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Systematics of *Erisma* (Vochysiaceae)

Kawasaki, Maria Lúcia, Ph.D.

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300 N. Zeeb Rd.
Ann Arbor, MI 48106

SYSTEMATICS OF *ERISMA* (VOCHYSIACEAE)

by

MARIA LÚCIA KAWASAKI

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The New York Botanical Garden

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Abstract

SYSTEMATICS OF ERISMA (VOCHYSIACEAE)

by

Maria Lúcia Kawasaki

Advisor: Dr. Scott A. Mori

Systematic studies on Erisma, one of the seven genera of the tropical family Vochysiaceae, are provided in this monograph. Erisma is distinguished from the other genera of the family by the inferior and unilocular ovary, the deciduous spurred-sepal, and the samaroid, four-winged fruits.

The 16 species of Erisma are tall trees predominantly in terra firme forests of the Amazon region, most of them with a limited distribution. Erisma uncinatum is the most common and widely distributed species of the genus with a range that follows the limits of Amazonia. Erisma arietinum, which is described as a new species from coastal forests of eastern Brazil, represents the first record of the genus outside Amazonia.

A key to the tribes and genera of Vochysiaceae is provided. A key to the species of Erisma, synonymy, descriptions, distribution, habitat, local names, uses, and specimens examined are presented. An overview of morphology and anatomy is provided and patterns of distribution, ecology, and phylogenetic relationships among the genera of Vochysiaceae and species of Erisma are discussed.

Erisma contains some of the most specialized members in the family. Erisma calcaratum, the only species in the genus found in inundated forests and with wingless fruits adapted for dispersal by water, is probably the most specialized member of the genus.

Resumo

SISTEMÁTICA DE ERISMA (VOCHYSIACEAE)

Maria Lúcia Kawasaki

Orientador: Dr. Scott A. Mori

Nesta monografia, são apresentados estudos sistemáticos em Erisma, um dos sete gêneros de Vochysiaceae, uma família de plantas tropicais. Erisma distingue-se dos outros gêneros pelo ovário ínfero e unilocular, pela sépala calcarada decídua, e pelos frutos samaróides, tetra-alados.

As 16 espécies de Erisma são árvores altas predominantemente em matas de terra firme, na maior parte, com distribuição restrita. Erisma uncinatum apresenta o mais amplo padrão de distribuição na área. Erisma arietinum, que é descrita como uma espécie nova das matas costeiras do leste do Brasil, representa o primeiro registro do gênero fora dos limites da região amazônica.

São apresentados uma chave de identificação para os gêneros de Vochysiaceae e para as espécies de Erisma,

sinonímia, descrições, distribuição, habitat, nomes vulgares, usos e espécimes examinados. Um resumo da morfologia e anatomia é fornecido e padrões de distribuição e ecologia, e relações filogenéticas entre os gêneros de Vochysiaceae e entre as espécies de Erisma são discutidos.

Erisma contém alguns dos membros mais especializados da família. Erisma calcaratum, a única espécie do gênero encontrada em matas inundáveis e com frutos sem alas, adaptados à dispersão por água, provavelmente é o representante mais especializado do gênero.

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INTRODUCTION

The family Vochysiaceae comprises seven genera and about 200 Neotropical species. Only the two species of the genus Erismadelphus Mildbraed are found in Africa. In Central and South America, the family occurs in tropical rainforests and savannas, especially those of Brazil.

According to the systems of Cronquist (1981), Takhtajan (1980), and Dahlgren (1980), the Vochysiaceae are included in the order Polygalales and are closely related to the Trigoniaceae. The Vochysiaceae, as here circumscribed, is distinguished from the other families in the order notably by the zygomorphic flowers with a single stamen.

Although some of the species of Vochysiaceae, including species of Erisma Rudge, are among the tallest and most representative trees of the Amazonian rainforests (Spruce, 1908; Ducke & Black, 1953; Kubitzki, 1985; Pires & Prance, 1985), the genus and the family as a whole are not well known. There are few good collections of these large trees (up to 50 m); in particular, species from remote areas are not well represented in herbaria. Ecological and biological aspects are still poorly understood, and a number of

taxonomic controversies at the generic and species level remain unresolved. Furthermore, phylogenetic relationships within the family and the genera have never been analyzed.

The 16 species of Erisma are the only representatives in the Neotropics of the tribe Erismeae of the Vochysiaceae. The species of this tribe, which also includes the two species of the African genus Erismadelphus (Keay & Stafleu, 1952), differ from the species of the Neotropical tribe Vochysieae by the stellate hairs, inferior, unilocular ovary, and indehiscent and winged fruits.

Erisma has been reported to be limited to the Amazon basin and the Guianas (Ducke, 1938; Stafleu, 1954). However, recent collections from the state of Espírito Santo in eastern Brazil have extended the geographic limits of the genus.

The distinctiveness, the reasonably small size, and the restricted geographic distribution of Erisma provide an appropriate starting point towards a better understanding of the taxonomy, geography, and phylogenetic relationships of the Vochysiaceae.

Because of many recent collections, new data are now available for the study of morphological variations within species and of distribution patterns. In this

contribution towards a monograph of the family, I recognize 16 species of Erisma, propose nine new synonyms, and describe one new species from eastern Brazil. The present study, refining the systematics of the group, has the objective of providing an updated taxonomic basis for ecological studies and for the comprehension of phylogenetic relationships.

TAXONOMIC HISTORY

The genus Erisma was established by Rudge in 1805. The type species, E. floribundum Rudge, from French Guiana, is described and illustrated in detail in Rudge's "Plantarum Guianae Rariorum." The author mistakenly interpreted the spurred and larger sepal as a petal. The characteristic winged fruits of most species of Erisma were described for the first time by Poeppig (1832). He based his fruit description on a species with purple flowers, which was probably the widespread Amazonian E. uncinatum.

The second described species of Erisma was E. calcaratum (Link) Warming (1875), from Pará, Brazil, which Link (1820) had described as a species of Qualea Aublet. Qualea calcarata Link had already been recognized as a species of Erisma by Martius (Martius & Zuccharini, 1824), who named it as E. violaceum Martius.

Martius cited Ditmaria Sprengel (1818) and Braya Schultes ex Mart. (Martius & Zuccarini, 1824) in the synonymy of Erisma and included the genus in the Vochysiaceae. The family "Vochysiae", when first described by Hilaire (1820), consisted only of the genera Qualea, Salvertia St. Hilaire, and Vochysia Poiret.

Candolle (1828) recognized three species in Erisma:

E. floribundum, E. violaceum, and a new species, E. nitidum. He included Debraea Roem. & Schult. in the synonymy of the genus and divided the Vochysiaceae into two sections, referring Erisma to a group of species with inferior ovaries and tetramerous flowers. Although Martius (Martius & Zuccarini, 1824) had already interpreted correctly the number of floral structures of the species of Erisma, Candolle described the calyx as tetramerous to pentamerous because of the ambiguous morphology of the larger sepal which is two-lobed and convolute, the outer side sepal-like and the inner side petal-like. The name Erisma was mistakenly interpreted as equivalent to Rixa in Latin, which means dispute. Candolle stated that it referred to the ambiguity of the calyx-lobe which, however, was not mentioned by Rudge (1805) when he described the genus.

Dumortier (1829) separated the genera of Vochysiaceae into two tribes, which are still recognized today: Vochysieae, consisting of the genera with superior ovaries, and Erismeae, consisting of the genera with inferior ovaries.

Four new species of Erisma were described by Warming (1875) in his treatment of the family for Flora Brasiliensis: E. laurifolium, E. japura, E. uncinatum, and E. micranthum. The author mentioned E. maliforme

and E. niveum as dubious species. These two species, described by Dietrich (1831), probably belong to the genus Callisthene Martius.

Ducke, in a series of papers published between 1915 and 1949 on new or poorly known plants from the Brazilian Amazon, described seven new species of Erisma (Ducke, 1925, 1932, 1935, 1938), some of which he later reduced to varieties of previously described species. Ducke was the first author to describe the unusual fruit of E. calcaratum (Ducke, 1922), mentioned earlier by Huber (1910). This species is the only one in the genus with wingless, nut-like fruits.

The last revision of the species of Erisma was made by Stafleu in 1954, in which a total of 16 species and six new varieties were recognized; of these, four species and four varieties were new to science. Subsequent to Stafleu's monograph, a few new species were described (Paula, 1967b; Marcano-Berti, 1986). The genus Erisma has been treated in several floristic studies (Benoist, 1915; Macbride, 1950; Stafleu, 1951; Bernardi & Spichiger, 1981).

MORPHOLOGY AND ANATOMY

Habit

The species of *Erisma* are characteristically emergent or canopy trees reaching up to 45 m high. Species of *Erisma* as well as other species of Vochysiaceae are very often among the tallest trees in Amazonia (Spruce, 1908; Huber, 1910; Ducke & Black, 1953; Kubitzki, 1985; Pires & Prance, 1985). *Erisma laurifolium* was described by Spruce on the label of the type specimen (*Spruce 2889*) as one of the tallest trees he had ever collected. The exceptional height of the trees explains in part the small number of collections for some of the species.

Wood and bark

The wood anatomy of Vochysiaceae has been studied by Quirk (1980), who observed consistent features at the generic level, and also by Chalk and Chattaway (1937), Mennega (1948), IPT (1974), Détienne and Mariaux (1982), and Détienne & Jaccquet (1983). Among all genera of Vochysiaceae, included phloem is present only in *Erisma* and *Erismadelphus*. These two genera also have banded parenchyma in common (Figs. 1A, 1C, 1E).

However, in Erisma, the rays are multiseriate and uniseriate (Figs. 1D, 1F), whereas in Erismadelphus, only uniseriate rays are present (Fig. 1B).

The wood of Vochysiaceae is economically exploited on a small scale. The wood of species of Erisma possesses a low degree of resistance and durability (Huber, 1910; IPT, 1974; Marnieri, 1983).

Bark characters have been emphasized as potentially useful for the identification of tropical trees (Roth, 1972, 1981; Mori et al., 1987; Pennington, 1990). In Erisma, for example, the bark of E. uncinatum is usually fissured with scales, whereas in E. floribundum, the bark is smooth and lenticellate. Nevertheless, the data available are still insufficient to determine the taxonomic significance of the bark for most species of Erisma.

Indument

The hairs of species of Erisma, when present, as of all species comprising the tribe Erismeae, are typically stellate (Figs. 9D, 10A, 11C). Stellate hairs are not found in other genera of Vochysiaceae. The color of the hairs, especially as seen on the inflorescences, is useful for distinguishing species. Erisma calcaratum, E.

micranthum, and E. uncinatum are characterized by grayish hairs; dark brown hairs are found only in E. fuscum and E. silvae; in all other species, the hairs are yellowish.

The density of the hairs, especially on the leaves, has been utilized to distinguish species and varieties (Ducke, 1935, 1938; Stafleu, 1954). However, the greater number of collections now available shows that this character is too variable to be of practical use.

Leaves

As in most species of Vochysiaceae, the leaves of Erisma are usually stipulate and opposite. In E. floribundum, and less often in E. uncinatum, they are also arranged in tetramerous whorls, which is the only arrangement of leaves seen in E. japura. This species is unique in the genus by its verticillate and emarginate leaves, with long petioles (2 to 4 cm). Among the other genera of Vochysiaceae, verticillate leaves are also present in Vochysia and in the monotypic genus Salvertia (Stafleu, 1948).

The stipules are usually subulate or unguiculate, persistent, often thickened at the base. They are absent in E. bicolor, E. floribundum, E. gracile, E. lanceolatum, and E. laurifolium. Although not useful in

Erisma, the morphology of the stipules is especially significant to distinguish species of Qualea from the other genera of Vochysiaceae. In this genus, the stipules are often transformed into glands or associated with extrafloral nectaries.

Characters of leaf anatomy of Erisma have been described by Solereder (1908), Metcalfe and Chalk (1979), Paula (1967a, b, c, 1969), and Roth (1984). The leaves are distinctly dorsiventral as in most species of Vochysiaceae. The stomata are anomocytic and occur only on the abaxial epidermis.

Cuticular characters are potentially useful in identification (Solereder, 1908; Stace, 1965; Wilkinson, 1979). SEM observations of the leaf surface show different patterns of variation in the leaves of Erisma (Figs. 2A-F). The cuticular surface is smooth and relatively undifferentiated, for example, in E. nitidum (Fig. 2A) and E. silvae (Fig. 2B), whereas it is striate in E. floribundum (Fig. 2C) and E. micranthum (Fig. 2D). The stomatal chamber is commonly surrounded by orbicular ridges, for example, in E. bracteosum (Fig. 2E) and E. blancoa (Fig. 2F). However, as a preliminary study, only two samples of each species were analysed. A more extensive survey correlating data on developmental stage with habitat is needed to determine the taxonomic

usefulness of cuticular characters in Erisma.

Roth (1984), comparing three species of Vochysiaceae, describes the leaves of E. uncinatum as characteristically xeromorphic, with thick-walled epidermal cells, long palisade cells, relatively compact spongy parenchyma, high density of small stomata, and vascular bundles surrounded by sclerenchyma. These anatomical features are also present in other species of the genus (Paula, 1967a, b, c). Nevertheless, considerable variation is observed in leaf anatomical characters of individual species of tropical forests, and, according to Roth (1984), these changes are associated with stratification and adaptation to specific microhabitats.

Leaf venation provides valuable characteristics for the identification of species of Erisma (Figs. 3, 4). The leaves are brochidodromous with the exception of E. fuscum (Fig. 3E) and E. uncinatum (Fig. 4G), both of which exhibit eucamptodromous leaves.

The midvein is prominent on the adaxial surface of the leaves of Erisma calcaratum, E. bracteosum, E. micranthum, and E. blancoa. The number of lateral veins, their angle with the midvein, and the tertiary venation are also useful in distinguishing species. Following the terminology proposed by Hickey (1980), five patterns of

tertiary venation are recognized in the leaves of Erisma: 1) randomly reticulate in E. nitidum (Fig. 3A), E. gracile (Fig. 3B), E. splendens (Fig. 3C), and E. arietinum (Fig. 3D); 2) percurrent, sinuous, oblique, predominantly opposite in E. fuscum (Fig. 3E), E. blancoa (Fig. 3F), E. silvae (Fig. 3G), and E. bicolor (Fig. 3H); 3) percurrent, sinuous, oblique, equally opposite and alternate in E. japura (Fig. 4A), E. micranthum (Fig. 4B), E. bracteosum (Fig. 4C), and E. calcaratum (Fig. 4D); 4) percurrent, sinuous, oblique, predominantly alternate in E. floribundum (Fig. 4E) and E. laurifolium (Fig. 4F); and 5) percurrent, sinuous, aproximately at right angles (perpendicular) in E. uncinatum (Fig. 4G) and E. lanceolatum (Fig. 4H).

Inflorescences and flowers

The inflorescences of all species of Erisma are typically terminal panicles of cincinni (Figs. 5A, 5B). Axillary and subterminal inflorescences are occasionally found in E. lanceolatum (e.g., Paula 300). The cincinni are composed of two to five bracteate flowers. Based on the morphology of these bracts, Warming (1875) divided the genus into two groups, which were formally named by Stafleu (1954) as sections Erisma and Rixa. According to

these authors, section Erisma has orbicular, persistent bracts larger than the buds (Figs. 10A, 10B). In this group, these outer bracts are conspicuously developed whereas the inner bracts are much smaller and linear or lanceolate in shape. The section Rixa is formed by species with early deciduous bracts which are smaller than the buds and linear or lanceolate in shape. In this section, the inner bracts are usually absent or early deciduous (Figs. 9A, 11A). This division, although a useful aid for recognizing species, is not supported by cladistic analysis (see Phylogeny, pg. 27) and, therefore, is not maintained in this treatment.

The flowers of Erisma, as in all other genera of Vochysiaceae, are strongly zygomorphic (Figs. 5C, 5D, 6). The calyx is formed by five unequal lobes which are connate at the base. The largest lobe is characteristically spurred and convolute in bud, half-sepaloid and half-petaloid, and villose internally.

The spur of the flowers of Vochysiaceae develops from the floral axis (Kopka & Weberling, 1984). The spurred sepal of Erisma, differing from all other genera of Vochysiaceae, is deciduous. The shape of the spur is an important taxonomic character (Fig. 7). Among the species of Erisma, three distinctive spur types can be recognized: globose in E. gracile (Fig. 7D), E. japura

(Fig. 7J), E. micranthum (Fig. 7F), E. splendens (Fig. 7K), E. silvae (Fig. 7M), and E. arietinum (Fig. 7N); cylindric in E. blancoa, E. bracteosum (Fig. 7A), E. floribundum (Fig. 7B), E. bicolor (Fig. 7C), E. laurifolium (Fig. 7E), E. calcaratum (Fig. 7I), and E. nitidum (Fig. 7L), and uncinate-incurved in E. uncinatum (Figs. 5D, 7G) and E. fuscum (Fig. 7H). There is only one petal, which is either purple (E. calcaratum, E. fuscum, and E. uncinatum) or yellowish (all other species). Because E. calcaratum and E. uncinatum are the two most commonly collected species, it is mistakenly thought that most species of Erisma usually have purple flowers. Flowers with a single petal are also a distinctive feature of the genera Qualea, Ruizterania Marcano-Berti, and Callisthene (Stafleu, 1952, 1953; Marcano-Berti, 1969).

As typically seen in all flowers of Vochysiaceae, there is only one stamen; however, its position in the flower varies according to the different genera (Fig. 6). In Erisma, the single stamen stands outside the plane of symmetry, opposite to the fifth sepal (Fig. 6F). In contrast, the stamen of Erismadelphus is in the plane of symmetry, in front of the spurred sepal (Fig. 6E). The pollen grains, although showing slight variations in size, are, as in Erismadelphus,

consistently striate and tricolporate (Fig. 8).

The gynoecial structure is one of the most important characters used to differentiate the two tribes of Vochysiaceae (Fig. 6). Superior and trilocular ovaries are typically found in the Vochysieae (Figs. 6A-D); in the Erismeae, the ovary is characteristically inferior and unilocular, with two ovules in Erisma (Fig. 6F) and only one ovule in Erismadelphus (Fig. 6E).

Fruits and seeds

The fruits of Vochysiaceae are either loculicidal capsules with few winged seeds (tribe Vochysieae) or samaroid with a single seed enclosed by the enlarged and persistent sepals (tribe Erismeae). In contrast with the five wings seen in the fruits of Erismadelphus, the winged fruits of Erisma have four wings because the spurred sepal in this genus is deciduous. The wings of fruits of Erisma are of unequal sizes, the one corresponding to the third sepal being distinctly larger than the others.

