mm long, the stigma 6-lobed, the lobes narrowly oblong, 2-2.5 mm long. Fruit a pyrene, spheroid to broadly ellipsoid, ca 7 mm diam., glabrous; seeds 1-1.2 mm long.

Distribution: restricted to the lower Amazon basin in Pará and Amapá, Brazil. Glaziou 9902 from Rio de Janeiro is probably a pirated collection and it does not represent a disjunct population (Wurdack, 1970). (Map 6).

Representative specimens examined: BRAZIL. AMAPA: Munguba, Perimetral Norte, 28 km E of Agua Fria, 20 km W of Campo Verde, Austin et al. 7204 (NY, UB, others to be distributed); Rio Araguari, Pires et al. 50704 (NY). PARA: Utinga, forest reserve for watershed of Belém, 1-2 km N of Belém, Archer 7610 (NY, US); Ilha de Mosqueiro near Pará, Killip & Smith 30654 (F, NY, US); Mun. Benevides, Faz. Marata, ca 30 km ENE of Belém on road to Benfica, Plowman et al. 8093 (F, MO, NY, UB); Mun. Paragominas, Belém-Brasilia hwy. (BR010); 17 km S of Ligação do Pará near km 1509, Plowman et al. 9452 (F, GH, MO, NY, UB, US); BR22, Capanema to Maranhão, km 98, Prance & Pennington 1910 (MO, NY, U). RIO DE JANEIRO: Quinta de São Christovão, Glaziou 9902 (P).

Isertia longifolia appears to be fairly common within

its restricted range. Most collections come from disturbed, secondary terra firme or várzea forests. Archer 7610 reports the common name "abiurana."

13. Isertia spiciformis DC.

Isertia spiciformis DC., Prodr. 4: 437. 1830. TYPE: FRENCH GUIANA: Cayenne, Patris s.n. (HOLOTYPE: G-DEL, photo F! neg. no. 6652).

Isertia commutata Miq., Stirp. Surin. Sel. 172. 1851. TYPE: SURINAM. BROKOPONDO: in sylvis reb. inter. ad fl. Surinam pr. Stationem Victoriam, Apr 1846, Kappler 1873 (LECTOTYPE: U!, herein designated; ISOLECTOTYPE: M!).

Isertia bullata K. Schum., Mart. Fl. bras. 6(6): 286. 1889. TYPE: BRAZIL. MARANHAO: habitat in provincia Maranhão, 1841, Gardner 6036 (LECTOTYPE: G-DEL, herein designated, photo F! neg. no. 25666; ISOLECTOTYPE: K!).

Isertia viscosa Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 260. 1922. TYPE: BRAZIL. PARA: Velha Pobre, 1 Jul 1919, Ducke s.n., RB accession number 15529 (HOLOTYPE: RB; ISOTYPES: U!, US!).

Isertia pterantha Bremek., Brittonia 8: 242. 1957. TYPE: FRENCH GUIANA: Montagne de Kaw, 11 Dec 1954, Cowan 38703 (HOLOTYPE: NY!; ISOTYPE: U!).

Shrub or small tree to 10 m tall, the branchlets subrotund or quadrangular, strigose to glabrescent. Leaves with blades membranaceous to subcoriaceous, obovate to ovate, 14-37 (47) x 5-22 cm, cuspidate at apex, the cusp 2-5 cm long, acute to rotund or decurrent at base, glabrous or scabrous above, glabrescent beneath; midrib strigose to glabrescent and prominulous above, strigulose to tomentose and prominent beneath; primary veins 19-21 pairs, planar and strigulose to glabrous above, prominulous and hispid to strigulose beneath; petiole 10-50 x 1-3 mm, glabrous to tomentose; stipules 2, intrapetiolar, triangular, 8-9 mm long, margin ciliolate. Inflorescence narrowly ellipsoid, 5-19 x 5-11 cm, with secondary rachises of a single flower, or of a simple 3-flowered dichasium, or of a simple 5-flowered dichasium, the ultimate branches having scorpioid cymes of 2 flowers, the secondary rachises lax and spreading at various angles from primary rachis, strigulose to tomentose, 3-25 x 1-2 mm, subtended by ovate to triangular cymbriform bracteoles, these glabrescent to puberulent with ciliolate margin, 2-3 mm long. Flowers: calyx red, cup-shaped, ca 3 x 3 mm, glabrous inside but with patches of red squamose cells near mouth, strigulose and somewhat rugulose outside, 4-lobed, the lobes 1 mm long, acute with ciliolate margins; corolla tube reddish, 32-45 mm long, strigulose outside, glabrous inside but