Erisma calcaratum is the only species in the genus with wingless fruits. In this species, which grows in periodically inundated riverine forests, the calyx is persistent but the sepals do not enlarge. The fruits are

nut-like, corky, verruculose, and dispersed by water.

The seed coat shows little differentiation among species compared to the other genera of Vochysiaceae (Boesewinkel & Venturelli, 1987). The oil obtained from the seeds of E. calcaratum is used in the manufacturing of soap and candles (Ducke, 1925; Stafleu, 1954). The seeds of E. japura are used as a minor food source by indigenous populations (Dufour & Zarucchi, 1979) and are eaten raw, toasted, or cooked and stored as a butter-like paste.

DISTRIBUTION AND ECOLOGY

Distribution

The tribe Erismeae, which consists of Erisma and Erismadelphus, has an American-African disjunct distribution. Erismadelphus is the only genus of Vochysiaceae that is not exclusively Neotropical. Its two species, E. exsul and E. sessilis, are both trees found in the rainforests of Equatorial West Africa. Erisma is a genus of trees found only in South America.

The American-African disjunct distribution at the levels of tribe, genus, and even species, is observed in many other groups of angiosperms, including Bromeliaceae, Turneraceae, Lecythidaceae, Annona, Hyptis, and Guarea. The impressive similarity between the African and Neotropical floras has been pointed out by Gentry (1982). According to several authors (Thorne, 1973; Smith, 1973), widely separate events of migration are explained by long-distance dispersal. This idea is supported by the disjunct distribution of Bromeliaceae, Cactaceae, and Humiriaceae (Smith, 1973), but very unlikely, by the disjunct distribution of Vochysiaceae. Among the Neotropical genera of the family, the African genus Erismadelphus is more closely related to Erisma.

Both genera possess wind-dispersed fruits, which are unlikely to be carried over wide oceanic barriers. In Erisma, the only species with water-dispersed fruits is E. calcaratum, a species only distantly related to Erismadelphus. Continental drift during the Cretaceous has been proposed as a more likely explanation for most American-African disjuncts (Raven and Axelrod, 1974), and this idea probably also explains the distribution of Erisma and Erismadelphus. The African Erismadelphus and the Neotropical Erisma probably diversified from a common stock originating in West Gondwanaland.

Erisma was believed to be limited to the Amazon basin and the Guianas (Ducke, 1938; Stafleu, 1954) but a recent collection from the state of Espírito Santo has extended the geographic range of the genus to Brazil's Atlantic coastal forests (Fig. 12). Erisma arietinum, a species described herein, represents the first record of the genus from outside the Amazon region (Fig. 12). This disjunct pattern between Amazonia and eastern Brazil is also observed in species of Caryocaraceae, Lecythidaceae, and in many other families (Prance & Mori, 1980; Andrade-Lima, 1966). These examples as well as geomorphological and paleoclimatic data (Ab'Saber, 1977; Bigarella & Andrade-Lima, 1980) support the theory that the forests of the Amazon and eastern Brazil were

once continuous. However, because of extreme climatic changes which began during the Pliocene, they are now separated by drier caatinga and cerrado vegetations of the Brazilian Planalto (Andrade-Lima, 1966; Smith, 1962; Mori et al., 1981).

With the exception of E. calcaratum, the species of Erisma are found in primary terra firme forests and do not grow in secondary vegetation. Erisma calcaratum, at first known only from forests inundated by muddy waters (várzea), is also commonly found in forests inundated by black waters (igapó). The fruits of this species differ remarkably from the characteristically winged fruits of the other species of Erisma. Associated with the unique habitat for the genus, these fruits are wingless and dispersed by water (Ducke, 1948). These floating, nut-like fruits seem to represent an efficient dispersal mechanism since this species has a broad distribution (Fig. 14). Nevertheless, it is important to emphasize that the geographic range of a species results not exclusively from effective methods of dispersal but also from the interaction of biotic and abiotic factors associated with those dispersal mechanisms (Kubitzki, 1985).

Although adaptations for wind dispersal are commonly observed in emergent and canopy trees, they do not

necessarily result in efficient dispersal, as evidenced by most species of Erisma. Significantly, among the species with winged fruits, only E. uncinatum is widely distributed in Amazonia and the Guianas whereas all other species are more restricted (Figs. 12-15). Moreover, local populations of Erisma species, including the widespread E. uncinatum, are actually composed only of few individuals and occupy restricted areas where they occur.

The winged fruits of Erisma are morphologically similar to the fruits of Dipterocarpaceae (Theales), the dominant family of trees in rainforests of Asia. This family is taxonomically very distinct from the Vochysiaceae, which has considerably less ecological importance in Neotropical forests. Nevertheless, Oldeman & Furdter (1986), studying similar patterns of regeneration and tree architecture, suggested that members of the two families have equivalent ecological strategies in their respective geographic areas.

Ducke and Black (1953) used the distribution of Hevea to delimit Amazonia. The geographic distribution of Erisma parallels that of Hevea, and, therefore, also coincides with the geographic limits of the rainforests of the Amazon.

Erisma uncinatum is undoubtedly the most common and

widely distributed species of the genus. Its range follows the limits of Amazonia (Fig. 15). In Neotropical groups of plants, it has been commonly observed that there is usually at least one species with a widespread distribution (Gentry, 1979).

Extremely uneven collecting in Amazonia (Nelson et al., 1990) practically guarantees that ranges of species will be extended in the future, as has been observed since Stafleu's treatment (1954). For some species such as E. lanceolatum (Fig. 13), E. micranthum, E. blancoa (Fig. 14), and E. silvae (Fig. 15), the distributions presented here are only preliminary representations of probably larger ranges. Significantly, between 1986 and 1991, more than 50 new records of Burseraceae for countries in Central and South America have been reported (D. Daly, pers. comm.).

Although several species of Erisma remain inadequately collected, it is possible to make inferences about the different distribution patterns of the genus. Taking into account the uneven sampling, areas of high diversity can be recognized by overlapping the species distributions (Figs. 12-15) on a single map (Fig. 16):

1. Erisma is clearly more diverse in the western Amazon Basin. Nine species (E. bicolor (Fig. 12); E. laurifolium, E. lanceolatum (Fig. 13); E. blancoa, E.

bracteosum, E. micranthum (Fig. 14); E. splendens, E. japura, E. silvae (Fig. 15) are found west of 63° W longitude (Manaus), whereas only two (E. gracile and E. nitidum (Fig. 13) are restricted to eastern Amazonia and the Guianas.

2. The Amazon River apparently has not restricted the range of the species, with the possible exception of E. gracile. Ducke and Black (1953) emphasized the importance of the Amazon River on the distributions of Amazonian plants. The Lower Amazon region (east) is divided into two different phytogeographic regions by the river whereas in the Upper Amazon region (west), this division does not occur. North-South orientations of phytogeographic limits in eastern Amazonia have been also observed by other authors to be more relevant than East-West oriented limits (Rizzini, 1963; Prance, 1977; Daly & Prance, 1989; Prance, 1989) and this is supported by the distribution of Erisma. In eastern Amazonia, the collections come mostly from the north of the river (E. floribundum (Fig. 13); E. calcaratum (Fig. 14); E. uncinatum (Fig. 15) and only very few reports exist from the south, which is, however, incompletely known botanically.

3. Apparently disjunct or endemic species, for example, E. fuscum (Fig. 15) and E. nitidum (Fig. 13), may be

widespread, but rare throughout their range. These two species occur in well collected areas - E. fuscum around Humaitá (Amazonas), and E. nitidum in French Guiana and Guyana. No recent collections, however, are known for either species.

It is unrealistic to expect to have complete collecting data before making inferences about patterns of distribution and endemism, especially considering the rapid rate of deforestation of the Amazonian forests (Fearnside, 1982, 1984; Alcântara & Conti, 1989). The destruction of primary forests and their consequent replacement by secondary vegetation severely threatens many species of Erisma, recognized as some of the most beautiful trees of the tropical rainforest.

The controversial refuge theory for plants proposed by Prance (1973), not supported by the distribution patterns of Erisma, is frequently considered in conservation planning but has been demonstrated to be biased towards collecting sites (Nelson et al., 1990). Conservation policies should be based on accurate and well-interpreted phytogeographic maps - and, in practical terms, on maps of areas being deforested, which would provide immediate data for priority areas for conservation - if true centers of endemisms are to be preserved.

The highest concentration of diversity and regional endemism of Erisma coincides with the areas suffering the least deforestation and demographic pressure - the western region of Amazonia. The largest national park of Brazil - Jaú National Park (61-64°W, 1-3°S), established in 1980 (Pádua, 1983) - represents a major effort towards conservation in the area. Large biological reserves in the lowlands, when carefully based on actual plant distributions, could protect a large part of Neotropical tree diversity (Gentry, 1982; Mori, 1991). For example, a large biological reserve in the Upper Rio Negro would protect 10 of the 16 species of Erisma, and the biological reserves proposed by Mori (1991) in central French Guiana and near the Essequibo River in Guyana would protect E. uncinatum, E. floribundum, and E. nitidum, the latter, a likely rare species in the genus, known only from the Guianas. Unfortunately, the areas with the most rapid alteration - the southeastern region of the Amazon forest - also constitutes the largest uncollected area in Amazonia and it is impossible to say what has been lost already. Similarly, with only a single known record of Erisma, the Atlantic coastal forest has already lost a significant percentage of its original area (Daly, 1990; Mori, 1989).

Phenology and pollination biology

The uneven sampling of Erisma seems to be intensified by the unusual height of some species, which makes the collection of fertile material a challenging task. The large stature of these trees also hampers studies on pollination biology, for which there is no complete information. However, bees have been observed visiting the flowers of E. calcaratum (Mori, pers. comm.). The flowers of Erisma present the characteristic syndrome of bee-pollination (Faegri & Pijl, 1979): zygomorphic, yellow or bluish flowers, petal with adequate surface for landing, weak odor, and few stamens (only one in Erisma). Pollinators are probably rewarded by nectar produced by superficial tissues in the spur of the flower.

It appears that most species of Erisma in the Amazonian region start flowering between September and November, and fruit between December and January. These periods correspond to late dry season and early rainy season, respectively, in the areas where most species are found. It has been verified in different communities of trees from different Neotropical regions that the beginning of the flowering for many species occurs during the dry season (Alencar et al., 1979; Frankie et al.,

1974; Janzen, 1967; Mori & Prance, 1987). According to Janzen (1967), the coincidence of the flowering period with the dry season promotes pollination success. This may be especially true for species of Erisma, which have numerous but very ephemeral flowers with a single stamen. In the rainy season, pollinators show reduced activity and may not be available. In addition, rain drops may destroy delicate flowers, wash away pollen, and dilute the nectar produced to atract pollinators.

PHYLOGENY

Phylogenetic systematics has been heralded as an advancement over traditional systematic methods (Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Wiley, 1981; Brooks & Wiley, 1985). Although extensively criticized by some authors (Ashlock, 1985; Cronquist, 1987; Hull, 1985, Mayr, 1985), the cladistic theory originally proposed by Hennig (1966) attempts to reconstruct the evolutionary history of a group using empirical methods, stressing shared derived characters.

A cladistic analysis was developed as an attempt to understand the phylogenetic relationships of the species of Erisma. This technique assumes that the taxon in study be monophyletic, i.e., to include all descendants of a common ancestor. It is based on a set of characters (data matrix) ordered into plesiomorphic and apomorphic states (polarization) so that a branching pattern (cladogram) can be produced (Wiley, 1981; Wiley et al., 1991). This study was conducted using compatible versions of MacClade 2.97 (Maddison and Maddison, 1989) and PAUP 3.0c (Swofford, 1990), which allow the use of polymorphic codings. Multistate characters were unordered.

Although several techniques can be used to polarize

the characters (Ridley, 1986), the outgroup comparison is the most commonly utilized method for polarization of character states (Funk, 1982; Brooks & Wiley, 1985; Loconte & Stevenson, 1990). The ideal outgroup is the sister group, which is the closest relative of the taxon under study (Wiley et al., 1991).

Cladistic analysis of the genera of Vochysiaceae

According to the traditional division proposed by Dumortier (1829), the family Vochysiaceae is formed by two tribes: Vochysieae and Erismeae. The affinities between Erisma and Erismadelphus are suggested since the tribe Erismeae comprises only these two genera. Thus, a cladistic analysis was initially performed to verify the phylogenetic relationships among the genera of Vochysiaceae and to confirm Erismadelphus as the sister group of Erisma.

Trigoniaceae has been widely accepted as being closely related to Vochysiaceae. These two families have in common the woody habit, usually stipulate leaves, zygomorphic flowers, and frequently trilocular ovaries with more than one ovule per locule. However, Vochysiaceae is unique in its spurred calyx, the single fertile stamen, and winged seeds. According to the

systems of Cronquist (1981, 1988), Takhtajan (1980), and Dahlgren (1980), the Vochysiaceae and the Trigoniaceae are included in the Order Polygalales. Thorne (1976) includes Vochysiaceae in the Order Geraniales, which basically unites the Orders Polygalales and Geraniales of Cronquist's, Takhtajan's, and Dahlgren's systems. In these three systems, Polygalales are mainly woody plants, with usually simple leaves and zygomorphic flowers, whereas Geraniales are mostly herbs, with either simple or compound leaves, and usually actinomorphic flowers.

Lleras (1978) removed Euphronia from Trigoniaceae and proposed its placement in Vochysiaceae, based on anatomical characters, such as the presence of libriform fibers and paratracheal parenchyma. The position of this genus, however, is still very questionable. If retained in Vochysiaceae, the three known Neotropical species of Euphronia (Steyermark, 1987) would be the only representatives with several fertile stamens in the Vochysiaceae, a family characteristically delimited by species with a single fertile stamen. Recently, a new family (Euphroniaceae) has been proposed to accomodate the species of Euphronia (Marcano-Berti, 1989b). Although Trigoniaceae was chosen as the outgroup of Vochysiaceae, Euphronia was excluded from this analysis because the taxonomic position of the genus remains

incompletely understood.

The cladistic analysis for the genera of Vochysiaceae identified only one parsimonious cladogram at 45 steps (Fig. 17) using the set of characters and the data matrix in Tables 1 and 2. The resulting cladogram supports Dumortier's traditional division of the family into Vochysieae and Erismeae, as well as Erismadelphus and Erisma as sister groups. The synapomorphies defining the tribe Erismeae are: stellate hairs (character 1), included phloem (5), inferior (19) and unilocular (20) ovaries, apical placentation (22), and winged (25), single-seeded (26) fruits.

Erisma is strongly corroborated as a monophyletic genus of Vochysiaceae and comprises some of the most specialized members of the family, which includes seven distinctly defined genera. The deciduous spurred sepal, ovaries with two ovules, and four-winged fruits are unique characteristics of Erisma.

It is significant to observe that the genera of the tribe Vochysieae are, in contrast, defined by only three synapomorphies: paratracheal parenchyma (4), which is a reversal in Callisthene, loculicidal capsules (24), and winged seeds (27). The several symplesiomorphies of the genera, for example, superior and trilocular ovaries, do not help to define the tribe as a monophyletic group.

Although a large number of homoplasies are shown, they do not have congruent patterns. Thus, for the present, the cladogram provided in this analysis is the most parsimonious result available.

Cladistic analysis of Erisma

The cladistic analysis of the species of Erisma, using the characters and the data matrix in Tables 3 and 4, resulted in only one parsimonious cladogram at 55 steps (Fig. 18). One of the two main phylogenetic lines is defined by elliptic (non-obverse) (4) and glabrous (5) leaves, and angle of lateral veins in relation to the midvein larger than 60° (10). Nevertheless, these three characters show reversals and an understanding of their plasticity requires further study.

Although the traditional divison of the genus into two sections (Erisma and Rixa) is not supported by cladistic analysis, the species formerly assigned to section Erisma (E. bicolor, E. floribundum, E. laurifolium, E. gracile, and E. bracteosum) form a clade defined by only one synapomorphy (21). The persistence (14) and size (15) of the outer bracts are the only characters differentiating the two sections (Warming, 1875; Stafleu, 1954). However, the most parsimonious

analysis resulted in reversals for these characters. Erisma lanceolatum, included by Stafleu (1954) in section Rixa, is closely related to this group but the flowers of this species have not been collected and, thus, the bract characters are unknown.

Several lines within Erisma reflect a great deal of parallel evolution. Percurrent tertiary venation (11), defining the second main phylogenetic line, apparently has evolved twice. This group comprises E. uncinatum and E. fuscum, two closely related species by the unique uncinate-incurved spur (17), E. silvae, an incompletely known species, and E. blancoa. This latter species is similar to E. micranthum in leaf morphological characters, which, however, do not represent synapomorphies. Erisma uncinatum, E. fuscum, and E. silvae also exhibit distinctive brown or gray hairs (1), a character, however, showing parallel evolution in the group formed by E. micranthum, E. calcaratum, and E. japura, three species with a sympatric distribution pattern.

Erisma arietinum, the only species occurring outside of Amazonia, is significantly isolated from the rest of the clade. The most widespread species of each main phylogenetic line, E. calcaratum and E. uncinatum, are also species in later branches. Within the genus, E.

calcaratum shows the largest number of generated autapomorphies (20, 21). This species is unique in the morphological specialization of its fruits, a response to selective pressures of the riverine habitat.

Although one of the objectives of cladistics, a cladistic classification is not provided in this study. As pointed out by Mayr (1985), the results of a cladistic analysis may not lend themselves for conversion into a classification scheme. Additional data and other interpretations of the character states will have to be considered before a predictive and informative infrageneric classification can be developed for Erisma. Nevertheless, cladistic analysis is extremely useful for the study of distribution of characters and delimitation of taxa, providing a framework for further studies in comparative biology.

KEYS TO THE GENERA OF VOCHYSIACEAE

The following keys are provided in order to summarize the main characteristics by which the tribes and genera of Vochysiaceae are distinguished, and to identify the taxonomic position of Erisma within the family.

KEY TO TRIBES OF VOCHYSIACEAE

1. Hairs simple. Ovary superior, trilocular. Fruit a loculicidal capsule; seeds 3 to several, winged .... tribe Vochysieae.
1. Hairs stellate. Ovary inferior, unilocular. Fruit samaroid by the accrescent and persistent sepals or nut-like; seed 1, without wings .... tribe Erismeae.

KEY TO GENERA OF VOCHYSIEAE

1. Petals 5 or usually 3; two ovules per locule.
    2. Petals 5, white; style incrassate, stigma lateral ..... Salvertia.

2. Petals usually 3, yellow; style cylindric, not incrassate, stigma terminal or lateral .... Vochysia.

1. Petal 1; several ovules per locule.

3. Stipules transformed into glands or associated with extrafloral nectaries. Capsule without a distinct central column; exocarp thick, attached to endocarp.

4. Spurred sepal to twice as long as other sepals; anther glabrous or pilose, not barbate ..... Qualea.

4. Spurred sepal 3 or more times longer than other sepals; anther barbate .... Ruizterania.

3. Stipules obsolete, not transformed into glands or associated with extrafloral nectaries. Capsule with a distinct central column; exocarp thin, not attached to endocarp .... Callisthene.

KEY TO GENERA OF ERISMEAE

1. Spurred sepal persistent; petals 5; one ovule per locule. Fruit with 5 wings. African trees .... Erismadelphus.

1. Spurred sepal deciduous; petal 1; two ovules per locule. Fruit with 4 wings or nut-like. Neotropical trees ..... Erisma.

SYSTEMATIC TREATMENT

Erisma Rudge, Pl. Guian. 1: 7, t. 1. 1805; Martius & Zuccarini, Nov. Gen, sp. pl. 1: 136-138. 1824; Candolle, Prodr. 3: 29-30. 1828; Dumortier, Analyse des familles des plantes, p. 41. 1829; Dietrich, in Linnaeus, Sp. pl. 1, 6 ed.: 101-103. 1831; Spach, Histoire naturelle des végétaux, Phanérogames. Les Vochysiées, v. 4, p. 328-329. 1835; Meisner, Pl. vasc. gen. 1: 119, 1837; Dietrich, Syn. pl. 1:21. 1839; Endlicher, Gen. pl. 2: 1179. 1840; Schomburgk, Reisen in Britisch Guiana 3: 1099. 1848; Bentham & Hooker, Gen. pl. 1: 975-978. 1867; Warming, in Martius, Fl. bras. 13(2): 106-114, t. 20-21. 1875; Baillon, The natural history of plants. Vochysiaceae, v.5, p. 96-97. 1878; Eichler, Bluthendiagr. 2: 360-363. 1878; Petersen, in Engler & Prantl, Nat. Pflanzenfam. 3(4): 319. 1897; Benoist, Bull. Soc. Bot. France 62: 235-248. 1915; Ducke, Arch. Jard. Bot. Rio de Janeiro 1: 50-51. 1915; Benoist, Bull. Soc. Bot. France 66: 319. 1919; Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 198. 1922; Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 105-107. 1925; Benoist, Arch. Bot. 5 mem. 1: 167-168. 1931; Ducke, Arq. Inst. Biol. Veg. 2(1): 54-56. 1935; Ducke, Arq. Inst. Biol. Veg. 4(1): 42-44. 1938;

Macbride, Field. Mus. Nat. Hist., Bot. ser. 13 part 3 (3): 872-875. 1950; Lemée, Flore de la Guyane Française 2: 237-244. 1952; Stafleu, Acta Bot. Neerl. 3(4): 459-480. 1954; Quirk, Int. Assoc. Wood Anat. News Bull. 1(4): 172-179. 1980; Bernardi & Spichiger, Candollea 36(1); 131-136. 1981.

Debraea Roemer & Schultes, Syst. veg. 1: 4. 1817.

Ditmaria Sprengel, Anleit. Kenntn. Gew. 2(2) ed.2: 704. 1818.

Braya Schultes ex Martius, Nov. Gen. sp. pl. 1: 136. 1824. In synon.

Emergent or canopy trees. Hairs yellowish, gray, or brown, stellate. Leaves simple, entire, opposite, rarely in tetramerous whorls, petioled; blades mostly coriaceous, variously pubescent, midvein sulcate or prominent above, prominent below, the venation usually brochidodromous, lateral veins to ca. 20 pairs, angle with midvein 40-80°, tertiary veins randomly reticulate or percurrent; petiole terete or canaliculate; stipules present or absent. Inflorescences panicles of cincinni, terminal, very rarely axillary, subterminal; cincinni with 2-5 flowers. Flowers zygomorphic, bracteate, mostly short-pedicellate; bracts deciduous, outer bracts

overlapping the buds or not, inner ones present or absent; calyx with 5 unequal lobes, connate at base, the largest one spurred, obcordate, convolute, the outer side sepal-like, the inner side petal-like and villose; spur globose, cylindric, or uncinate-incurved, deciduous with the larger calyx-lobe; petal one, in front of spurred sepal, white to yellow, or purple, puberulous, convolute in bud, obcordate, unguiculate, deciduous; stamen one, in front of fifth sepal, outside the plane of symmetry; anther sagittate, dorsifixed; pollen grains tricolporate, exine striate; staminodes 0-4; style one, pilose at base or glabrous, stigma terminal, capitate; ovary inferior, unilocular, with two apical ovules. Fruits indehiscent, samaroid, 4-winged by the unequally enlarged and persistent calyx-lobes; wings elliptic to oblong, the major and second major wing corresponding to third and second sepals, respectively, the two smallest wings corresponding to first and fifth sepals; fruits wingless and nut-like only in E. calcaratum; seed 1, lacking endosperm, the cotyledons fleshy.

Type. Erisma floribundum Rudge. The name Erisma is derived from the Greek ἐρείδω , which means to support. It refers to the overlapping bracts that subtend the flowers.

Distribution (Figs. 12-16). The genus Erisma comprises sixteen species predominant in the non-flooded forests of the Amazon Basin and the Guianas with only one species found in the coastal forests of Espírito Santo, in eastern Brazil.

KEY TO SPECIES OF ERISMA

1. Outer bracts overlapping the buds, late deciduous; major wing of fruits oblong.
    2. Midvein of leaves prominent above; mature buds 1 cm or longer ..... 5. E. bracteosum.
    2. Midvein of leaves sulcate above; mature buds less than 1 cm.
        3. Leaves strongly coriaceous; lateral veins ribbed below, distinctly parallel .... 2. E. bicolor.
        3. Leaves chartaceous to coriaceous; lateral veins not ribbed below, curved upwards.
            4. Leaves chartaceous; bracts to 4 mm long; spur globose ..... 6. E. gracile.
            4. Leaves subcoriaceous to coriaceous; bracts 7 mm or longer; spur cylindric.
                5. Lateral veins 14-20; petiole usually corky; spur incurved .... 3. E. floribundum.
                5. Lateral veins 8-10; petiole smooth; spur straight .... 4. E. laurifolium.

1. Outer bracts very small, not overlapping the buds, early deciduous; major wing of fruits ovate or elliptic, rarely oblong, or fruits wingless.
    6. Midvein of leaves prominent above.
        7. Fruits without wings; inundated forests ..... 9. *E. calcaratum*.
        7. Fruits with wings; non-inundated forests.
            8. Fruits to 3 cm long; stipules ca. 1 mm long, thickened at base .... 8. *E. micranthum*.
            8. Fruits longer than 3 cm; stipules ca. 4 mm long, not thickened at base .... 16. *E.blancoa*.
    6. Midvein of leaves sulcate above.
        9. Petioles 1.5 cm or longer.
            10. Leaves in whorls, apex emarginate .... 10. *E. japura*.
            10. Leaves opposite, apex acuminate.
                11. Leaves shiny, coriaceous, base acute; stipules present .... 12. *E. splendens*.
                11. Leaves opaque, chartaceous, base obtuse; stipules absent .... 7. *E. lanceolatum*.
        9. Petioles to 1 cm long.

12. Spur uncinate-incurved; flowers purple.
    13. Hairs brown; base of leaves subcordate ..... 14. E. fuscum
    13. Hairs gray; base of leaves acute, attenuate ..... 13. E. uncinatum.
12. Spur cylindric or globose; flowers white or yellow.
    14. Leaves to 10 cm long; eastern Brazil ..... 1. E. arietinum.
    14. Leaves longer than 10 cm; Guianas.
        15. Hairs yellow; lateral veins 7-9; spur cylindric, straight ..... 11. E. nitidum.
        15. Hairs brown; lateral veins 12-13; spur globose .... 15. E. silvae.

1. Erisma arietinum Kawasaki, Mem. New York Bot. Gard.00: 000-000. 1992. Type. Brazil. Espírito Santo: Linhares, Companhia Vale do Rio Doce Reserve, carneiro road, old 243-A4, km 0.6, T.408, right side, 9 Jun 1978 (fl), Folli 008/78 (holotype, CVRD; isotypes, NY-2 sheets). Figs. 3D, 7N, 8A, 9, 12.

Ab E. laurifolio bracteis externis deciduis (nec longe persistentibus) parvis lanceolatis (nec late ovatis gemmis longioribus) et calcari brevi subgloboso (nec cylindrico) differt.

Tree 20-30 m high, to 120 cm DBH; hairs when present yellowish; young twigs pubescent. Leaves opposite; blade coriaceous, elliptic to narrowly elliptic, 7.5-10 x 3.5-5.5 cm, glabrous; apex acute or obtuse-acuminate; base obtuse to subcordate; midvein sulcate above, prominent below; lateral veins 8-10 pairs, immersed above, prominent below, angle with midvein 70-80°; tertiary veins randomly reticulate; marginal vein 1-2 mm from margin; petiole canaliculate, 8-10 mm long; stipules subulate, 1-2 mm long. Inflorescences terminal, to 15 cm long, peduncles and lateral branches tomentose; cincinni 2-3 cm long, tomentose; outer bracts lanceolate, to 3 mm long; inner bracts absent; pedicel 0-1 mm long; buds ca.

9 mm long; spurred sepal ca. 10 mm long, spur subglobose, 1-3 mm long; other sepals 1-5 mm long; petal yellow, ca. 10 x 10 mm; stamen ca. 5 mm long; style ca. 6 mm long, pilose at the base. Fruits winged, puberulous, glabrescent, 5.5-8 cm long; major wing elliptic or narrowly ovate, 4.5-6 x 2.5-3 cm; second major wing widely elliptic to elliptic, 2.5-3 x 1.5-2 cm.

Distribution (Fig. 12). Known only from the type locality in the coastal forests of Espirito Santo, southeastern Brazil. Flowers have been collected in June, and fruits in April and December.

Specimens examined. Brazil. Espirito Santo: Linhares, Companhia Vale do Rio Doce Reserve, Carneiro Road (old 243-A4), km 1.8, left side, 26 Apr 1983 (fr), Folli 444 (CVRD, NY-2 sheets), km 0.6, 12 Dec 1989 (fr), Kawasaki et al. 400 (CVRD, NY).

Local name. Brazil: carneiro.

Erisma arietinum is similar in leaf characteristics to E. laurifolium, from which it is distinguished by the morphology of the outer bracts and the calyx-spur. In E. arietinum, the outer bracts are early deciduous, lanceolate, and smaller than the buds; the spur is short and subglobose. The outer bracts of E. laurifolium are

characteristically larger than the buds and remain on the inflorescences until the fruits start to develop; the spur is distinctly cylindric.

This new species represents the first record of a species of Erisma outside of the Amazon basin and the Guianas. It is a tall tree, locally common in the moist forests of coastal Espírito Santo, eastern Brazil. Several other examples of this disjunct pattern of distribution at the generic level have been reported (Rizzini, 1963; Andrade-Lima, 1966; Prance & Mori, 1980; Mori et al., 1981; Daly, 1990).

The epithet "arietinum" refers to the local name of the species, which means ram. It may be an allusion to the yellowish and somewhat woolly pubescence on the inflorescences and flowers.

2. Erisma bicolor Ducke, Bull. Mus. Hist. Nat. (Paris) 4: 740-741. 1932. Type. Brazil. Amazonas: Non-flooded forest, near Borba on lower Rio Madeira, 20 Jan 1930 (fl), Ducke RB 23500 [holotype, RB; isotypes, G, n.v., IAN-2 sheets (photos at NY), K (photo at NY), NY, P, n.v. (photo at NY), R-2 sheets (photos at NY), RB, S, n.v., U, n.v. (photo at NY), US-2 sheets]. Figs. 1C, 1D, 3H, 5A, 7C, 12.

Erisma petiolatum Gleason, Bull. Torrey Bot. Club 60(5): 363-364. 1933. Type. Brazil. Mato Grosso: Non-flooded forest, near Tabajara, upper Machado River region, 12 Nov 1931 (fl), Krukoff 1334 [lectotype (Stafleu, 1954), NY; isolectotypes, A, n.v., F, G, n.v., K (photo at NY), MO, P, n.v. (photo at NY), S, n.v., U, n.v.].

Erisma macrophyllum Ducke, Arq. Inst. Biol. Veg. 4: 44. 1938. Type. Brazil. Amazonas: In forest on high banks of Rio Curicuriary (affluent of Rio Negro), below Bucú Falls, 21 Feb 1936 (fr), Ducke RB 34685 [lectotype (Stafleu, 1954), RB (photo at NY); isolectotypes, K (photo at NY), RB, U, n.v. (photo at NY), US].

Erisma bicolor Ducke var. macrophyllum (Ducke) Stafleu, Acta Bot. Neerl. 3: 465. 1954. Type. Based on E. macrophyllum Ducke.

Erisma costatum Stafleu var. costatum, Acta Bot. Neerl. 3: 466. 1954. Type. Brazil. Amazonas: Non-flooded forest, Tabatinga, 24 Nov 1945 (fl), Ducke 1842 (=RB 60347) [holotype, U, n.v. (photo at NY); isotypes, F, GH, n.v., NY-2 sheets, R (photo at NY), RB-5 sheets (photo at NY), US].

Erisma costatum Stafleu var. gracilipes Stafleu, Acta Bot. Neerl. 3: 467. 1954. Type. Brazil. Amazonas: Igarapé Jandiatuba, on terra firme, Jan (fl), Fróes

23921 [holotype, U, n.v. (photo at NY); isotype, IAN].

Tree 12-30 m high, to 50 cm DBH; hairs when present yellowish-brown; young twigs pubescent. Leaves opposite; blade coriaceous, widely to narrowly elliptic or narrowly obovate, 11.5-25 x 5.2-10.5 cm, glabrous above, tomentose below, glabrescent; apex acute, obtuse-acuminate or acuminate; base acute or obtuse; midvein sulcate above, prominent below; lateral veins 15-18 pairs, immersed above, prominent below, angle with midvein 50-60°; tertiary veins percurrent, sinuous, oblique to midvein, arrangement predominantly opposite; marginal vein ca. 1 mm from margin; margin often revolute; petiole canaliculate, 15-25 mm long; stipules absent. Inflorescences terminal, 14-23 cm long, peduncles and lateral branches tomentose; cincinni 1-2 cm long, tomentose; outer bracts ca. 7 x 7 mm; inner bracts linear, ca. 1 mm long; pedicel 1-2 mm long; buds 5-6 mm long; spurred sepal ca. 7 x 9 mm, spur cylindric, ca. 2 mm long.; other sepals 2-5 mm long; petal cream, yellow, or white, ca. 12 x 15 mm; stamen ca. 6 mm long; style ca. 6 mm long, pilose at the base. Fruits winged, puberulous, 5.5-6.5 cm long; major wing narrowly oblong, 4.5-5.5 x 1.5-2 cm; second major wing elliptic, ca. 2 x 1 cm.

Distribution (Fig. 12). In terra firme forests of Peruvian and central Brazilian Amazon. It flowers from November to January and fruits have been collected in January, February, May, and July.

Specimens examined. PERU. Loreto: Prov. Requena, Dtto. Sapuena, basin of Río Ucayali, Jenaro Herrera and vicinity, 3 km E of Jenaro Herrera, 2 km ENE of Centro de Investigaciónes Jenaro Herrera, 4°55'S, 73°45'W, 24 Nov 1988 (fl), Daly et al. 5756 (NY); Jenaro Herrera Arboretum, 140 m, 17 Jul 1980 (fr), Vásquez & Jaramillo 299 (MO, NY); Jenaro Herrera, 170 m, 13 Nov 1987 (fl), Vásquez & Jaramillo 10031 (MO, NY). Prov. Maynas, Dtto. Alto Nanay, Santa María del Nanay, 150 m, 15 Dec 1967 (fl), R. Rodríguez 39 (F, NY), 52 (F, MO, NY); Nauta, Nauta-Iquitos Road, 4°29'S, 73°35'W, 150 m, 9 Jan 1988 (fr), Vásquez & Jaramillo 10293 (MO, NY); Sargento Lores, Esperanza, Río Tahuayo, 4°10'S, 73°15'W, 120 m, 12 Dec 1989 (fl), Vásquez & Jaramillo 13206 (MO, NY). Without locality, Vásquez 1026 (MER).

BRAZIL. Amazonas: Manaus, 15 May 1933 (fr), Ducke RB 23796 (K), 16 May 1933 (fr), Ducke 214 (US); Reserva Florestal Ducke, Q9, tree #1011, 15 Jan 1964 (fl), W. Rodrigues & Osmarino 5664 (INPA, MER, RB), 28 Jan 1964 (fl), W. Rodrigues & Osmarino 5703 (INPA, MER); São Paulo

de Olivença, basin of creek Belém, 26 Oct-11 Dec 1936 (fl), Krukoff 8892 (F, MO, NY, US-2 sheets). Acre: Upper Rio Moa, near Fazenda Arizona, 7°29'S, 73°39'W, 10-16 Oct 1985 (st), Campbell et al. 6239 (NY). Rondônia: Porto Velho, Usina Hidrelétrica Samuel, end of E dike road, 50 km SE of dam, 9°06'S, 63°13'W, 12-24 Sep 1988 (st), Thomas 6510 (NY). Mato Grosso: Near Tabajara, upper Machado River region, Nov-Dec 1931 (fl), Krukoff 1376 (NY).

Local names. Brazil: maueira, maueira-roxa.

Erisma bicolor is closely related to E. floribundum, having in common with it markedly bracteate flowers and a recurved calyx-spur. However, the leaves of E. bicolor are more coriaceous and wider, the lateral veins are characteristically straight and parallel (not curved), and the petioles are longer.

Stafleu (1954) recognized two varieties of this species, bicolor and macrophyllum, differing basically in leaf pilosity which is extremely variable, ranging from densely tomentose to glabrous. In adition, Stafleu (1954) described E. costatum with two varieties, costatum and gracilipes. The type specimens of this species show the same floral and leaf morphology as E. bicolor. Both species have the characteristic long-petiolate leaves

with ribbed lateral veins, and largely bracteate flowers with a recurved spur, and, therefore, I have considered E. costatum a synonym of E. bicolor.

3. Erisma floribundum Rudge, Pl. guian. 1: 7-8, t. 1. 1805. Type. French Guiana. Without locality, no date (fl), Martin s.n. [holotype, BM, n.v. (photo at NY); isotypes, BR, n.v., M, n.v., MO, U-2 sheets, n.v. (photos at NY)]. Figs. 1E, 1F, 2C, 4E, 5B, 7B, 8B, 8E, 8F, 10, 13.