with copious yellow pubescence near mouth, the lobes 6, yellow, oblong, 3-6 mm long, villous pubescent inside, acute and cucullate at apices; stamens 6, the anthers narrowly oblong, ca 5 mm long, the filaments 3-4 mm long; ovary 5-6-celled; style glabrous, 35-40 mm long, the stigma 5-6-lobed, the lobes narrowly oblong, 2-3 mm long. Fruit a pyrene, obloid, 4-6 mm diam., smooth and strigulose or glabrescent; seeds 1-1.3 mm long.

Distribution: French Guiana, Surinam, and northeast Amazonian Brazil (Map 5).

Representative specimens examined: BRAZIL. MARANHAO: ca 50 km from Santa Luzia on hwy. to Açailandia, Daly et al. D727 (NY, others to be distributed); Maracassumé River region, Candido Mendes, Frões 1711 (F, GH, NY, U, US). PARA: island of Marajó, Kauffmann 32 (F). FRENCH GUIANA: Saül, Boom & Mori 1869 (CAY, NY); Rivière Petite Ouaiqui, de Granville 1915 (CAY, NY, U); Rivière Grand Inini, de Granville B-3690 (CAY); Route Acarouany, Sastre & Sastre 306 (CAY, NY, P, U, VEN). SURINAM. BROKOPONDO: between villages Afobaka and Brownsveg, Donselaar 2405 (U). MAROWIJNE: Rikanau prope Moengo, Lindeman 6063 (U); circa portum aeronaut. ad flum. Oelemari, Wessels Boer 1124 (F, NY, U, VEN).

Within this species one finds quite a range of variation in leaf texture and shape, in the extent of branching of secondary inflorescence rachises, and in

pubescence. Schumann (1889) recognized I. bullata as distinct from I. spiciformis based on leaf blade shape and texture (obovate and bullate in the former, obovate-oblong to lanceolate and non-bullate in the latter). Isertia bullata is said to have a more branched inflorescence than I. spiciformis. Also, there is an apparent geographic separation of these two species; the collections from Brazil generally conform to I. bullata, while those from Surinam and French Guiana conform to I. spiciformis. It is possible that further study will support the recognition of both of these species, but based on my work to date there is no justification for keeping them separate. The entire range of leaf blade shape and texture, and of inflorescence branching can be found in collections from Surinam and French Guiana.

The argument for maintaining I. pterantha is rather convincing when that species is contrasted only with I. rosea or I. parviflora; Steyermark (1967), for example, listed ten ways in which I. pterantha is distinct from I. rosea. However, when I. pterantha is compared with I. spiciformis, the distinctions of the former are quickly blurred. In fact, collections referable to I. pterantha generally appear to represent morphologically diverse introgressants between I. rosea and I. spiciformis.

If further research can demonstrate the hybrid origin of these plants, and if reasonably consistent morphological characters can be found to satisfactorily circumscribe these species, then perhaps I. pterantha should be maintained as a species. For the present I prefer to lump these collections with I. spiciformis, clearly the species with which they are most closely related. The following collections of I. spiciformis suggest introgression with I. rosea: de Granville 1828 & 1915; Oldeman B-3557, B-4155, & B-4287; Wessels Boer 1124.

14. Isertia rosea Spruce ex K. Schum.

Isertia rosea Spruce ex K. Schum., Mart. Fl. bras.

6(6): 284. 1889. TYPE: BRAZIL. AMAZONAS: prope Panure ad Rio Vaupes, Spruce 2894 (LECTOTYPE: K!; ISOLECTOTYPES: BR!, K!, P!).

Isertia commutata Sagot, Pl. Exicc. no. 308, nomen nudum, non Miq., 1851.