Erisma parvifolium Gleason, Bull. Torrey Bot. Club 60(5): 362-363. 1933. Type. Brazil. Mato Grosso: Non-flooded forest, near Tabajara, upper Machado River region, 23 Nov 1931 (fl, fr), Krukoff 1401 [lectotype (Stafleu, 1954), NY; isolectotypes, A, n.v., F, G, n.v., K (photo at NY), MO, P, n.v. (photo at NY), RB-3 sheets (photo at NY), S, n.v., U, n.v., US].

Erisma pallidiflorum Ducke, Arq. Inst. Biol. Veg. 2: 54-55. 1935. Type. Brazil. Amazonas: Near Igarapé Mioá, below Camanaos on Rio Negro, 19 Dec 1931 (fl), Ducke RB 24102 [lectotype (Stafleu, 1954), RB (photo at NY); isolectotypes, K (photo at NY), P, n.v. (photo at NY), S, n.v., U, n.v. (photo at NY), US].

Erisma tomentosum Ducke, Arq. Inst. Biol. Veg. 2: 55.

1935. Type. Brazil. Amazonas: In non-flooded forest, Manaus, near source of Igarapé do Crespo, 13 Dec 1932 (fl), 18 Apr 1933 (fr), Ducke RB 24100 [holotype, RB (photo at NY); isotypes, K (photo at NY), P, n.v. (photo at NY), RB, S, n.v., U, n.v., US].

Erisma parvifolium Gleason var. pallidiflorum (Ducke) Ducke, Arq. Inst. Biol. Veg. 4: 43. 1938. Type. Based on E. pallidiflorum Ducke.

Erisma parvifolium Gleason var. tomentosum (Ducke) Ducke, Arq. Inst. Biol. Veg. 4: 43. 1938. Type. Based on E. tomentosum Ducke.

Erisma floribundum Rudge var. tomentosum (Ducke) Stafleu, Acta Bot. Neerl. 3(4): 468-469. 1954. Type. Based on E. tomentosum Ducke.

Tree 15-35 m high, to 65 cm DBH; hairs when present yellowish-brown; young twigs pubescent. Leaves opposite or in 4-merous whorls; blade coriaceous, narrowly oblong, elliptic or narrowly obovate, 8.5-15 x 2.5-5.5 cm, glabrous above, tomentose or pubescent, glabrescent below; apex shortly acuminate; base obtuse; midvein sulcate above, prominent below; lateral veins 14-20 pairs, sulcate above, prominent below, angle with midvein 60-80°; tertiary veins percurrent, sinuous, oblique to midvein, arrangement predominantly alternate; marginal vein 1-3 mm from margin; petiole transversely rimose,

3-10 mm long; stipules absent. Inflorescences terminal, 10-18 cm long, peduncle and lateral branches pubescent; cincinni up to 3 cm long, pubescent; outer bracts rounded or broadly ovate, 9-10 x 6-8 mm; inner bracts elliptic, 3 mm long; pedicel 1-3 mm long; buds 6-8 mm long; spurred sepal 7-8 x 9-10 mm, spur cylindric, usually recurved, 3-5 mm long; other sepals 2-5 mm long; petal white or yellowish, ca. 15 x 15 mm, villose at base, glabrescent; stamen ca. 6 mm long; staminodes 1-2 mm long; style 5-6 mm long, glabrous. Fruits winged, minutely puberulous, glabrescent; major wing narrowly oblong, 5-5.5 x 1.3-1.8 cm; second major wing narrowly oblong or narrowly elliptic, 2-2.5 x 1.5-1.8 cm.

Distribution (Fig. 13). This species grows in terra firme and swamp forests of the Amazon basin and French Guiana. It flowers from September to February. Fruits have been collected in November, December, and April.

Specimens examined. VENEZUELA. Amazonas: Yavita, 128 m, 1942 (fl), Williams 14111 (F, MER, NY, RB, US-2 sheets).

FRENCH GUIANA. Saül, Mont La Fumée, 3°37'N, 53°12'W, 200-400 m alt., 12 Oct 1982 (st), Boom & Mori 1974 (NY); Saül, Route de Belizon, between Saül and Eaux Claires, ca. 200-300 m alt., 12 Nov 1990 (fl), Mori et al. 21630

(NY).

BRAZIL. Amazonas: Manaus, 13 Dec 1935 (fl), Ducke RB 32144 (K, RB-2 sheets, US); Manaus, Estrada do Aleixo, 26 Dec 1936 (fl), Ducke 104 (F, MO, NY, R, US); Manaus, Tarumã, 28 Nov 1931 (fl), Ducke RB 24101 (RB, US). Pará: Rio Jari, along road Monte Dourado to Planalto, 19 Jan 1968 (fl), Oliveira 3913 (INPA, NY); Monte Dourado, Gleba Pacanari, tree #1047, 00°40'S, 52°35'W, 18 Feb 1988 (fl), M. J. Pires & N. T. Silva 2003 (MG). Mato Grosso: Alta Floresta, road of Hidrelétrica do Salto do Rio Apiacás, 110 km from Alta Floresta, 10°15'S, 56°50'W, 29 Sep 1985 (fl), Cid et al. 6281 (INPA, MG, NY); Alta Floresta, ca. 3 km on road from Alta Floresta to Rio Apiacá (MT 208), 44.5 km E of Rio Apiacá, 9°56'S, 56°38'W, 29 Sep 1985 (fl), Thomas et al. 4096 (INPA, MG, NY); near Tabajara, upper Machado River region, Nov-Dec 1931 (fl), Krukoff 1332 (F, MO, NY, US); source of the Jatuaraha River, Machado River region, Dec 1931 (fr), Krukoff 1679 (F, K, MO, NY, US).

Erisma floribundum is morphologically very similar to E. bicolor in floral structure. Although having in common the largely bracteate flowers with recurved spurs, these two species are very distinct in leaf characters.

Erisma floribundum also shows affinities with E.

laurifolium both in leaf and floral morphology. The differences between the two species are discussed under E. laurifolium.

Stafleu (1954) recognized two varieties of this species, floribundum and tomentosum, which he distinguished by the pubescence of the leaves and petal. However, pubescence ranges from densely tomentose to glabrous, thereby obscuring the delimitation of the two varieties.

4. Erisma laurifolium Spruce ex Warming, in Martius, Fl. bras. 13(2): 109, t. 20. 1875. Type. Brazil. Amazonas: Near Panuré, at Uaupés River, Oct 1852-Jan 1853 (fl), Spruce 2889 [lectotype (Stafleu, 1954), C, n.v. (photos at F, GH, and MO); isolectotypes, BR, n.v., F-frag, G, n.v., GOET, n.v., K (photo at NY), LD, n.v., NY, OXF, n.v., P-2 sheets, n.v. (photos at NY), RB (photo at NY), W, n.v.]. Figs. 4F, 7E, 13.

Erisma tessmannii Pilger, Notizbl. Bot. Gart. Berlin-Dahlem 11: 295. 1931. Type. Peru. Loreto: In non-flooded forest, San Antonio, near Pongo de Manseriche on the Marañon River, 14 Jan 1924 (fl), Tessmann 4932 [lectotype (Stafleu, 1954), B, not extant (photos at F, MO, and NY).

Tree 40-45 m high; hairs when present yellowish; young twigs pubescent. Leaves opposite; blade coriaceous, elliptic to narrowly elliptic, 7-14 x 2.5-5.5 cm, glabrous above, pubescent to puberulous below; apex acuminate; base obtuse; midvein sulcate above, prominent below; lateral veins 8-10 pairs, immersed above, prominent below, angle with midvein 60-80°; tertiary veins percurrent, sinuous, oblique to midvein, arrangement predominantly alternate; marginal vein 2-3 mm from margin; petiole canaliculate, 5-15 mm long; stipules absent. Inflorescences terminal or axillary-subterminal, 9-15 cm long, peduncles and lateral branches pubescent; cincinni tomentose; outer bracts widely ovate, 7-8 x 4-5 mm; inner bracts lanceolate, 2-3 mm long; pedicels ca. 1 mm long; buds ca. 5 mm long; spurred sepal ca. 9 x 7 mm, spur cylindric, straight, 2-3 mm long.; other sepals 2-5 mm long; petal white or white-yelowish, ca. 15 x 10 mm; stamen ca. 6 mm long; style ca. 6 mm long, glabrous. Fruits winged, pink-yellowish, puberulous, glabrescent, 5-7 cm long; major wing narrowly oblong, 4-6 x 1-1.5 cm; second major wing elliptic or oblong, 2-2.5 x 1-1.5 cm.

Distribution (Fig. 13). A tall tree in non-flooded forests of the Colombian, Peruvian, and western Brazilian Amazon. It flowers from November to June; fruits have

been collected in February and June.

Specimens examined. COLOMBIA. Amazonas: Río Caquetá, left margin, in front of Isla de Mariname, Jul 1989 (st), Urrego 786 (NY).

PERU. Loreto: Maynas, Allpahuayo (estación IIAP), 4°10'S, 73°30'W, 150 m, 6 Jun 1985 (fl, fr), Vásquez et al. 6596 (MER, MO, NY); Iquitos, Iquitos-Nauta Road, km 44, 4°10'S, 73°20'W, 150 m, 14 Dec 1988 (fl), Vásquez & Jaramillo 11427 (MO, NY); Iquitos, Puerto Almendras, Río Nanay, 3°48'S, 73°25'W, 122 m, 29 Mar 1990 (fl), Vásquez & Jaramillo 13677 (MO, NY).

BRAZIL. Amazonas: São Paulo de Olivença, 6 Feb 1937 (fr), Ducke RB 34680 (K, US); Rio Curicuriari, affluent of Rio Negro, Buçú falls, 21 Feb 1936 (fl), Ducke RB 34681 (RB-2 sheets, U, US); Humaitá to Lábrea Road, km 80, between Rio Ipixuna and Rio Itaparana, 24 Nov 1966 (fl), Prance et al. 3249 (B, NY, R, US).

This species is morphologically similar to E. arietinum, as discussed earlier, and to E. floribundum, from which it can be distinguished by the smooth leaves with fewer lateral veins, smooth petiole, and straight spur. In E. floribundum, the leaves are very often bullate because of the impressed and numerous lateral

veins, the petiole is usually distinctly corky, and the spur is curved upwards.

It is also similar to E. gracile which is, however, easily recognized by its small and delicate flowers, the globose calyx-spur, and chartaceous leaves, which are uncommon in the genus.

Pilger (1931) described the Peruvian E. tessmannii, the lectotype of which is not extant and for which no isolectotypes are known. The description and phototype of E. tessmannii do not differ from E. laurifolium and therefore E. tessmannii is considered a new synomym of E. laurifolium.

5. Erisma bracteosum Ducke, Bull. Mus. Hist. Nat. (Paris) 4: 740. 1932. Type. Brazil. Amazonas: In humid, non-flooded forest, near Borba on lower Rio Madeira, 16 Jan 1930 (fl), Ducke RB 23502 [holotype, RB (photo at NY); isotypes, G, n.v., K (photo at NY), NY-2 sheets, P, n.v. (photo at NY), R (photo at NY), RB-4 sheets, S, n.v., U, n.v., US]. Figs. 2E, 4C, 7A, 14.

Erisma djalma-batistae Paula, Bol. Mus. Paraense Hist. Nat. 28: 2-3. 1967. Type. Brazil. Amazonas: Lower falls of the Tarumã, 26 Dec 1962 (fl), W. Rodrigues & D. Coêlho 4940 (holotype, INPA-2 sheets; isotype, MG).

Tree 10-20 m high, to 35 cm DBH; hairs when present yellowish; young twigs puberulous. Leaves opposite; blade subcoriaceous or coriaceous, elliptic or narrowly elliptic, 9.5-23 x 4-11 cm, glabrous; apex acuminate; base acute, obtuse or subcordate; midvein prominent on both surfaces; lateral veins 7-10 pairs, prominent on both surfaces, angle with midvein 60-70°; tertiary veins percurrent, sinuous, oblique to midvein, arrangement alternate and opposite; marginal vein 3-6 mm from margin; petiole terete, 4-9 mm long; stipules subulate, 2 mm long, deciduous. Inflorescences terminal, 11-20 cm long, peduncles and lateral branches pubescent; cincinni 2-2.5 cm long; outer bracts cordate, ca. 12 x 12 mm; inner bracts linear, ca. 2 mm long; pedicel 2 mm long; buds 10-12 mm long, tomentose; spurred sepal up to 12 x 12 mm, spur oblong, recurved, ca. 5 mm long; other sepals 4-8 mm long; petal yellow, ca. 20 x 20 mm; stamen ca. 8 mm long; style ca. 8 mm long, pilose at the base. Fruits winged, puberulous, glabrescent, to 11 cm long; major wing oblong, to 8 x 2.5 cm; second major wing oblong, to 4 x 1.5 cm.

Distribution (Fig. 14). In terra firme forests of western and central Brazilian Amazon. It flowers from October to February. I have not seen fruits of this species even though they were mentioned for the specimen

collected in February (W. Rodrigues 8683).

Specimens examined. BRAZIL. Amazonas: São Jeronimo, Rio Solimões, below Tabatinga, 25 Oct 1931 (fl), Ducke RB 24038 (RB-2 sheets, U, US); São Paulo de Olivença, Rio Solimões, 31 Oct 1931 (fl), Ducke RB 24037 (K, US); São Paulo de Olivença, near Palmares, 11 Sep-26 Oct 1936 (fl), Krukoff 8504 (US); Carauarí, 8 Oct 1975 (fl), Pena 565 (MG); Humaitá to Lábrea Road, km 80, between Rio Ipixuna and Rio Itaparana, 24 Nov 1966 (fl), Prance et al. 3250 (F, INPA, NY, R, RB); Cacau Pireira to Manacapuru Road, km 35, 5 Jan 1967 (fl), Prance et al. 3915 (F, INPA, NY, R); Manaus-Itacoatiara Road, km 65, Reserva Walter Egler, 27 Jan 1970 (fl), W. Rodrigues 8672 (INPA, MER, MG, MO), 4 Feb 1970 (fl), W. Rodrigues 8683 (INPA, MO-2 sheets). Rondônia: Porto Velho, 22 Nov 1949 (fl), N. T. Silva 369 (IAN, NY, R, US).

Erisma bracteosum is easily recognized from the other species of the genus with large and persistent bracts by the prominent midvein on the upper surface of the leaves. Among these species, the calyx-spur is recurved in E. bracteosum, E. floribundum, and E. bicolor. However, the outer bracts and buds of E. bracteosum are larger than those of the other two species.

Erisma djalma-batistae was described as closely related

to E. bracteosum (Paula, 1967b) but differing in height, size and number of flowers of the inflorescences, shape of inner bracts, curvature of the spur, and pilosity of the style. The features used to characterize E. djalma-batistae are often also observed in young specimens of E. bracteosum and they are not consistent enough to maintain it as a distinct species.

Erisma bracteosum, E. calcaratum, E. blancoa, and E. micranthum are distinguished from the other species of the genus by the distinctly prominent venation on the upper surface of the leaves. Among these species, E. bracteosum is the only one with large-bracteate flowers.

6. Erisma gracile Ducke, Arq. Inst. Biol. Veg. 2: 55-56. 1935. Type. Brazil. Amazonas: Near Manaus, in riverine forest, at lesser falls of the Tarumã River, 14 Feb 1933 (fl), 20 Apr 1933 (fr), Ducke RB 24103 [holotype, RB (photo at NY); isotypes, INPA, K (photo at NY), NY, P, n.v. (photos at F, MO, and NY), S, n.v., U, n.v., US]. Figs. 3B, 7D, 13.

Tree 8-25 m high, to ca. 60 cm DBH; hairs yellowish when present; young twigs pubescent. Leaves opposite; blade chartaceous, elliptic or narrowly elliptic, 6.5-10.5 x 2.3-4.3 cm, glabrous; apex acuminate; base

acute to subobtuse; midvein sulcate above, prominent below; lateral veins ca. 7-9 pairs, angle with midvein 60-70°; tertiary veins randomly reticulate; marginal vein 2-5 mm from margin; petiole canaliculate, 6-7 mm long, stipules absent. Inflorescences terminal, up to 12 cm long, peduncles and lateral branches pubescent; cincinni with 3-6 flowers, up to 1.5 cm long, densely tomentose; outer bracts suborbicular, ca. 4 x 4 mm; inner bracts linear, 0.5-1 mm long; pedicels 0.5-2 mm long; buds 3-4 mm long; spurred sepal ca. 5 mm long; spur globose, ca. 1 mm diam.; other sepals 1-5 mm long; petal yellow, obcordate, unguiculate, ca. 10 x 8 mm; stamen ca. 6 mm long; style ca. 5 mm long, pilose at base. Fruits winged, glabrous, 4.5-5 cm long; major wing oblong, 3.5-4.5 x 1-1.3 cm; second major wing 1.5-2 x 0.8-1 cm.

Distribution (Fig. 13). Tall trees in riverine or terra firme forests known only from Central Amazonian Brazil. Flowers have been collected from November to February and fruits in February and April.

Specimens examined. BRAZIL. Amazonas: Manaus, Igarapé da Bolívia, 29 Jan 1963 (fl), Castellanos INPA 27547 (INPA, MER); Manaus, lower falls of Tarumã River, 16 Apr 1958 (fr), Chagas INPA 6354 (INPA, MER), 30 Dec 1936 (fl), Ducke 371 (F, MER, MO, NY, R, US), 7 Feb 1958 (fl),

Pessoal do CPT INPA 6048 (INPA, MER); Humaitá-Lábrea Road, km 80, between Ipixuna and Itaparana rivers, 24 Nov 1966 (fl), Prance et al. 3251 (F, INPA, MG, NY, R). Pará: Porto Trombetas, 10 Jan 1986 (fl), Soares 81 (INPA). Rondônia: Porto Velho, Usina Hidrelétrica de Samuel, Rio Jamari, 18 Jan-11 Feb 1989 (fl, fr), Maciel & Rosário 1711, 1737 (MG).

E. gracile is easily recognized by its chartaceous leaves and small flowers, comparable in size only to those of E. micranthum, which is, however, an unrelated species. The calyx-spur is characteristically globose.

This species could be confused with young forms of E. laurifolium but is distinguished by the texture of the leaves and especially by the spur morphology. In E. laurifolium, the leaves are coriaceous and the spur is cylindric.

7. Erisma lanceolatum Stafleu, Acta Bot. Neerl. 3(4): 470-471, fig. 3a-b. 1954. Type. Brazil. Amazonas: Rio Castanha, affluent of Rio Negro, 27 Apr 1942 (fr), Fróes 12527/221 [holotype, A-2 sheets, n.v. (photos at NY); isotype, F]. Figs. 4H, 13.

Erisma megalophyllum Stafleu, Acta Bot. Neerl. 3(4):

471-472, fig. 3c-d. 1954. Type. Brazil. Amazonas: Non-flooded forest, Igarapé Belém, Rio Solimões, 18 Dec 1948 (fl), Fróes 23741 [holotype, U, n.v. (photo at NY); isotype, IAN (photo at NY)].

Tree to 30 m high, to 100 cm DBH; hairs when present yellowish; young twigs pubescent. Leaves opposite; blade chartaceous, elliptic or narrowly elliptic, 10-21 x 4-7.5 cm, glabrous; apex shortly acuminate; base acute to obtuse; midvein sulcate above, prominent below; lateral veins 8-9 pairs, sulcate above, prominent below, angle with midvein 40-50°; tertiary veins percurrent, sinuous, perpendicular to midvein; marginal vein 3-5 mm from margin; petiole canaliculate, 15-20 mm long; stipules absent. Inflorescences terminal and axillary, to 30 cm long, peduncles and lateral branches pubescent; cincinni to 2.5 cm long, tomentose; outer and inner bracts not seen; pedicel ca. 1 mm long; buds, spurred sepal, and spur not seen; other sepals 3-6 mm long; petal and stamen not seen; style ca. 5 mm long, pilose at base. Fruits winged, puberulous, glabrescent, 6-7.5 cm long; major wing elliptic to narrowly elliptic, 4.5-6 x 2-3 cm; second major wing elliptic, 2.5 x 1-1.5 cm.

Distribution (Fig. 13). A species known only from the type locality and from two collections in non-flooded

forests in northern and western Brazilian Amazonia. Good flowering specimens have not been collected. Old flowers were collected in December and material with fruits in April and August.

Specimens examined. BRAZIL. Amazonas: Pari, Cachoeira do Rio Itiquiê, 23 Aug 1966 (fr), Paula 300 (MG).

This species shows affinities with E. gracile, having in common with it elliptic, glabrous, and chartaceous leaves with fewer lateral veins. The leaves of E. lanceolatum are, however, larger and the petioles are longer; its flowers and fruits are also larger.

Erisma lanceolatum was described from only a fruiting collection (Stafleu, 1954), but it is undoubtedly a distinct species of Erisma. Erisma megalophyllum was described from a collection with old flowers (Stafleu, 1954), and therefore, several floral structures are still unknown. Nevertheless, the type of E. megalophyllum seems to represent an individual of E. lanceolatum with larger leaves. Erisma lanceolatum is the only species of the genus in which axillary panicles have been observed, but the significance of this character can not be determined because only few specimens are available for study.

8. Erisma micranthum Spruce ex Warming, in Martius, Fl. bras. 13(2): 112. 1875. Type. Brazil. Amazonas: Rio Negro, near San Carlos, Dec 1854 (fl), Spruce 3767 [lectotype (Stafleu, 1954), C, n.v. (photo at NY); isolectotypes, B, n.v. (photos at F, MO, and NY), BR, n.v., F, G, n.v., GH, n.v., GOET, n.v. (photo at NY), K (photo at NY), OXF, n.v., P-2 sheets, n.v. (photos at NY), W, n.v.]. Figs. 2D, 4B, 7F, 14.

Tree ca. 10 m high; hairs when present grayish; young twigs puberulous. Leaves opposite; blade coriaceous, narrowly ovate or elliptic to narrowly elliptic, 10-15 x 4.5-8 cm; coriaceous, glabrous; apex acuminate; base obtuse; midvein prominent on both surfaces of the leaf; lateral veins 7-9 pairs, prominent on both surfaces, angle with midvein 60-80°; tertiary veins percurrent, sinuous, oblique to midvein, arrangement alternate and opposite; marginal vein 2-4 mm from margin; petiole terete, 5-10 mm long; stipules 1 mm long, base thickened. Inflorescences terminal, to 15 cm long, peduncles and lateral branches puberulous; cincinni 1 cm long, tomentose; outer bracts linear, 1 mm long; inner bracts absent; pedicel to 1 mm long; buds 3-4 mm long; spurred sepal ca. 3 x 4 mm long, spur globose, ca. 1 mm long; other sepals 1-2 mm long; petal yellowish, red at

base, ca. 5 x 4 mm; stamen ca. 2 mm long; style ca. 2 mm long, glabrous. Fruits winged, puberulous, glabrescent, 3-3.5 cm long; major wing elliptic, ca. 2 x 1 cm; second major wing widely elliptic to elliptic, 1-1.5 x 0.5-1 cm.

Distribution (Fig. 14). In riverine forests of the Venezuelan and northern Brazilian Amazon. Flowers have been collected in November, December, and May, and fruits in February and July.

Specimens examined. VENEZUELA. Amazonas: Yavita, Alto Orinoco, 128 m, 2 Feb 1942 (fr), Williams 14156 (MER, NY).

BRAZIL. Amazonas: Rio Curicuriari, affluent of Rio Negro, Cuina Falls, 30 Nov 1936 (fl), Ducke RB 34684 (K, US); along Rio Curicuriari, ca. 0°20'S, 66°55'W, 13 Jul 1979 (fr), Poole 1994 (F, INPA, MG, MO, NY); Rio Negro, Içana, cachoeira Tunui, 5 May 1947 (fl), Fróes 22276 (MER).

This species is similar to E. calcaratum in the grayish inflorescences and salient venation on the upper surface of the leaves. However, E. micranthum grows in non-flooded forests and has the smallest flowers and fruits of the genus. In contrast, E. calcaratum, found in inundated forests, with its peculiar wingless

fruits and very large flowers, is one of the most distinct species of Erisma.

Erisma micranthum is also similar to E. blancoa in leaf morphology, but these two species differ in the color of the pubescence (grayish in E. micranthum and yellowish in E. blancoa) and dimensions of flowers (petal ca. 5 mm long in E. micranthum and ca. 10 mm in E. blancoa) and fruits (to 3.5 cm in E. micranthum and to 10.5 cm in E. blancoa).

9. Erisma calcaratum (Link) Warming, in Martius, Fl. bras. 13(2): 111-112. 1875. Type. Based on Qualea calcarata Link. Figs. 4D, 5C, 7I, 8C, 14.

Qualea calcarata Link, Jahrb. Gewächsk. 1(3): 24-25. 1820. Type. Brazil. Pará: Probably from around Belém, no date (fl), Hoffmannsegg s.n. [holotype, B, n.v. (photo at NY)].

Erisma violaceum Martius, Nov. Gen. sp. pl. 1: 137-138, t. 82. 1824. Type. Brazil. Pará: Marajó, at mouth of Tocantins River, on banks of Igarapé Mirim and Tagipurú, Sep (fl), Martius s.n. [holotype, K (photo at NY); isotype, MO].

Tree 10-20 m high, to 40 cm DBH; hairs when present grayish-tomentose. Leaves opposite; blade coriaceous, elliptic or narrowly elliptic, 12-28 x 4.5-11.5 cm, glabrous; apex acute or acuminate; base obtuse, rounded or subcordate; midvein prominent on both surfaces of the leaf; lateral veins 7-9 pairs, prominent on both surfaces, angle with midvein 60-70°, anastomosing irregularly; tertiary veins percurrent, sinuous, aprox. at right angles and oblique to midvein, arrangement alternate and opposite; petiole terete, 5-10 mm long; stipules subulate, ca. 3 mm long. Inflorescences terminal, 16.5-23 cm long, peduncles and lateral branches densely pubescent; cincinni 1.5-4 cm long; outer bracts oval-orbicular, ca. 2 x 2 mm, deciduous; inner bracts linear, ca. 1 mm long; pedicel 1-2 mm long; buds 10-13 mm long; spurred sepal ca. 10 x 10 mm, spur conical, 5-6 mm long, incurved; other sepals 7-9 mm long; petal blue or purplish, ca. 15 x 15 mm; stamen ca. 9 mm long; staminodes 1-3, 1-5 mm long, style ca. 9 mm long, pilose at base. Fruits without wings, woody, longitudinally ridged, rugose, 5.5-6.5 x 2.5-3 cm, glabrescent.

Distribution (Fig. 14). A locally common species in inundated forests of both white and black water rivers. It blooms mainly from September to December. Fruits have been collected from January to May.

Representative specimens. VENEZUELA. Amazonas: El Sipapo forest reserve, Sipapo River, May 1971 (fr), Blanco 1233 (MER, NY, US); Río Autana, 26 Oct 1982 (fl), Lasi 3 (MER); San Carlos de Rio Negro, ca. 20 km S of confluence of Rio Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 119 m, 29 Apr 1981 (fr), Clark & Maguirino 7991 (MO, NY); San Carlos, upper Rio Negro, 15 Dec 1947 (fl), Schultes & López 9378 (NY, US); Rio Cassiquiare, between mouth of river and El Merey, 1°58'N, 66°55'W, 150 m, 20-30 Oct 1986 (fl), Stergios et al. 9575 (MER, NY).

PERU. Loreto: Maynas, Río Nanay, Puerto Almendras, 3°48'S, 73°25'W, 122 m, 20 Jul 1982 (fl), Vásquez & Jaramillo 3163 (MER, MO, NY); Río Mamón, near Río Nanay, 1 Sep 1972 (fl), Croat 19878 (AAU, F, MER, MO, NY); Alto Río Nanay, between Santa María de Nanay and Diamante Azul, 140 m, 25 Mar 1979 (fl), Gentry et al. 26206 (NY); Iquitos, Nanay river from Bellavista to Pampachica, ca. 105 m, 30 Jul 1975 (fl), Rimachi 1808 (MO, NY).

BRAZIL. Roraima: São Luíz do Amauá, Manaus-Caracaraí Road (BR-174), km 330, to São José do Boraçu village, 36 km on BR-174, 0°10'S, 61°02'W, 22 Aug 1987 (fl), Cid 9092 (NY). Amapá: Macapá, Igarapé do Lago, 26 Oct 1980 (fl), Rabelo 877 (MG-2 sheets); Ariramba, 26 Jun 1982 (fl), Rosa & Alfeu 4386 (MG, NY). Amazonas: Upper Rio Negro basin, Cucuí, 7 Dec 1947 (fl), Schultes & López 9252 (NY,

US); Tapuruquara, 21 Oct 1971 (fl), Prance et al. 15761 (F, MER, MG, NY); Rio Negro, right side of Ilha Tamanduá (locality Ilha Marajó), 0°06'N, 67°16'W, 20 Oct 1987 (fl), Maas et al. 6809 (NY); São Gabriel da Cachoeira, left margin of Rio Negro, Lago Ataana, 10 Oct 1978 (fl), Nascimento 582 (MG, NY); Barcelos, at mouth of Rio Ararirá, right margin of Rio Negro, 0°30'S, 63°30'W, 8 Oct 1987 (fl), Cid 9278 (INPA, NY); Rio Negro, Ponta do Pagodão, 6 Sep 1987 (fl), Kawasaki & Mori 80 (INPA, NY); Rio Negro, Arquipélago das Anavilhanas, 29 Sep 1975 (fl), Kubitzki 75-103 (HBG); Rio Negro, near mouth of Rio Cuieiras, 70-100 m, 7 Oct 1988 (fl), Mori & Gracie 19251 (NY); Manaus, igarapé do São Raimundo, 20 Sep 1956 (fr), D. Coêlho s. n. (F, INPA); Manaus, lower falls of Tarumã river, 17 Nov 1966 (fl), Prance et al. 3193 (INPA, NY, R); Manaus, Sep 1851 (fl), Spruce 1798 (K, NY); Presidente Figueiredo, Rio Uatumã, Igarapé Barreto, Balbina, 1°30'-2°00'S, 59°30'-60°00'W, 17 Sep 1986 (fl), Cid et al. 8172 (NY); between Maraã and Japurá, Rio Japurá, 8 Nov 1982 (fl), Cid & Lima 3519 (F, K, MG, MO, NY, US). Pará: Caripi, Aug 1849 (fl), Spruce 125 (K-2 sheets); Rio Jari, Munguba, 6 Aug 1969 (fl), N. T. Silva 2608 (INPA, NY); Gurupá, 25 Sep 1916 (fl), Ducke MG 16536 (R, US); Rio Amazonas, Antonio Lemos, Igarapé Pixuna, Tajupurú river, 19 Jul 1948 (fl), Black 48-2951 (US);

Ilha do Marajó, sítio Campina on Pracuubamirim, ca. 1 hour by boat upstream from São Sebastião de Boa Vista, 20 Oct 1984 (fr), Sobel et al. 4756 (NY); Rio Xingu, Vitória, 21 Nov 1943 (fr), Fróes 20296 (NY); Rio Acará, between Tomé-Açu and Acará, 2 Jun 1969 (fl), Cavalcante 2231 & Austin 4104 (MG, MO).

Local names. Venezuela: chimaco (Baré language). Peru: sacha caca-huillo, cacahuillo. Brazil: jaboti-da-várzea, cachimbo-de-jaboti, jaboti, vergalhão-de-jaboti, aburana.

Erisma calcaratum is the only species of the genus typical of inundated forests, both in várzeas and igapós, and has wingless fruits that float and are dispersed by water. The species was originally described in Qualea of the tribe Vochysieae (Link, 1820). This tribe is characterized by genera with superior, trilocular ovaries, and dehiscent fruits. However, E. calcaratum undoubtely belongs to the tribe Erismeae because of its inferior and unilocular ovary and indehiscent fruits. The unusual and distinct fruits of this species were first described by Ducke in 1922.

This species is also characterized by the prominent midvein on the upper surface of the leaves, the grayish inflorescences, the large buds with incurved spur, and the purple flowers. Erisma calcaratum and E. uncinatum

are by far the two most common species of the genus, widely distributed throughout the Amazon basin. Within the genus, the grayish inflorescences with purple flowers are found only in these two species, which are, however, unrelated species distinguished by habitat, leaf venation, spur shape, and fruit morphology.

Erisma calcaratum is closely related to E. micranthum, as already mentioned by Warming (1875), and it also shows affinities with E. japura. It is similar in leaf morphology to E. blancoa, which is, however, an unrelated species. The differences among E. calcaratum, E. micranthum, E. japura, and E. blancoa are summarized in the key to the species.

10. Erisma japura Spruce ex Warming, Fl. bras. 13(2): 109-110. t. 21, fig. 1. 1875. Type. Brazil. Amazonas: Near Panuré on the Vaupés River, Oct 1852-Jan 1853 (fl, fr), Spruce 2613 [lectotype (Stafleu, 1954), C, n.v.; isolectotypes, BR, n.v., F-2 sheets, G, n.v., GH, n.v., GOET, n.v., K-4 sheets (photos at NY), NY, OXF, n.v. (photo at NY), P-3 sheets, n.v. (photos at NY), RB (photo at NY), S, n.v., US-2 sheets, W, n.v.]. Figs. 4A, 7J, 15.

Tree to 30 m high, to 50 cm DBH; hairs where present grayish; young twigs pubescent. Leaves in 4-merous

whorls, long-petiolate; blade coriaceous, elliptic, narrowly elliptic, narrowly obovate, or oblanceolate, 11-20 x 4.5-8 cm, glabrous; apex emarginate; base cuneate, decurrent; midvein sulcate above, prominent below; lateral veins 15-17 pairs, immersed or slightly sulcate above, slightly prominent below, angle with midvein 60-70°; tertiary veins percurrent, sinuous, oblique to midvein, arrangement alternate and opposite; marginal vein 1-2 mm from margin; petiole canaliculate, 20-40 mm long; stipules lanceolate, ca. 3 mm long, deciduous. Inflorescences terminal, to 18 cm long, peduncles and lateral branches pubescent; cincinni 3-3.5 cm long, tomentose; outer bracts ca. 8 x 5 mm, early deciduous; inner bracts linear, ca. 3 mm long, deciduous; pedicel 3-4 mm long; buds 10-12 mm long; spurred sepal ca. 12 x 12 mm, spur subglobose, ca. 3 mm diam.; other sepals 4-7 mm long; petal yellow, ca. 20 x 25 mm; stamen ca. 14 mm long; staminodes ca. 3 mm long; style ca. 12 mm long, glabrous. Fruits winged, puberulous, glabrescent, 10-13 cm long; major wing narrowly ovate or narrowly elliptic, 9-11 x 3-4 cm; second major wing narrowly oblong or narrowly ovate, ca. 5 x 2.3 cm.

Distribution (Fig. 15). In terra firme forests of the Upper Rio Negro and Vaupés region. Collected in flower from October to April, and in fruit in February and April.

Specimens examined. COLOMBIA. Vaupés: Alto Río Papurí, near Yapú, Apr 1977 (fr), Patmore & Dufour 78 (K, US), 13 Mar 1978 (fl), Patmore & Dufour 164 (K).

BRAZIL. Amazonas: Rio Curicuriarí, affluent of Rio Negro, Mirapora, 25 Feb 1936 (fr), Ducke RB 34678 (US); São Gabriel, Rio Negro (Cabari), 30 Oct 1932 (fl), Ducke RB 23798 (INPA-2 sheets, K, RB-3 sheets, US); Marabitanas, Rio Negro, 20 Apr 1947 (fl), J. M. Pires 470 (NY-2 sheets, US); Rio Negro, at its confluence with Rio Uaupés, upper slopes and summit of Serra Camaleão, 200-250 m. 0°07'N, 67°18'W, 22 Nov 1987 (fl), Stevenson et al. 1012 (INPA, K, NY, US).

Local names. Colombia: batí (Tayuto language), yapurá (Língua Geral). Brazil: japurá.

Erisma japura is one of the most distinctive species of Erisma. It is easily recognized by its emarginate leaves with long petioles arranged in tetramerous whorls, its grayish inflorescences with yellow flowers, and its large fruits. Erisma japura is also characterized by large buds (10-12 mm long), which can be compared in size only to those of E. bracteosum (10-12 mm long) and E. calcaratum (10-13 mm long).

The epithet "japurá" is the indigenous name given to this species. The japurá paste obtained from its seeds, already mentioned by Spruce on the label of the type specimen (Spruce 2613) collected on the Upper Rio Negro, is known as a food source among the indigenous population of the northwestern Amazon (Dufour & Zarucchi, 1979).

11. Erisma nitidum DC., Prodr. 3: 30. 1828. Type. French Guiana. Roura Mountain, no date (fl) Martin s.n. [lectotype (Stafleu, 1954), FI, n.v.; isolectotypes, G-DEL, n.v. (photo at NY), P-3 sheets, n.v. (photos at F, MO, and NY)]. Figs. 2A, 3A, 7L, 13.