Shrub or small tree to 13 m tall, 20 cm diam., the branchlets subrotund, glabrescent or pulverulent. Leaves with blades membranaceous, oblanceolate to obovate, 19-48 x 6-17 cm, cuspidate at apex, the cusp 1.5-2 cm long, acute to acuminate or attenuate at base, glabrous above, glabrous beneath or rarely short ciliate and proximally prominent beneath; primary veins 12-19 pairs, prominent above and beneath, glabrous or rarely ciliolate

beneath; petiole 15-35 (50) x 1.5-2 mm, glabrescent; stipules 2, intrapetiolar, widely depressed ovate, ca 3 mm long, margin with several low teeth. Inflorescence ellipsoid to ovate, 8-14 x 7-8 cm, with secondary rachises of a compound 11-flowered dichasium, the ultimate branches having scorpioid cymes of 2 flowers, the secondary rachises spreading at ca 45 degree angles from primary rachis, glabrescent to ciliolate, 15-20 x 1.5-2.5 mm, subtended by widely ovate, cymbriform bracteoles, these glabrescent to puberulent with aciliolate margin, ca 1.5 mm long. Flowers: calyx red, cup-shaped, ca 3.5 x 3.5 mm, mostly glabrous but with small patches of red squamose cells inside near mouth, glabrescent and smooth or slightly rugose outside, indistinctly 4-lobed; corolla reddish-violet proximally, grading to pink distally, the tube 35-50 mm long, with copious pinkish-purple- or yellow-villous pubescence inside restricted to around mouth, mostly glabrous but rarely puberulent outside, the lobes 5-6, oblong, 6-8 mm long, acute and cucullate at apices; stamens 6, the anthers narrowly oblong, 5.5-6 mm long, the filaments lamninar, ca as long as anthers; ovary (5) 6-celled; style 29-42 mm long, the stigma 4-6-lobed, the lobes narrowly oblong, 2-3 mm long. Fruit a pyrene, spheroidal, ca 8.5 mm diam., smooth, glabrous; seeds 1.2-1.3 mm long.

Distribution: lowland Amazonian regions of Brazil, Colombia, Peru, and Venezuela at elevations of 25-300 m (Map 7).

Representative specimens examined: BRAZIL. ACRE: tract from km 20, road Cruzeiro do Sul-Japiim to Vila Maitá, Prance et al. 2862 (NY, US). AMAZONAS: Manaus, Campos Sales, km 10, estrada da Forquilha, Chagas 67 (F, US); above mouth of Rio Brancinho, Prance et al. 17725 (MO, NY, U); along margin of Rio Cauaburí between Maturaca and Rio Yá, N. Silva & Brazão 60958 (F, MO, NY). PARA: Belém, area de Pesq. Ecológicas do Guama, Schubert 2233 (US). COLOMBIA. AMAZONAS: Río Igara-Parana (affl. Río Putumayo), corr. La Chorrera, Gasche & Desplats 179 (P, US, VEN); Río Putumayo, carretera entre Caucaya (Puerto Leguizamo) y La Tagua, Schultes 3744 (VEN). VAUPES: Río Piraparana, environs of Catholic mission of San Miguel, downstream on the Canon Colorado, Davis 138 (F, GH); Río Apaporis, entre el Río Pacoa y el Río Kananari, Soratama, Schultes & Cabrera 13211 (F, U, US); San Felipe and vicinity (below confluence of Río Guainia and Río Casiquiare), Schultes et al. 18302 (F, U, US); Mitú and vicinity, along stream near base of Cerro de Mitú, Zarucchi & Balick 1761 (F, GH, US). PERU. LORETO: Iquitos, Asplund 14395 (NY, US); ca 6 km up Río Itaya from Iquitos, Croat 19057 (F, MO, NY, U); Florida, Río Putumayo at mouth of Río Zubineta, Klug 2269 (F, GH, MO, NY, US); Mishuyacu,