Tree to 30 m high, to 40 cm DBH; hairs when present yellowish-brown. Leaves opposite; blade chartaceous, shiny above, elliptic, 10-18 x 5-8 cm, glabrous; apex shortly acuminate; base obtuse; midvein sulcate above, prominent below; lateral veins 7-9 pairs, prominent on both surfaces, densely reticulate, angle with midvein 60-70°; tertiary veins randomly reticulate; marginal vein 5-10 mm from margin; petiole canaliculate, 6-8 mm long; stipules subulate, ca. 2 mm long, deciduous. Inflorescences terminal, ca. 20 cm long, peduncles and lateral branches pubescent; cincinni with 2-5 flowers,

ca. 2 cm long, tomentose; outer and inner bracts deciduous; pedicel ca. 1 mm long; buds ca. 6 mm long; spurred sepal ca. 5 mm long, spur cylindric, straight, ca. 4 mm long; other sepals 2-5 mm long; petal white, yellow in center, ca.10 x 10 mm; stamen ca. 5 mm long; style ca. 5 mm long, pilose at the base. Fruits winged, puberulous, glabrescent; major wing elliptic to narrowly elliptic, 5-5.5 x 2 cm; second major wing elliptic, 2-3 x 1.2-1.6 cm.

Distribution (Fig. 13). Known only from non-flooded forests on white sand in French Guiana and Guyana. Collected in flower in October and November. One report of fruits collected in November (Stafleu, 1954).

Specimens examined. GUYANA. Kangaruma, Potaro River, Essequibo, Oct 1922 (fl), Abraham 347 (K, US); Mahdia, Potaro River, Bartica-Potaro road, 1 Nov 1943 (fl), Forest Dept. British Guiana 3743 (NY-2 sheets); Potaro River, Cobanatuk falls, Oct 1898 (fl), Jenman 7439 (K, NY).

Erisma nitidum is distinguished by the shiny, chartaceous leaves with few pairs of lateral veins joining to form marginal vein 5-10 mm from the margin, and by flowers with a cylindric and straight spur. It is

the only species of the genus restricted to the Guianas and is probably rare in the region. Although one of the first species of Erisma described (Candolle, 1828), it remains poorly collected. I have not studied any recent collections of this species.

12. Erisma splendens Stafleu, Acta Bot. Neerl. 3: 476-477, fig. 4. 1954. Type. Brazil. Amazonas: Manaus, Mindú River, 28 Nov 1935 (fl), Ducke RB 34682 [holotype, U, n.v. (photo at NY); isotypes, G, n.v., K (photo at NY), P, n.v. (photo at NY), RB-11 sheets (photo at NY), S, n.v., U, n.v., US)]. Figs. 3C, 7K, 8D, 15.

Tree 8-30 m high, 8-50 cm DBH; hairs when present yellowish; young twigs glabrous. Leaves opposite; blade coriaceous, discolor, shiny, yellowish-green above, brownish below, elliptic to widely elliptic, 9-17 x 4-11.5 cm, glabrous; apex acuminate; base acute; midvein sulcate above, prominent below; lateral veins 10-13 pairs, prominent on both surfaces of the leaf, angle with midvein 60-70°; tertiary veins randomly reticulate; marginal vein 1-2 mm from margin; petiole canaliculate, 20-25 mm long, stipules subulate, ca. 3 mm long. Inflorescences terminal, up to 17 cm long, peduncle and

lateral branches puberulous; cincinni to 1.5 cm long, tomentose; bracts deciduous; pedicel ca. 2 mm long; buds 4-5 mm long; spurred sepal ca. 5 mm long; spur subglobose, ca. 1 x 1 mm; other sepals 1-3 mm long; petal yellow internally, white or pale lilac externally, ca. 10 x 9 mm; stamen ca. 6 mm long; style ca. 5 mm long, pilose at the base. Fruits winged, glabrous, 7.5-8 cm long; major wing narrowly elliptic, 6-7.5 x 2-2.5 cm; second major wing elliptic, 2.5-3 x 1.5-2 cm.

Distribution (Fig. 15). Trees in terra firme forests of the Colombian, Venezuelan, and Central Brazilian Amazon. In Colombia and Venezuela, flowers were collected in May and fruits in June. In Brazil, it flowers from November to February, and fruits from December to April.

Specimens examined. COLOMBIA. Amazonas: Río Atabapo, Chamochina, Guainía, 14 May 1979 (fl), R. Rodríguez & E. Acero 192 (INPA).

VENEZUELA. Amazonas: Atabapo, Cucurital de Caname, SE bank of the middle part of Caño Caname, 3°40'N, 67°22'W, 100 m, 30 Apr-1 May 1979 (fl), Davidse et al. 17003 (MER); Caño San Miguel, just above Limoncito, 15 km from Guainía River, 28 Jun 1959 (fr), Wurdack & Adderley 43227 (NY).

BRAZIL. Amazonas: Manaus, 2 Feb 1930 (fl), Ducke RB 23501 (INPA, K, MG, R, RB, US); Manaus, lower falls of Tarumã River, 18 Apr 1967 (fr), Albuquerque & Elias 67-30 (INPA, MER), 7 Jan 1963 (fl), Chagas & W. Rodrigues 4947 (INPA), 6 Dec 1955 (fl), D. Coêlho s.n. (INPA), 6 Dec 1955 (fl), L. Coêlho INPA 3038 (INPA, MG), INPA 3054 (INPA, MG), 27 Apr 1966 (fr), D. Coêlho & W. Rodrigues 7723 (INPA, MER), 30 Dec 1936 (fl), Ducke RB 34683 (US), 7 Feb 1958 (fr), Pessoal do CPT INPA 6049 (INPA, MER, MG), 27 Dec 1962 (fr), W. Rodrigues & D. Coêlho 4947 (MER); Manaus, Igarapé de São Raimundo, 27 Jan 1956 (fr), D. Coêlho s.n. (INPA, MER); Manaus, Cachoeira Grande, 30 Nov 1935 (fl), Ducke 96 (F, K, MO, NY, R, US); Manaus, near lodging of Experimental Reserve, 23 Nov 1976 (fl), Mello 5 (INPA); Manaus-Caracaraí Road, near biological reserve of Km 60, 18 Feb 1977 (fr), J. R. Nascimento & J. G. Oliveira 517 (INPA); Presidente Figueiredo, Balbina, road to Cachoeira Morena, 11 km from Balbina, left side of Uatumã River, 1-2 Km S, 59-60 W, 14 Mar 1986 (fr), Cid et al. 6764 (INPA, NY).

Erisma splendens is characterized by long-petiolate (20-25 mm long), shiny and discolorous leaves, which are yellowish-green above, brownish below; by the marginal vein at 1-2 mm from the margin; by inflorescences with

yellowish pubescence; and by small flowers with globose spur.

In the features of the shiny leaves with randomly reticulate tertiary venation and color of pubescence, it is similar to E. nitidum. However, E. nitidum has short petioles (6-8 mm long), leaves with the marginal vein at 5-10 mm from margin, and flowers with cylindric spurs.

13. Erisma uncinatum Warm., in Martius, Fl. bras. 13(2): 110-111. 1875. Type. Brazil. Amazonas: Ega, 1831 (fl), Poeppig 2633 [lectotype (Stafleu, 1954), W, n.v.; isolectotypes, BM, n.v., F, G-DEL, n.v. (photos at F and MO), GOET, n.v., L, n.v., P, n.v. (photo at NY), US)]. Figs. 4G, 5D, 7G, 11, 15.

Erisma pulverulentum Poepp. ex Warm., Vidensk. Meddel. Naturhist. Foren. Kjoebenhavn 1889: 28. 1889. nom. nud.

Tree to 40 m high, to 150 cm DBH; hairs when present grayish; young twigs pubescent. Leaves opposite or in tetramerous whorls; blade coriaceous, elliptic, narrowly elliptic or narrowly obovate, 8.5-23 x 4.5-9.5 cm, glabrous above, puberulous, glabrescent below; apex obtuse or obtuse-acuminate; base acute, attenuate;

midvein immersed or sulcate above, prominent below; lateral veins 5-9 pairs, sulcate above, prominent below, angle with midvein 40-60°; tertiary veins percurrent, sinuous, perpendicular to midvein, predominantly opposite; marginal vein absent; petiole 8-13 mm long; stipules subulate, ca. 2 mm long, deciduous. Inflorescences terminal, 17-28 cm long, peduncles and lateral branches tomentose; cincinni 1.5-2 cm long, tomentose; outer bracts suborbicular, 2-3 x 2-3 mm, deciduous; inner bracts linear, 1-2 mm long; pedicels ca. 1 mm long; buds 6-9 mm long; spurred sepal ca. 7 x 8 mm long, spur uncinate-incurved, 2-2.5 mm long.; other sepals 2-3 mm long; petal blue or purple, ca. 10 x 12 mm; stamen ca. 6 mm long; style 5-6 mm long, pilose at the base. Fruits winged, bluish-green, puberulous, glabrescent; major wing narrowly elliptic or oblong, 5.3-7 x 1.8-2.5 cm; second major wing elliptic, 1.3-1.8 x 2-3.5 cm.

Distribution (Fig. 15). The most common species of Erisma, widespread in terra firme forests of the Guianas and the Amazon basin. It blooms mainly from August to January, but flowering collections have also been made in March, May, and July. Fruits have been collected mostly from December to February, but also from July to September.

Representative specimens. COLOMBIA. Vichada: Parque Nacional Natural El Tuparro, ca. 7 km of El Tapon, 5°10'N, 69°06'W, 110 m, 19 Mar 1985 (fl), Zarucchi & Barbosa 3763 (MER, MO, NY).

VENEZUELA. Amazonas: Río Manapiare, Guara village, southeast trail to Caño Garrafón, 5°15 N, 66°03 W, 140 m, 25 Jan 1977 (fr), Huber & Canales 408/21.24.30 (MER, NY-2 sheets); Cerro Duida, Río Cunucunuma, return to Culebra from Cerro Duida Camp, 26 Nov 1950 (fl), Maguire et al. 29737 (NY); Cerro Moriche, Río Ventuari, 500 ft, 16 Jan 1951 (fl), Maguire et al. 30974A (F, NY, US), 30974B (NY, US); Atabapo, Río Cunucunuma, between Culebra and Huachamacari villages, between Cerro Duida and Huachamacari, 180-210 m, 3°40'N, 65°45'W, 28-30 Jan to 6-8 Feb 1982 (fl), Steyermark et al. 125854 (MER, NY). Bolívar: El Palmar to Río Grande, Serra Imataca, 300 m, 16 Feb 1959 (fr), Bernardi 7078 (MER, US); NE of Upata, 8°16'N, 62°13'W, 500 m, 19 Mar 1966 (fl), Breteler 5049 (MER, MG, NY); El Tigre-La Soledad Road, 29 May 1965 (fl), Marcano-Berti 736 (B, F, MO, NY-2 sheets, US-2 sheets); Nuría, between El Cruzero and slightly beyond pica 101, ESE of Villa Lola, 315 m, 15 Jul 1960 (fr), Steyermark 86371 (F, K, NY); along road S of El Dorado, between km 42 and 65, 26 Jul 1960 (fr), Steyermark 86678 (NY); vicinity of Caño Sucio, upstream from Raudal Catua,

4 km E of Río Asa, S of La Paragua, 290 m, 3 Aug 1960 (fr), Steyermark 86818 (NY); 3-4 km SE of Los Patos, N of Río Hacha and N of Río Supamo, 30 km S of El Manteco, 365 m, 9 Aug 1960 (fr), Steyermark 87077 (NY); along Río Parguaza just below Raudal Maraca, 115 m, 30 Dec 1955 (fl), Wurdack & Monachino 41036 (NY). Delta Amacuro: E of Río Grande, E-NW of El Palmar, near border of Bolívar, Nov 1965 (fl), Blanco 512 (MER, NY-2 sheets, US); El Palmar-Raudal Trail, upper Río Toro drainage, 270-470 m, 20 Nov 1955 (fl), Wurdack & Monachino 39685 (F, NY, US).

GUYANA. Wabuwak, Kanuku Moutains, lower slopes on N side of Kanuku Mountains, Oct 1948 (fl), Forest Dept. British Guiana WB387/5801 (K, NY, US); Iramaipang, Kanuku Mountains, Nov 1948 (fl), Forest Dept. British Guiana WB530/5929 (K, NY).

SURINAM. Sectie 0, 3 Oct 1907 (fl), Boschwezen 46 (K, MO, NY); Zanderij I, tree #48, 9 Jan 1918 (fr), collector unknown herb.3580 (K, NY, US); Brokopondo, National Park Brownsberg, 12 Jul 1974 (fl), Vreden LBB 13726 (K, NY).

FRENCH GUIANA. Yaroupi river, 0-5 km from its confluence with Rio Oiapoque, 2°48'N, 52°28-31'W, 25 Sep 1960 (fl), Irwin et al. 48472 (F, NY, US); Saül, La Fumée West, 3°37'N, 53°12'W, ca. 200-300 m alt., 14 Sep 1989 (fl), Mori et al. 20890 (NY), 25 Apr 1983 (seedlings), Mori & Pipoly 15667 (NY); Saül, on Route de Belizón south

of Eaux Claires, 3°37'N, 53°W, ca. 200-300 m alt., 9 Nov 1990 (fl), Mori et al. 21585 (NY); Cayenne, P.K. 14200, left side and 150 m from road, 7 Nov 1957 (fl), colector unknown 7750 (NY); Mana-Gallo road, km 12500, left side, at 50 m of road, 23 Dec 1955 (fr), collector unknown 7121 (NY).

ECUADOR. Napo: Jatun Sacha Biological Station, 8 km E of Misahualli, 1°04'S, 77°36'W, 450 m, 17-21 Nov 1988 (fl), Cerón & Iguago 5629 (MO, NY), 4 Nov 1987 (fl), Neill & Manning 7988 (NY).

PERU. Loreto: Coronel Portillo, Callería, 150 m, vivero florestal Pucallpa, 3 Nov 1967 (fl), Cáceres 8 (F, NY). San Martín: Mariscal Cáceres, Uchisa, 650 m, km 30 of the road bordering the forest, 21 Sep 1967 (fl), Rodríguez del Aguila 4 (F, MO, NY).

BRAZIL. Amapá: Rio Oiapoque, about 1-3 km N of Cachoeira Três Saltos, 2°12-13'N, 52°52-53'W, 12 Sep 1960 (fl), Irwin et al. 48205 (MO, NY, US); Mazagão, Camaipi, EMBRAPA reserve and vicinity, 30 km NW of Mazagão, 0°10'N, 51°37'W, 23 Dec 1984 (fr), Mori et al. 17515 (NY). Amazonas: Without locality, no date (fl), Riedel s.n. (NY); Borba, Rio Madeira, Aug 1936 (fl), Ducke 264 (F, MO, NY, R, US); São Paulo de Olivença, 4 Nov 1927 (fl), Ducke RB 20560 (US); Santo Antonio do Abonari, Manaus-Caracaraí Road, km 220, 26 Nov 1976 (fl), Prance

et al. 24309 (MER, NY). Pará: Lower falls of Tapajós river, Periquito, 6 Dec 1919 (fl), Ducke RB 13691 (US); Serra Iricoumé, forest by field by Shuurutirir Camp, 11 Sep 1952 (fl), Forest Dept. British Guiana G565/7580 (NY-3 sheets, US); Peixe-Boi, Belém-Bragança Road, Sep 1907 (fl), Ducke 8322 (R, US); Belém, Reserva Utinga, 3 Nov 1989 (fr), Kawasaki et al. 396 (INPA, MG, NY, K, US); Belém, grounds of Instituto Agronômico do Norte, 17 Aug 1964 (fl), Prance & N. T. Silva 58748 (LS72) (B, NY-2 sheets, US); Marabá, Carajás, Serra Norte, PA-275, 10 km from camp site, 3 Aug 1982 (fl), Maciel et al. 726 (MG, NY); Rio Jari, Monte Dourado, Planalto B, between Pilão and Repartimento, 31 Oct 1968 (fl), N. T. Silva 1347 (NY, US). Maranhão: Maracaçumé river region, 15 Oct 1932 (fl), Fróes 1939 (F, K, MO, NY, US); Turiaçu, km 6 of BR 106 Maracaçumã-Santa Helena, fazenda Maracaçumã Agro-Industrial Grupo Mesbla, 30 Nov 1978 (fl), Rosa & Vilar 2755 (F, MER, MG, MO, NY). Acre: Near mouth of Rio Macauhan, tributary of Rio Yaco, 22 Aug 1933 (fl), Krukoff 5603 (NY-2 sheets, US). Rondônia: Brasília-Acre Road, 1 km beyond camp, 66 km W of Vilhena, 5 Sep 1963 (fl), Maguire et al. 56585 (MG, NY, US). Mato Grosso: Aripuanã, km 245 da BR 174, Projeto Juina, linha 4, 18 Jan 1979 (fr), M. G. Silva & Pinheiro 4320 (F).

BOLIVIA. Pando, N. Suárez, estación experimental, 27

km of Pando, 25 Oct 78 (fl), Meneces 796 (NY-2 sheets).

Local names. Venezuela: daujen, mureillo, salado. Guyana: prumaye. Surinam: mowsi-kwari, singri-kwari. French Guiana: couali, man-onti-kouali (Paramaka language). Peru: asta-de-veado-negro. Brazil: bruto, jaboti-da-terra-firme, quaruba-antã, quarubarana. Bolivia: guarú.

This species is characterized by the distinctly eucamptodromous leaves, the grayish inflorescences with purple flowers, and the uncinate-incurved calyx-spur. Within the genus, this type of spur and the eucamptodromous leaves are also found only in E. fuscum, and affinities between these two species are here suggested.

Erisma uncinatum is the most commonly collected species of the genus. The large number of specimens of this species can only be compared to the number of collections of E. calcaratum, which grows in inundated forests. Erisma uncinatum has in common with the latter species the grayish inflorescences with purple flowers. Nevertheless, these two species are very distinct from each other, differing markedly in their habitat, leaf morphology, and the type of fruits.

14. Erisma fuscum Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 105-106. 1925. Type. Brazil. Pará: In non-flooded forest, near Antonio Lemos, by the Tajapurú River in the Amazon estuary by Breves, 18 Feb 1922 (fl), 19 Mar 1923 (fr), Ducke RB 17745 [holotype, RB (photo at NY); isotypes, G, n.v., K (photo at NY), P, n.v. (photos at F, MO, and NY), S, n.v., U, n.v. (photo at NY), US]. Figs. 3E, 7H, 15.