near Iquitos, Klug 2523 (F, GH, NY, U); Maynas, Dtto. Alto Nanay, trail from mouth of Quebrada Anguilla to interior, McDaniel et al. 21512 (F); Coronel Portillo, Dtto. Calleria, carretera a Tournavista, km 7, Schunke 5253 (F, GH, NY); Amazon River near Iquitos, Williams 8239 (F, US). VENEZUELA. AMAZONAS: Alto Orinoco, entre Ocamo y Mavaca, a lo largo del Río Orinoco, Aristeguieta & Lizot 7427 (F, MO, NY, U, VEN); alrededor de Macuruco, Río arriba de Santa Barbara del Orinoco, Berry 687 (MO, NY, VEN); Depto. Atures, carretera Puerto Ayacuho-Sanariapo, desde Puerto Ayacucho hasta el km 35 hacia Sanariapo, Bunting et al. 3496 (U, VEN); 1 km E of San Carlos de Río Negro, ca 30 km S of confluence of Río Negro and Brazo Casiquiare, Liesner 7131 (MO); Esmeralda, upper Orinoco, Williams 15394 (F, US).

The following common names have been recorded for I. rosea: Colombia, "erilloquei" or "fizido reigai," (Gasche et al. 179); Peru, "isico-ey," (Klug 2269); Venezuela, "carisillo," (Liesner 7131), "caruto," (Liesner 6383).

Isertia rosea is a common species of poorly drained soils of the Amazon and Orinoco basins. Generally, the inflorescences are completely glabrous, but in some specimens (e.g., Schultes & Cabrera 15012) the axes are irregularly puberulent. One collection (Ducke 101, 12 Jun 1935) is especially notable due to its pubescent leaf

undersurfaces and corolla tubes. None of these variations in pubescence can be correlated with other characters or geographic distribution, however, and are not consistent enough in themselves to warrant the recognition of varieties. I cannot substantiate Bremekamp's (1957) claim that I. rosea has a 4-locular ovary. In the specimens I have dissected the ovary is 5-6-locular.

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Numbers in parentheses following each collector refer to the following taxa of Isertia: (1) I. krausei, (2) I. reticulata, (3) I. verrucosa, (4) I. laevis, (5) I. scorpioides, (6) I. pittieri, (7) I. hypoleuca, (8) I. coccinea, (9a) I. haenkeana var. haenkeana, (9b) I. haenkeana var. mirandensis, (10) I. parviflora, (11) I. wilhelminensis, (12) I. longifolia, (13) I. spiciformis, (14) I. rosea.

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2937 (7); 3068 (10); 3201 (10).

Smith, C. 3285 (9a); 3303 (9a); 3441 (4).

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4050 (10); 4407 (10).

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Splitgerber 650 (10); 741 (13); 935 (13).
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3633 (10); 3878 (4); 4846 (4).
Stahel 410 (11); 419 (8); 3037 (10).
Standley 24721 (9a); 26832 (9a); 26940 (9a); 27011 (9a);
27741 (9a); 28111 (9a); 28605 (9a); 29753 (9a);
30072 (9a); 30340 (9a); 41056 (9a); 72561 (9a);
72698 (9a).
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Steyermark 42040 (9a); 56743 (9a); 60604 (7); 75410 (7);
87079 (9b); 87612 (10); 90138 (9b); 90579 (7);
90918 (10); 96524 (9a); 97527 (9b); 99924 (9a);
99983 (9a); 102693 (3); 106577 (9a); 107177 (7);
113877 (14); 116627 (9b); 117782 (7); 119026 (4);
119557 (9a); 120432 (9a).
Stier 7 (9a); 201 (9a).
Stimson s.n. (9a); 5062 (9a); 5100 (9a); 5254 (4).
Sucre 8 (9a); 237 (4).
Sullivan 85 (9a).
Swabey 12236 (10).
Sytsma 1024 (9a); 1280 (4).
Tamayo 1716 (9a).

Tejera 122 (9a).
Terán 3487 (4); 5034 (3).
Terry 1404 (9a).
Tessmann 3535 (14); 4432 (4).
Teunissen 14115 (10).
Thomas 2425 (10).
Tillett 45022 (7); 45396 (7); 45444 (7).
Toro 583 (4).
Torrea 383 (4).
Tresling 145 (8).
Triana s.n. (9a); 1838 (4); 1839 (6); 1840 (4); 3311
(4); 3324 (9a).
Tutin 654 (7).
Tyson 1144 (9a); 2040 (9a); 2196 (4); 3330 (4); 4051 (4);
4551 (4); 5527 (9a); 5537 (5); 6842 (9a).
Ule 5488 (4); 5846 (7); 8338 (10).
Uribe 2623 (9a); 3763 (4).
Utley 4895 (4); 4946 (9a).
Vaillant s.n. (7).
Valverde 1384 (4).
Vareschi 7583 (10).
Vargas 7775 (4); 15359 (4).
Vergara 33 (9a).
Versteeg 617 (8).
Viera 856 (7).
Vogel 147 (4).
Wachenheim 24 (7); 62 (13); 64 (13).

Weberbauer 7054 (4); 7066 (1).

Webster 9656 (10); 16424 (9a).

Wedel 580 (4); 1937 (4); 2488 (9a); 2539 (9a).

Wessels Boer 671 (10); 1124 (13); 1140 (8).

Wetmore 41A (9a).

White, J. 67 (4).

White, P. 141 (9a).

Whitmore 56 (9a).

Whitton 336 (7).

Wilber 11140 (4).

Williams, L. 41 (12); 1111 (14); 1159 (14); 1743 (7);
2071 (7); 2200 (7); 4418 (4); 7856 (4); 8239 (14);
11743 (10); 11847 (10); 13331 (10); 13402 (10);
14141 (3); 14422 (14); 14501 (14); 15034 (14);
15148 (14); 15394 (14); 15649 (14); 15877 (10);
15984 (14).

Williams, R. 754 (9a); 1480 (2); 1563 (2).

Witherspoon 8692 (9a).

Woodson 964 (9a); 1333 (9a); 1366 (9a).

Woodworth 358 (9a).

Wright 2665 (9a).

Wullschlaegel 241 (10).

Wurdack 266 (10); 40936 (10); 43553 (14).

Zarucchi 1088 (4); 1164 (14); 1177 (14); 1602 (14).

Zelaya 430 (9a).

Zuccarini s.n. (7).

LIST OF LOCAL NAMES

abiurana (Archer)	<u>I. longifolia</u>	Brazil
aieato (Bena)	<u>I. coccinea</u>	French Guiana
asaquíro (Mexia)	<u>I. laevis</u>	Peru
asquiru (Klug)	<u>I. laevis</u>	Peru
bois pian (BAFOG)	<u>I. coccinea</u>	French Guiana
caaynum (Berlin)	<u>I. laevis</u>	Peru
café negro (Williams)	<u>I. parviflora</u>	Venezuela
cagnum (Kayap)	<u>I. laevis</u>	Peru
canelito (Croat)	<u>I. haenkeana</u>	Panama
carisillo (Liesner)	<u>I. rosea</u>	Venezuela
chaparrillo		
rebalseo (Steyermark)	<u>I. hypoleuca</u>	Venezuela
coralito (Steyermark)	<u>I. haenkeana</u>	Venezuela
coralleira (Krukoff)	<u>I. hypoleuca</u>	Brazil
corolillo (Pennell)	<u>I. haenkeana</u>	Colombia
carrutillo		
morichalero (Steyermark)	<u>I. parviflora</u>	Venezuela
caruto (Liesner)	<u>I. rosea</u>	Venezuela
erilloquei (Gasche)	<u>I. hypoleuca</u>	Colombia
fizido reigai (Gasche)	<u>I. rosea</u>	Colombia
isico-ey (Klug)	<u>I. rosea</u>	Peru
jaboncillo (Archer)	<u>I. pittieri</u>	Colombia
jambo de mata (Prance)	<u>I. hypoleuca</u>	Brazil
kandrahoedoe (Lanjouw)	<u>I. coccinea</u>	Surinam

lyrio do matto (Krause)	<u>I. hypoleuca</u>	Brazil
mamayahooka (Kribs)	<u>I. hypoleuca</u>	Guyana
manáse-yek (Steyermark)	<u>I. hypoleuca</u>	Venezuela
masamorro (Solís)	<u>I. pittieri</u>	Ecuador
panga panga (Mennega)	<u>I. hypoleuca</u>	Surinam
pin-pin (Lanjouw)	<u>I. coccinea</u>	Surinam
sacha rifari (Plowman)	<u>I. hypoleuca</u>	Peru
takoewiden (Wessels Boer)	<u>I. spiciformis</u>	Surinam
tsagnum (Ancuash)	<u>I. laevis</u>	Peru
tsánum (Kujikat)	<u>I. laevis</u>	Peru
tukuí-mariru (Cardona)	<u>I. hypoleuca</u>	Venezuela
velero (Steyermark)	<u>I. haenkeana</u>	Venezuela