Tree ca. 25 m high; hairs when present brown; young twigs pubescent. Leaves opposite; blade coriaceous, narrowly obovate to obovate, 14-16 x 6.5-9 cm, glabrous above, puberulous, glabrescent below; apex obtuse, shortly acuminate, mucronate; base subcordate, folded; midvein sulcate above, prominent below; lateral veins 9-10 pairs, sulcate above, prominent below, angle with midvein 50-60°; tertiary veins percurrent, sinuous, oblique to midvein, arrangement opposite; marginal vein absent; petiole canaliculate, ca. 5 mm long; stipules unguiculate, 6-8 mm long. Inflorescences terminal, to 25 cm long, peduncles and lateral branches pubescent; cincinni tomentose; outer bracts linear, ca. 2 mm long; inner bracts absent; pedicel to 1 mm long; buds 6-7 mm long; spurred sepal ca. 6 x 7 mm, spur uncinate-incurved, ca. 3 mm long; other sepals 2-4 mm long; petal purple,

ca. 13 x 13 mm; stamen ca. 6 mm long; style ca. 6 mm long, pilose at the base. Fruits winged, puberulous, glabrescent, to 8.5 cm long; major wing elliptic, ca. 6.5 x 3 cm; second major wing widely elliptic, ca. 2 x 1.5 cm.

Distribution (Fig. 15). Known only from two collections from non-flooded forests: the type from eastern Brazilian Amazonia and a second collection from central Brazilian Amazonia. It probably flowers from October to February and fruits in March.

Specimens examined. BRAZIL. Amazonas: Humaitá, near Livramento, on Rio Livramento, 12 Oct-6 Nov 1934 (fl), Krukoff 6927 (NY).

Erisma fuscum is characterized by short-petiolate, obovate, eucamptodromous leaves with a subcordate, folded base; by inflorescences covered with dark-brown hairs; and by purple flowers with uncinate-incurved spur. It is very similar to E. uncinatum, having in common with this species unusual characters in the genus such as the eucamptodromous leaves, the uncinate-incurved spur, and the purple flowers. If it were not for the dark-brown pubescence and subcordate leaves of E. fuscum, in contrast to the grayish hairs and acute leaves

of E. uncinatum, the two names could be synonymous. Erisma fuscum is known from only two collections whereas E. uncinatum is the most commonly collected species of the genus. In the numerous collections studied of the latter species, the color of the inflorescences and the leaf bases are consistent.

It is likely that E. fuscum is an extremely rare species. Only a single tree was seen by Ducke, who first collected and described the species (Ducke, 1925). The only other known collection is from Humaitá, in the Brazilian Amazon. This area and the type locality near Belém, in the state of Pará, represent some of the most extensively collected sites in the Brazilian Amazon. However, no recent collections of this species have been made.

15. Erisma silvae Marcano-Berti, Pittieria 13: 15-18. 1986; Pittieria 18: 12. 1989. Type. Brazil. Amazonas: Neblina, margin of Rio Maturacá, between Salesiana Mission and the Rio Cauaburí, 8 Jan 1966 (fl), N. T. Silva & U. Brazão 60790 [lectotype (Marcano-Berti, 1989), VEN, n.v.; isolectotypes, F, NY-3 sheets, P, n.v. (photo at NY), RB]. Figs. 2B, 3G, 7M, 15.

Tree to 30 m high, to 60 cm DBH; hairs when present brown; young twigs pubescent. Leaves opposite; blade coriaceous, oblong or ovate to narrowly ovate, 17-30 x 7.5-16.5 cm, glabrous above, puberulous to glabrous below; apex shortly acuminate; base obtuse or subcordate; midvein sulcate above, prominent below; lateral veins 12-13 pairs, sulcate above, prominent below, angle with midvein 50-60°; tertiary veins percurrent, sinuous, oblique to midvein, arrangement predominantely opposite; marginal vein 2-5 mm from margin; petiole canaliculate, 5-10 mm long; stipules unguiculate, 4-7 mm long. Inflorescences terminal, 18-26 cm long, peduncle and lateral branches pubescent; cincinni ca. 1.5 cm long, tomentose; outer bracts ca. 4 x 4 mm; inner bracts linear-lanceolate, ca. 3 mm long; pedicel ca. 1 mm long; buds 6-7 mm long; spurred sepal ca. 7 x 7 mm, spur globose, ca. 1 x 1 mm; other sepals 3-5 mm long; petal yellow, ca. 10 x 10 mm; stamen ca. 4 mm long, staminodes 1-2 mm long, pilose; style ca. 5 mm long, pilose at the base. Fruits unknown.

Distribution (Fig. 15). Known only from the type locality. Flowers were collected in January. I have not seen any collections with fruits.

I have studied only the type collection of E. silvae. It differs in the dark-brown pilosity of the inflorescences, a feature in common only with E. fuscum. However, the flowers of E. fuscum are purple and the calyx-spur is typically uncinate-incurved, whereas in E. silvae the flowers are yellow and the spur is globose. Although the type specimens of E. silvae show variations in leaf morphology, I am unable to suggest closer affinities between these two species because of the differences in the spur morphology which I have observed as being uniform for each species of Erisma.

16. Erisma blancoa Marcano-Berti, Pittieria 13: 12-15. 1986; Pittieria 18: 12. 1989. Type. Venezuela. Amazonas: El Sipapo Forest Reserve, margins of Río Cuao, between El Sipapo and the Danto Rapids, May 1971 (fr), Blanco 1271 [lectotype (Marcano-Berti, 1989), VEN; isolectotypes, MER, NY]. Figs. 2F, 3F, 15.

Tree to 25 m high, to 80 cm DBH; hairs where present yellowish; young twigs pubescent. Leaves opposite; blade coriaceous, narrowly oblong or narrowly elliptic to elliptic, 14.5-27 x 5-10 cm, glabrous, usually with few hairs in axils of lateral veins below; apex acuminate; base obtuse or subcordate; midvein prominent on both

sides of leaf; lateral veins 8-11 pairs, prominent on both sides of leaf, angle with midvein 40-50°; tertiary veins percurrent, sinuous, oblique to midvein, arrangement predominantly opposite; marginal vein 1-2 mm from margin; petiole terete, ca. 5 mm long; stipules to 4 mm long. Inflorescences terminal, 11-23 cm long, peduncles and lateral branches puberulous; cincinni to 1.5 cm long; outer bracts suborbicular, ca. 3 x 2.5 mm; inner bracts linear, ca. 1 mm long; spurred sepal ca. 9 mm long, spur cylindric, 2-3.5 mm long; petal yellowish, ca. 10 mm long; stamen ca. 8 mm long; staminodes ca. 3 mm long; style ca. 5 mm long, pilose at base. Fruits winged, puberulous, glabrescent, 6.5-10.5 cm long; major wing ovate to narrowly ovate, 4.5-7.5 x 2.5-3 cm; second major wing elliptic to widely elliptic, 2.5-4.5 x 1.5-2.5 cm.

Distribution (Fig. 15). A species of non-flooded forest known only from Venezuelan Amazonia and northern Brazil, near the border with Venezuela. I have only studied fruiting specimens collected in May, July, and August. Although flowers have been described, the isolectotypes at MER and NY have fruits only.

Specimens examined. VENEZUELA. Amazonas: Reserva Florestal El Sipapo, left margin of Río Sipapo, Bloque 1,

May 1971 (st), Blanco 1162 (MER), (fr), Blanco 1168 (MER); 2-3 km above mouth of Río Cuao, near Raudal Murciélago to Salto Danto, 120 m, 23 Aug 1973 (fr), Morillo & Ishikawa 3520 (MER).

BRAZIL. Amazonas: Rio Curicuriarí, between Rio Negro and Igarapé Arabú, 00°20'S, 66°50'W, 8-9 Jul 1979 (fr), Alencar 501 (MG, MO, NY-2 sheets); margin of Rio Cauaburí, between cachoeira Manajós and cachoeira Tomáz, 5 Feb 1966 (fr), Silva & Brazão 60984 (NY-3 sheets).

Local name. Venezuela: yuri.

Erisma blancoa and E. micranthum are similar in leaf morphology. Stipules can be useful to distinguish sterile specimens. The stipules of E. blancoa are conspicuous (ca. 4 mm long) whereas in E. micranthum, they are shorter (ca. 1 mm long) and thickened at the base.

The flowers and fruits of these two species are very distinct. In E. blancoa, the hairs are yellow, and the flowers and fruits are much bigger than those of E. micranthum, which possesses gray hairs and the smallest flowers and fruits in the genus.

Excluded Names

Erisma maliforme Link ex A. Dietrich, Sp. pl. ed. 6: 102. 1831. Type. Brazil. No further information given in protologue (holotype, B, not extant).

Warming (1875) and Stafleu (1954) considered this name among "species dubiae". Syntypes have not been found. I cannot accurately recognize this species on the basis of the original description. However, it is unlikely that it represents a species of Erisma because its inflorescences were decribed as axillary racemes. The inflorescences of all species of Erisma are typically panicles of cincinni. Warming (1875) suggested that E. maliforme was probably a species of Callisthene.

Erisma niveum Link ex A. Dietrich, Sp. pl. ed. 6: 102. 1831. Type. Brazil. No further information given in protologue (holotype, B, not extant).

This name was also considered as dubious by Warming (1875) and Stafleu (1954). Syntypes have not been found. The description of its inflorescences as axillary racemes indicates that it does not belong to Erisma.

NUMERICAL LIST OF TAXA

Erisma

01. E. arietinum Kawasaki
02. E. bicolor Ducke
03. E. floribundum Rudge
04. E. laurifolium Spruce ex Warming
05. E. bracteosum Ducke
06. E. gracile Ducke
07. E. lanceolatum Stafleu
08. E. micranthum Spruce ex Warming
09. E. calcaratum (Link) Warming
10. E. japura Spruce ex Warming
11. E. nitidum A. P. de Candolle
12. E. splendens Stafleu
13. E. uncinatum Warming
14. E. fuscum Ducke
15. E. silvae Marcano-Berti
16. E. blancoa Marcano-Berti

LIST OF EXSICCATAE

Abraham, 347 (11).

Albuquerque, B. W. P. de & J. Elias, 67-30 (12).

Albuquerque, B. W. P. de et al., 685 (13).

Alencar, L., 501 (16).

Amaral, I. L. et al., 225 (09); 580 (09).

Arends, E. & F. Matos, 08-AM (13).

Bastos, M., 137 (13).

Bernardi, A. L., 1457 (13); 7078 (13).

Black, G. A., 48-2951 (09).

Black, G. A. et al., 50-9795 (09).

Blanco, C., 173 (13); 261 (13); 512 (13); 516 (13); 1162 (16); 1168 (16); 1233 (09); 1271 (16).

Boom, B. & S. Mori, 1974 (03).

Boom, B. & S. Wentzel, 6659 (13); 6706 (13).

Boschbeheer, 46 (13).

Breteler, F. J., 4998 (13); 5000 (13); 5049 (13); 5072 (13).

Bruijn, J. de, 1642 (13); 1654 (13).

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B.W., 1402 (13); 2475 (13); 3380 (13); 3544 (13); 3580 (13); 5434 (13); 5564 (13).

Cáceres, J., 8 (13).

Campbell, D. G. et al., 6239 (02); 6315 (02), 6328 (02);

6380 (02); 6607 (02); 6641 (02); P21842 (09).

Campbell, W. & Osmarino, INPA 15218 (13).

Cavalcante, P., 2231 & D. F. Austin, 4104 (09).

Castellanos, A., INPA 27547 (06).

Cerón, C. & C. Iguago, 5629 (13).

Chagas, J., s.n. (09); INPA 6354 (06).

Chagas, J. & W. Rodrigues, 4947 (12).

Chota, J., 2 (09).

Cid, C. A., 9092 (09); 9278 (09).

Cid, C. A. & J. Lima, 3519 (09).

Cid, C. A. et al., 176 (09); 451 (09); 6281 (03); 6764 (12); 7072 (09); 8172 (09).

Clark, H. L. & P. Maquirino, 7991 (09).

Coêlho, D., s.n. (09); s.n. (12); INPA 3038 (12).

Coêlho, D. & W. Rodrigues, 7723 (12).

Coêlho, L., INPA 3054 (12).

Collector unknown, 314M (13); 318M (13); herb.3580 (13); 7121 (13); 7717 (13); 7750 (13); 9791 (13).

Croat, T. B., 19878 (09).

Daly, D. et al., 5756 (02).

Davidse, G. et al., 17003 (12).

Delascio, F. & F. Guánchez, 10939 (13).

Díaz, C. & J. Jaramillo, 579 (09).

Ducke, A., 96 (12); 104 (03); 214 (02); 264 (13); 371 (06); 756 (09); 897 (09); 1842 (=RB 60347) (02); 8322

(13); 8827 (13), MG 16536 (09); RB 13691 (13); RB 17745 (14); RB 20560 (13); RB 23500 (02); RB 23501 (12); RB 23502 (05); RB 23796 (02); RB 23798 (10); RB 24037(05); RB 24038 (05); RB 24100 (03); RB 24101 (03); RB 24101 (03); RB 24103 (06); RB 32144 (03); RB 34678 (10); RB 34679 (13); RB 34680 (04); RB 34681 (04); RB 34682 (12); RB 34683 (12); RB 34684 (08); RB 34685 (02).

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Ferreira, C. A. C. (see Cid, C. A.)

Folli, D., 008/78 (01); 444 (01).

Foster, R., 12105 (13).

Forest Dept. of British Guiana, WB387/5801 (13); WD530/5929 (13); G565/7580 (13); 3743 (11).

Fróes, R. L., 1939 (13); 11953 (13); 12527/221 (07); 20296 (09); 22677 (09); 22276 (08); 23741 (07); 23921 (02); 26423 (13).

Gentry, A. & L. Emmons, 38025 (09).

Gentry, A. & J. Revilla, 20631 (09).

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Glaziou, A. F. M., 3809 (09).

Goeldi, A., 8322 (13).

Guedes, M., 2136 (13).

Guppy, N., 565 (13).

Hoffmannsegg, J. C., s.n. (09).

Holst, B. & R. Liesner, 2815 (13).

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Hurtado, F., 2626 (13).

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Klug, G., 1541 (09).

Krukoff, B. A., 1334 (02); 1332 (03); 1376 (02); 1401 (03); 1679 (03); 5603 (13); 6927 (14); 8084 (13); 8504 (05); 8892 (02).

Kubitzki, K., 75-103 (09).

Lao, R., s.n. (13).

Lasi, M., 3 (09).

Lins, A. et al., 205 (09).

Maas, P. J. M. et al., 6809 (09).

Maciel, U. N. & C. Rosário, 1711 (06); 1737 (06).

Maciel, U. N. et al., 726 (13).

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Maguire, B. et al., 29737 (13); 30974A (13); 30974B (13); 56585 (13).

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Martins, J., s.n. (03); s.n. (11).

Martius, K. F. P., s.n. (09).

Mélinon, E., 1863 (13).

Mello, F., s.n. (09); 5 (12).

Meneces, E., 796 (13).

Mexia, Y., 6056 (09).

Molina, R., 1-A (13); 2-A (13); 3-A (13); 4-A (13).

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Nascimento, J. R. & J. G. Oliveira, 517 (12).

Nascimento, O. C., 582 (09).

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Paula, J. E., 300 (07).

Pena, B. S., 565 (05).

Pessoal do CPF, INPA.6048 (06); INPA.6049 (12).

Pires, J. M., 470 (10); 51788 (13).

Pires, M. J. & N. T. Silva, 2003 (03); 2028 (06).

Pires, O. & Piatã, ABC270 (09).

Plowman, T. et al., 12366 (09).

Poeppig, E., 2633 (13).

Poole, J. M., 1994 (08).

Prance, G. T., 15159 (09); 30176 (09).

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Prance, G. T. et al., 3193 (09); 3249 (04); 3250 (05); 3251 (06); 3915 (05); 11508 (09); 14874 (09); 15761 (09); 24309 (13); 30176 (09).

Prévost, M. F. & D. Sabatier, 2846 (03); 2854 (13).

Rabelo, B. V., 877 (09); 1260 (09).

Revilla, J., 165 (09).

Riedel, L., s.n. (13).

Rimachi, Y., 1808 (09); 1857 (09).

Rodrigues, W. 6718, (09); 8672 (05); 8683 (05); 8818 (09).

Rodrigues, W. & D. Coêlho, 4030 (09); 4940 (05); 4947 (12).

Rodrigues, W. & L. Emygdio, 2886 (09).

Rodrigues, W. & Osmarino, 5664 (02); 5703 (02).

Rodríguez del Aguila, L. T., 4 (13).

Rodríguez, R., 39 (02); 52 (02).

Rodríguez, R. & E. Acero, 192 (12).

Rosa, N. A. & Alfeu, 4386 (09).

Rosa, N. A. & E. Vilar, 2755 (13).

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Rosário, C. S. & M. das Graças, 1272 (09).

Sabatier, D. & M. F. Prévost, 2218 (13).

Schultes, R. E. & F. Lópes, 9252 (09); 9378 (09).

Schultes, R. E. & J. M. Pires, 8997B (09).

Schwacke, W., 556 (col. III) (09).

Silva, A., s.n. (09).

Silva, M., s.n. (13).

Silva, M. G. & A. Pinheiro, 4320 (13).

Silva, N. T., 369 (05); 1347 (13); 2608 (09).

Silva, N. T. & U. Brazão, 60790 (15); 60984 (16).

Simpson, D. R., 793 (09).

Siqueira, R., 8827 (13).

Soares, E., 81 (06).

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Spruce, R., 125 (09); 1798 (09); 2613 (10); 2889 (04); 3767 (08).

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Stergios, B. & G. Aymard, 7316 (09).

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Stevenson, D. W. et al., 1012 (10).

Steyermark, J. A., 86371 (13); 86678 (13); 86818 (13); 87077 (13); 87597 (13).

Steyermark, J. A. et al., 125854 (13).

Tessmann. G., 4932 (04); 5330 (09).

Thomas, W., 6510 (02).

Thomas, W. et al., 4096 (03).

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Urrego, L. E., 786 (04); 1820 (13).

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Vieira, M. G. et al., 1034 (13).

Vreden, C., LBB13726 (13).

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White, O. E., 1823 (13).

Williams, Ll., 14111 (03); 14156 (08); 16184 (09).

Wurdack, J. J. & L. S. Adderley, 43227 (12).

Wurdack, J. J. & J. V. Monachino, 39628 (13); 39685 (13); 41036 (13).

Zarucchi, J. L. & C. E. Barbosa, 3763 (13); 3795 (13).