LITERATURE CITED

- Aublet, J.B.C.F. 1775. Guettarda. In: Histoire des plantes de la Guiane française 1: 317-320, pl. 123.
- Baillon, H.E. 1880. Isertia. In: Histoire des plantes 7: 257-546.
- Bartlett, H.H. 1907. Isertia deamii Bartlett. Proc. Amer. Acad. 43: 59.
- Bentham, G. 1841. Brignolia and Isertia. In: J. Bot. (Hooker) 3: 219-220.
- Bentham, G. & J.D. Hooker. 1873. Isertia and Cassupa. In: Genera plantarum 2: 65.
- Bolten, A.B. & P. Feinsinger. 1978. Why do hummingbird flowers secrete dilute nectar? Biotropica 10(4): 307-309.
- Bremekamp, C.E.B. 1934. Isertia. In: Notes on the Rubiaceae of Surinam. Recueil Trav. Bot. Néerl. 31: 263.
- _____. 1957. Rubiaceae. In: R.C. Cowan & Collaborators. New species and new records of plants in Guiana. Brittonia 8(4): 241-245.
- Brizicky, G.K., W.L. Stern & L. Chambers. 1958. A collection of woody plants from Panama. Trop. Woods 109: 61-80.
- Candolle, A.P. de. 1830a. Cassupa H. & B. In: Prodromus systematis naturalis regni vegetabilis 4: 373.
- _____. 1830b. Isertia Schreb. In: Prodromus systematis naturalis regni vegetabilis 4: 437.

- _____. 1830c. Brignolia DC. In: Prodrum
systematis naturalis regni vegetabilis 4: 444.
- Chang, Y.-P. 1951. Anatomy of wood and bark in the
Rubiaceae. Unpublished Doctoral Dissertation, Univ.
of Michigan, Ann Arbor. 333 pp.
- Croat, T.B. 1978. Flora of Barro Colorado Island.
Stanford: Stanford Univ. Press. 943 pp.
- Ducke, A. 1922. Isertia viscosa Ducke. Arch. Jard. Bot.
Rio de Janeiro 3: 260.
- _____. 1925. Isertia glabra Ducke. Arch. Jard.
Bot. Rio de Janeiro 4: 179.
- Dwyer, J.D. 1980. 49. Isertia. In: Family 179.
Rubiaceae--Part 1. In: R.E. Woodson, Jr. & W.
Schery & Collaborators. Flora of Panama. Ann.
Missouri Bot. Gard. 67(1): 246-250.
- Eldredge, N. & J. Cracraft. 1980. Phylogenetic patterns
and the evolutionary process. New York: Columbia
Univ. Press.
- Endlicher, S.L. 1838a. 3231. Brignolia. In: Genera
plantarum 6-7: 547.
- _____. 1838b. 3234. Isertia. In: Genera plantarum
6-7: 547.
- _____. 1838c. 3311. Cassupa. In: Genera plantarum
8: 563.
- Foster, R.C. 1958. Isertia. In: A catalogue of the
ferns and flowering plants of Bolivia. Contr. Gray
Herb. 184: 194.

- Gaertner, C.F. von. 1806. Isertia. In: Supplementum
carpologicae 1(2): 57-128.
- Gmelin, J.F. 1791. Isertia. In: Syst. nat. 2: 567.
- Grisebach, A.H.R. 1864. Isertia. In: Flora of the
British West Indian Islands. London: Lorell
Reeve & Co. 789 pp.
- Haffer, J. 1982. General aspects of the refuge theory.
In: G.T. Prance, ed. Biological Diversification in
the Tropics. 714 pp.
- Humboldt, F.W.H.A. von & A.J.A. Bonpland. 1806. Cassupa.
In: Plantae aequinoctiales 1: 42-45, pl. 12.
- Janssonius, H.H. 1926. Mikrographie des Holzes der auf
Java vorkommenden Baumarten. IV. Leiden.
- Jussieu, A.H.L. de. 1820. Cassupa H. & B. Mém. Mus.
Hist. Nat. 6: 389-399.
- Kirkbride, J.H., Jr. 1982. Rubiaceae types in the Triana
collections in the Instituto de Ciencias Naturales, Univ.
Nacional, Bogota, Colombia. Taxon 31(2): 303-332.
- Kirkbride, M.C.G. 1979. Review of the neotropical
Isertieae (Rubiaceae). Brittonia 31(3): 313-332.
- Koek-Noorman, J. 1972. The wood anatomy of Gardenieae,
Ixoreae, and Mussaendeae (Rubiaceae). Acta Bot.
Néerl. 21: 301-320.
- Krause, K. 1925. Isertia hoehnei Krause. Archiv. Bot.
Estado São Paulo 1: 115.
- Kribs, D.A. 1928. The Persaud collection of British
Guiana woods. Trop. Woods 13: 7-46.

- Meacham, C.A. 1980. Phylogeny of the Berberidaceae with an evaluation of classifications. Syst. Bot. 5(2): 149-172.
- Meisner, C.F. 1838. Cassupa, Isertia, Brignolia. In: Plantarum vascularium genera 5: 161-164.
- Metcalf, C.R. & L. Chalk. 1950. 164. Rubiaceae. In: Anatomy of the Dicotyledons. Vol. II. Oxford: Clarendon Press. pp 759-776.
- Miquel, F.A.W. 1843. 29. Bruinsmania. Linnaea 17: 72-74.
- _____. 1844. Isertia flava Miq. Linnaea 18: 613.
- _____. 1851a. Isertia. In: Stirpes surinamensis selectae. pp 169-172.
- _____. 1951b. Bruinsmania. In: Stirpes surinamensis selectae. pp 173-174.
- Prance, G.T. 1982. Forest refuges: evidence from woody angiosperms. In: G.T. Prance, ed. Biological Diversification in the Tropics. 714 pp.
- Radford, A.E., W.C. Dickison, J.R. Massey & C.R. Bell. Vascular Plant Systematics. New York: Harper & Row. 891 pp.
- Rafinesque, C.S. 1820. Tableau analytique des ordres naturels, familles naturelles et genres, de la classe Endogynie, sous classe Corisantherie. Ann. Gén. Sci. Phys. 6: 76-89.
- Record, S.J. 1927. The Editor again visits Central America. Trop. Woods 10: 1-47.

- _____. 1928. Contributions to the arborescent
flora of western Panama. Trop. Woods 16: 9-35.
- _____. 1929. Trees and shrubs collected by F.C.
Englesing in northeastern Nicaragua. Trop. Woods
17: 18-38.
- Richard, A. 1830a. Isertia Schreb. In: Mémoire sur la
famille des Rubiacées. 224 pp, 15 pl.
- _____. 1830b. Cassupa H. & B. In: Mémoire sur la
famille des Rubiacees. 224 pp, 15 pl.
- Roemer, J.K. & J.A. Schultes. 1819. Psychotria longifolia
Hoffsgg. Syst. Veg. 5: 190.
- Rusby, H.H. 1896. Isertia reticulata Britton. Mem.
Torrey Bot. Club 6(1): 46.
- Schlechtendal, D.F. L. von. 1856. Psychotria longifolia
Hoffsgg. Linnaea 28: 511.
- Schmid, R. 1982. Sonication and other improvements on
Jeffrey's technique for macerating wood. Stain
Tech. 57 (5): 293-299.
- Schreber, J.C.D. 1789. 602. Isertia. In: Genera
plantarum 1: 1-379.
- Schumann, K. 1889. Trib. XVI. Mussaendeae Hook. fil.
In: Rubiaceae, trib. VII-XIX. In: C.F.P. von
Martius. Flora brasiliensis 6(6): 279-318.
- _____. 1891. Isertia and Cassupa. In: H.G.A
Engler & K.A.E. Prantl. Die natürlichen
Pflanzenfamilien 4, Abt. 4: 1-96.

- _____. 1907. Cassupa. Bot. Jahrb. Syst. 40: 148.
- _____ & K. Krause. 1908a. Cassupa. Verh. Bot. Vereins Prov. Brandenburg 50: 98.
- _____ & _____. 1908b. Isertia and Cassupa. Bot. Jahrb. Syst. 40: 321-322.
- Smith, J.D. 1916. Isertia deamii var. stenophylla. Bot. Gaz. 61: 374.
- Sprague, T.A. 1905. Isertia. Trans. & Proc. Bot. Soc. Edinb. 22: 434.
- Standley, P.C. 1914. Cassupa pittieri. Contr. U.S. Natl. Herb. 17(5): 445.
- _____. 1916. Cassupa panamensis. Contr. U.S. Natl. Herb. 18: 135.
- _____. 1926. Isertia. In: Trees and Shrubs of Mexico. Contr. U.S. Natl. Herb. 23(5): 1313-1721.
- _____. 1929. Isertia. Publ. Field Columbian Mus., Bot. Ser. 4(8): 277.
- _____. 1930a. 31. Cassupa H. & B. and 32. Isertia Schreb. In: The Rubiaceae of Colombia. Publ. Field Columbian Mus., Bot. Ser. 7(1): 44-46.
- _____. 1930b. Isertia leiantha. Publ. Field Columbian Mus., Bot. Ser. 8(3): 163.
- _____. 1930c. A second list of the trees of Honduras. Trop. Woods 21: 9-41.
- _____. 1931a. 14. Isertia Schreb. In: The Rubiaceae of Ecuador. Publ. Field Columbian Mus.,

- Bot. Ser. 7(2): 211.
- _____. 1931b. 24. Isertia. In: The Rubiaceae of Bolivia. Publ. Field Columbian Mus., Bot. Ser. 7(3): 283.
- _____. 1931c. Creatantha and Isertia. In: Studies of American plants V. Publ. Field Columbian Mus., Bot. Ser. 8(5): 344-346.
- _____. 1931d. 30. Isertia. In: The Rubiaceae of Venezuela. Publ. Field Columbian Mus., Bot. Ser. 7(4): 384-385.
- _____. 1932. Vernacular names of trees of the Tapaj6z River, Brazil. Trop. Woods 29: 6-13.
- _____. 1936a. 36. Isertia. In: The Rubiaceae of Peru. Pub. Field Columbian Mus., Bot. Ser. 8(6): 77-80.
- _____. 1936b. Isertia krausei Standl. Publ. Field Mus. Nat. Hist., Bot. Ser. 11(5): 216.
- _____ & L.O. Williams. 1975. Isertia Schreber. In: Flora of Guatemala. Fieldiana, Bot. 24, 11(1-3): 116-117.
- Steudel, E.G. 1840. Isertia breviflora Mart. In: Nomenclator botanicus (ed. 2) 1: 825.
- Steyermark, J.A. 1967. Isertia Schreber. In: Rubiaceae. In: B. Maguire & Collaborators. The Botany of the Guayana Highland--Part VII. Mem. New York Bot. Gard. 17(1): 291-299.

- _____. 1974. Isertia Schreb. In: Rubiaceae. In:
T. Lasser, ed. Flora de Venezuela 9(1): 461-478.
- _____ & O. Huber. 1978. Isertia. In: Flora del
Avila. Madrid: INCAFO. 971 pp.
- Triana, J.J. 1858. Cassupa. Ann. Sci. Nat. (Paris) Ser.
IV. 9: 44.
- Vahl, M.H. 1798. Isertia. In: Eclogae Americinae 2:
27-29.
- Wagner, W.H., Jr. 1980. Origin and philosophy of the
groundplan-divergence method of cladistics. Syst.
Bot. 5(2): 173-193.
- Watrous, L. & Q. Wheeler. 1981. The outgroup method of
phylogeny reconstruction. Syst. Zool. 30: 1-16.
- Wiley, E.O. 1981. Phylogenetics: The Theory and
Practice of Phylogenetic Systematics. New York:
John Wiley and Sons. 439 pp.
- Williams, L. 1941. Forests of the Venezuelan Guiana.
Trop. Woods 68: 13-40.
- _____. 1947. Forests of the upper Orinoco. Trop.
Woods 91: 17-38.
- Wurdack, J.J. 1970. Erroneous data in Glaziou collections
of Melastomataceae. Taxon 19: 911-913.