TABLES AND FIGURES FOR TEXT

TABLE 1

Characters and character states of Vochysiaceae

characters	characters states		
	0	1	2
01.Hairs	simple	stellate	
02.Multiseriate rays	present	absent	
03.Ray cells	heterocellular	homocellular	
04.Parenchyma	apotracheal	paratracheal	
05.Included phloem	absent	present	
06.Stipules	interpetiolar	regular	obsolete
07.Stipular glands and extrafloral nectaries	absent	present	
08.Bracts	persistent	deciduous	
09.Perulate buds	absent	present	
10.Spurred sepal 3 or more times longer than other sepals	absent	present	
11.Spur	absent	persistent	deciduous
12.Papilionaceous corolla	present	absent	
13.Number of petals	5	3	1
14.Disc glands	present	absent	
15.Number of stamens	more than 1	1	
16.Stamen position	symmetrical	assymmetrical	
17.Anther	basifixed	dorsifixed	
18.Pollen	triporate	tricolporate	
19.Ovary	superior	inferior	
20.Number of carpels	3	1	
21.Many ovules per locule	present	absent	
22.Placentation	axile	apical	
23.Stigma	terminal	lateral	
24.Fruit	septicidal capsule	loculicidal capsule	samaroid
25.Fruit with accrescent sepals	absent	present	
26.Number of seeds	3 to several	1	
27.Seed wing	absent	lateral	circular

TABLE 2

Data matrix for the cladistics of Vochysiaceae

characters	taxa							
	Tr	Sa	Vo	Qu	Ru	Ca	El	Er
01.	0	0	0	0	0	0	1	1
02.	0	0	0	0	0	0	1	0
03.	0	1	0	1	1	0	0	0
04.	0	1	1	1	1	0	0	0
05.	0	0	0	0	0	0	1	1
06.	0	1	1	1	1	2	1	1,2
07.	0	0	0	1	1	0	0	0
08.	0	1	1	1	1	0	0	0,1
09.	0	0	0	1	1	1	0	0
10.	0	0	1	0	1	1	0	0
11.	0	1	1	0,1	1	1	1	2
12.	0	1	1	1	1	1	1	1
13.	0	0	1	2	2	2	0	2
14.	0	1	1	1	1	1	1	1
15.	0	1	1	1	1	1	1	1
16.	0	0	0	1	1	1	0	1
17.	0	0	0	1	1	0	0	1
18.	0	1	1	1	1	1	1	1
19.	0	0	0	0	0	0	1	1
20.	0	0	0	0	0	0	1	1
21.	0	1	1	0	0	0	1	1
22.	0	0	0	0	0	0	1	1
23.	0	1	0,1	0	0	0	0	0
24.	0	1	1	1	1	1	2	2
25.	0	0	0	0	0	0	1	1
26.	0	0	0	0	0	0	1	1
27.	0	1	1	1	1	2	0	0

Tr=Trigoniaceae; Sa=*Salvertia*; Vo=*Vochysia*; Qu=*Qualea*; Ru=*Ruizterania*; Ca=*Callisthene*; El=*Erismadelphus*; Er=*Erisma*.

TABLE 3

Characters and character states of Erisma

characters	character states		
	0	1	2
01.Hair color	yellow	brown	gray
02.Twig pubescence	pilose	glabrous	
03.Bicolor leaves	absent	present	
04.Obverse leaves	present	absent	
05.Leaf pubescence	tomentose	glabrous	
06.Subcordate leaves	present	absent	
07.Midvein	sulcate	prominent	
08.Number of lateral veins	13 or less	more than 13	
09.Lateral veins	sulcate	prominent	
10.Angle of lateral veins more than 60°	absent	present	
11.Tertiary venation	reticulate	percurrent	
12.Marginal vein	absent	present	
13.Stipules	present	absent	
14.Bracts	persistent	deciduous	
15.Bract size	enclosing buds	not enclosing buds	
16.Spurred sepal	persistent	deciduous	
17.Spur shape	globose	cylindric	uncinate
18.Petal color	white to yellow	purple	
19.Style base	pilose	glabrous	
20.Number of wings	5	4	0
21.Wing shape	elliptic	oblong	

TABLE 4

Data matrix for the cladistics of *Erisma*

characters	taxa																
	El	ar	bi	bl	br	ca	fl	fu	gr	ja	la	lu	mi	ni	si	sp	un
01.	0	0	0	0	0	2	0	1	0	2	0	0	2	0	1	0	2
02.	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	0
03.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
04.	0	1	0	0	1	1	0	0	1	0	1	1	1	1	0	1	0
05.	0	1	0	0	1	1	0	0	1	1	1	0	1	1	0	1	0
06.	0	0	1	0	0	0	1	0	1	1	1	1	1	1	0	1	1
07.	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0
08.	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0
09.	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0
10.	0	1	0	0	1	1	1	0	1	1	0	1	1	1	0	1	0
11.	0	0	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1
12.	0	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0
13.	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0
14.	0	1	0	1	0	1	0	1	0	1	?	0	1	1	1	1	1
15.	0	1	0	1	0	1	0	1	0	1	?	0	1	1	1	1	1
16.	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
17.	0	0	1	1	1	1	1	2	0	0	?	1	0	1	0	0	2
18.	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1
19.	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0	0
20.	0	1	1	1	1	2	1	1	1	1	1	1	1	1	?	1	1
21.	0	0	0	1	0	2	1	0	1	0	0	1	0	0	?	0	0

El=*Erismadelphus*; ar=*Erisma arietinum*; bi=*bicolor*; bl=*blancoa*; br=*bracteosum*; ca=*calcaratum*; fl=*floribundum*; fu=*fuscum*; gr=*gracile*; ja=*japura*; la=*lanceolatum*; lu=*laurifolium*; mi=*micranthum*; ni=*nitidum*; si=*silvae*; sp=*splendens*; un=*uncinatum*; ?=missing data.

FIGURE 01. Wood anatomy of Erismadelphus and Erisma. A-B: Erismadelphus exsul (collector unknown U20822). A. Cross section showing banded parenchyma; B. Tangential section showing uniseriate rays. C-D: Erisma bicolor (Krukoff 1334). E-F: Erisma floribundum (Krukoff 1401). C, E: Cross section showing banded parenchyma; D, F: Tangential section showing uniseriate and multiseriate rays. Bars = 100 um.

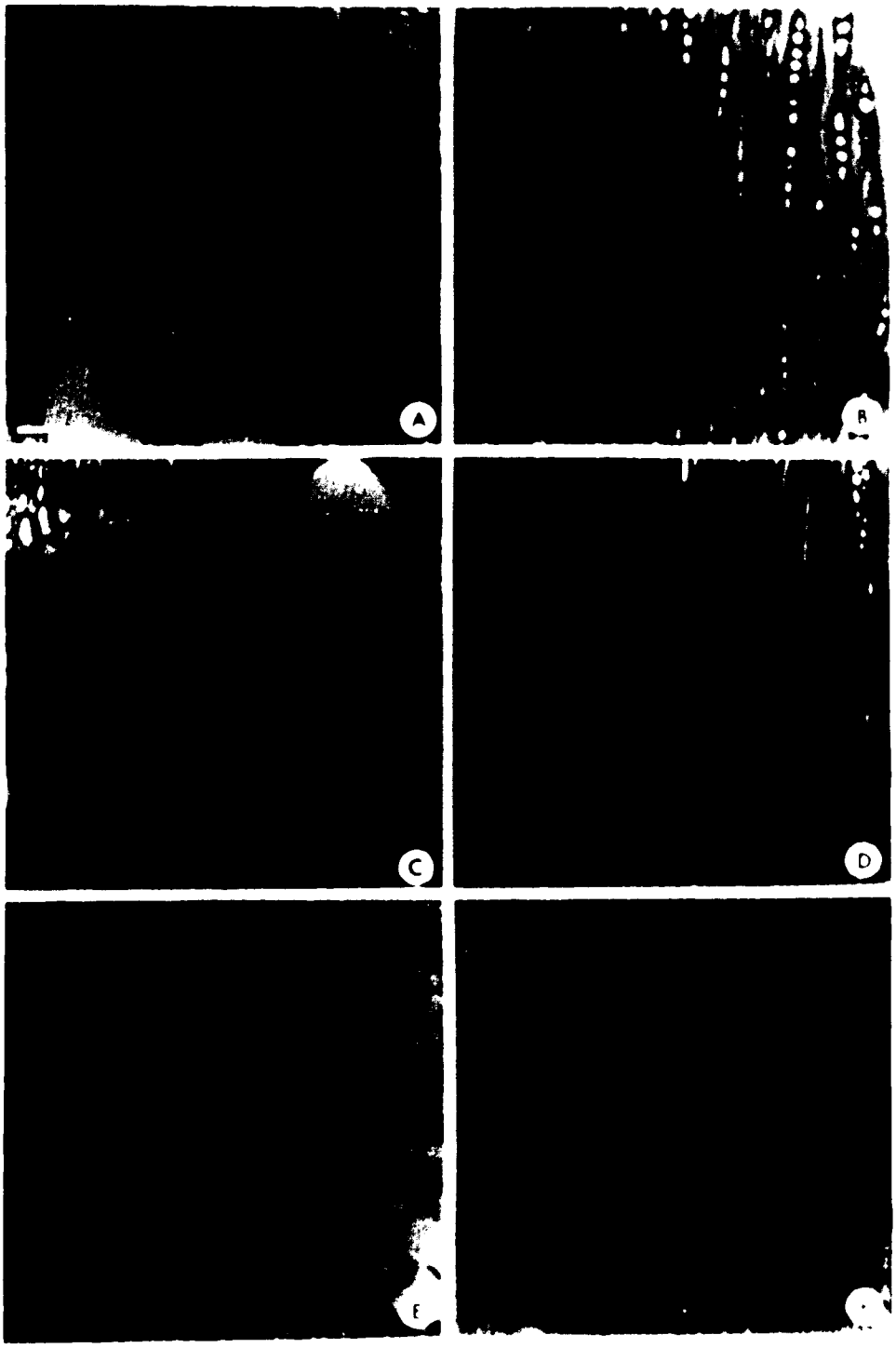

A
B
C
D
E

FIGURE 02. SEM of abaxial leaf surface in selected species of Erisma. A-B: smooth and relatively undifferentiated. A. E. nitidum (Forest Dept. of British Guiana 3743); B. E. silvae (N. T. Silva & Brazão 60790). C-D: striate. C. E. floribundum (Thomas et al. 4096); D. E. micranthum (Poole 1994). E-F: stomatal chamber distinctly surrounded by orbicular ridges. E. E. bracteosum (Prance et al. 3250); F. E. blancoa (N. T. Silva & Brazão 60984). Bars= 30 um.

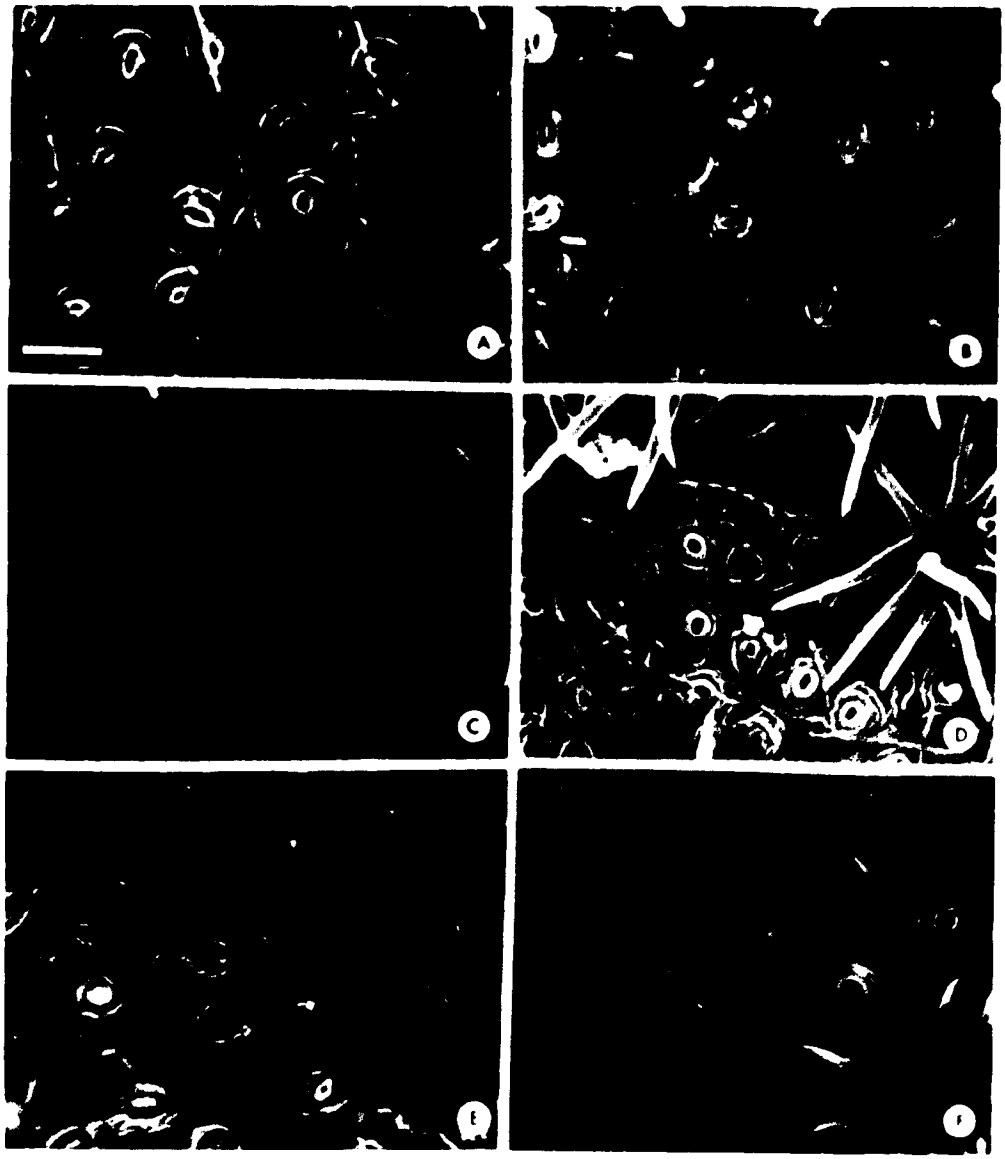

A
B
C
D
E
F

FIGURE 03. Leaf venation of Erisma. A-D: randomly reticulate. A. E. nitidum (Martin s.n.); B. E. gracile (Prance et al. 3251); C. E. splendens (Cid 6764); D. E. arietinum (Kawasaki 400). E-H: oblique, predominantly opposite. E. E. fuscum (Ducke RB 17745); F. E. blancoa (N. T. Silva & Brazão 60974); G. E. silvae (N. T. Silva & Brazão 60790); H. E. bicolor (R. Rodríguez 52).

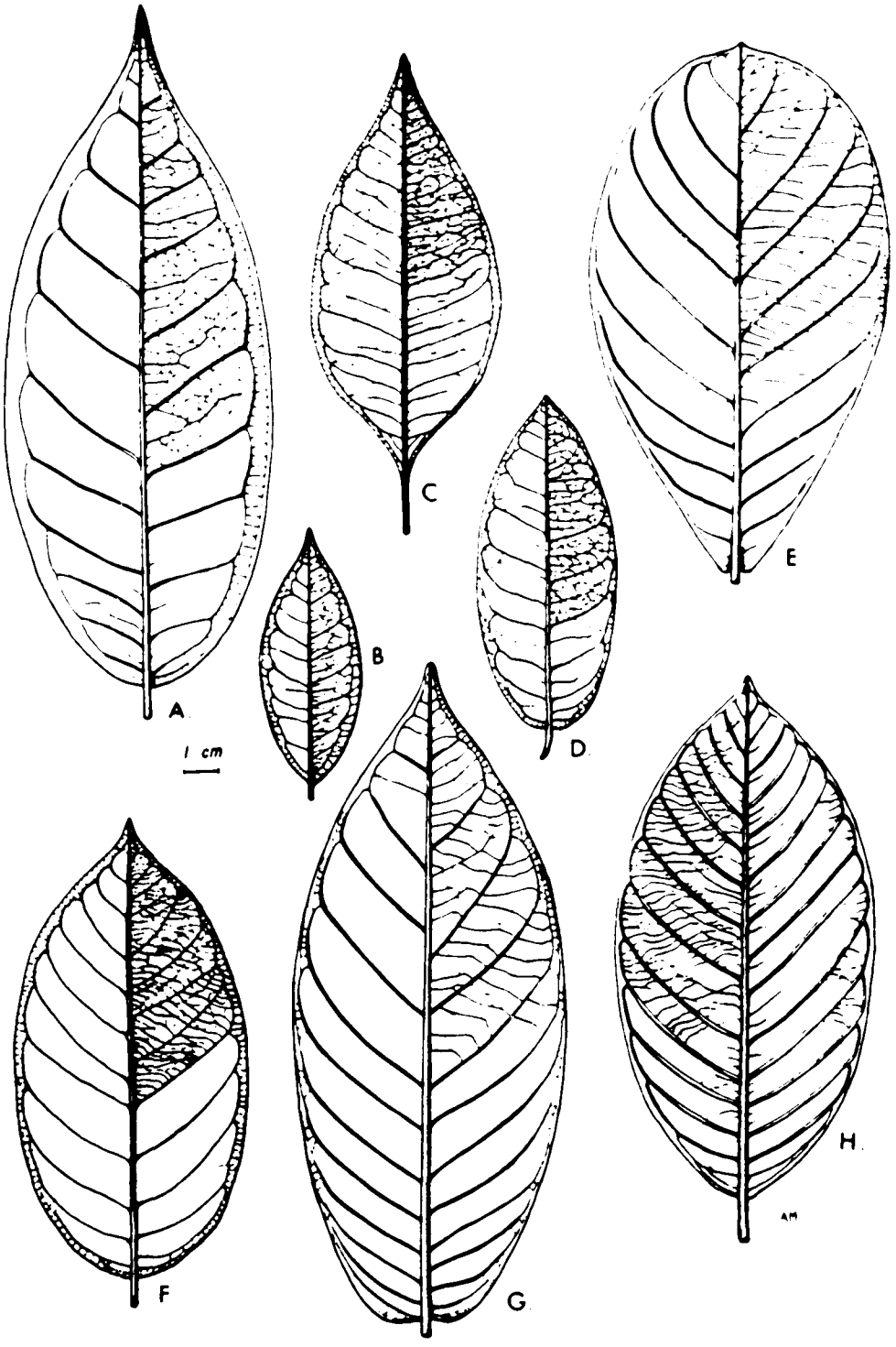

A
B
C
D
E
F
G
H
1 cm

FIGURE 04. Leaf venation of Erisma. A-D: oblique, equally opposite and alternate. A. E. japura (Stevenson 1012); B. E. micranthum (Spruce 3767); C. E. bracteosum (Prance et al. 3250); D. E. calcaratum (Plowman et al. 12366). E-F: oblique, predominantly alternate. E. E. floribundum (Cid 6281); F. E. laurifolium (Spruce 2889). G-H: perpendicular. G. E. uncinatum (Kawasaki 396); H. E. lanceolatum (Fróes 12527/221).

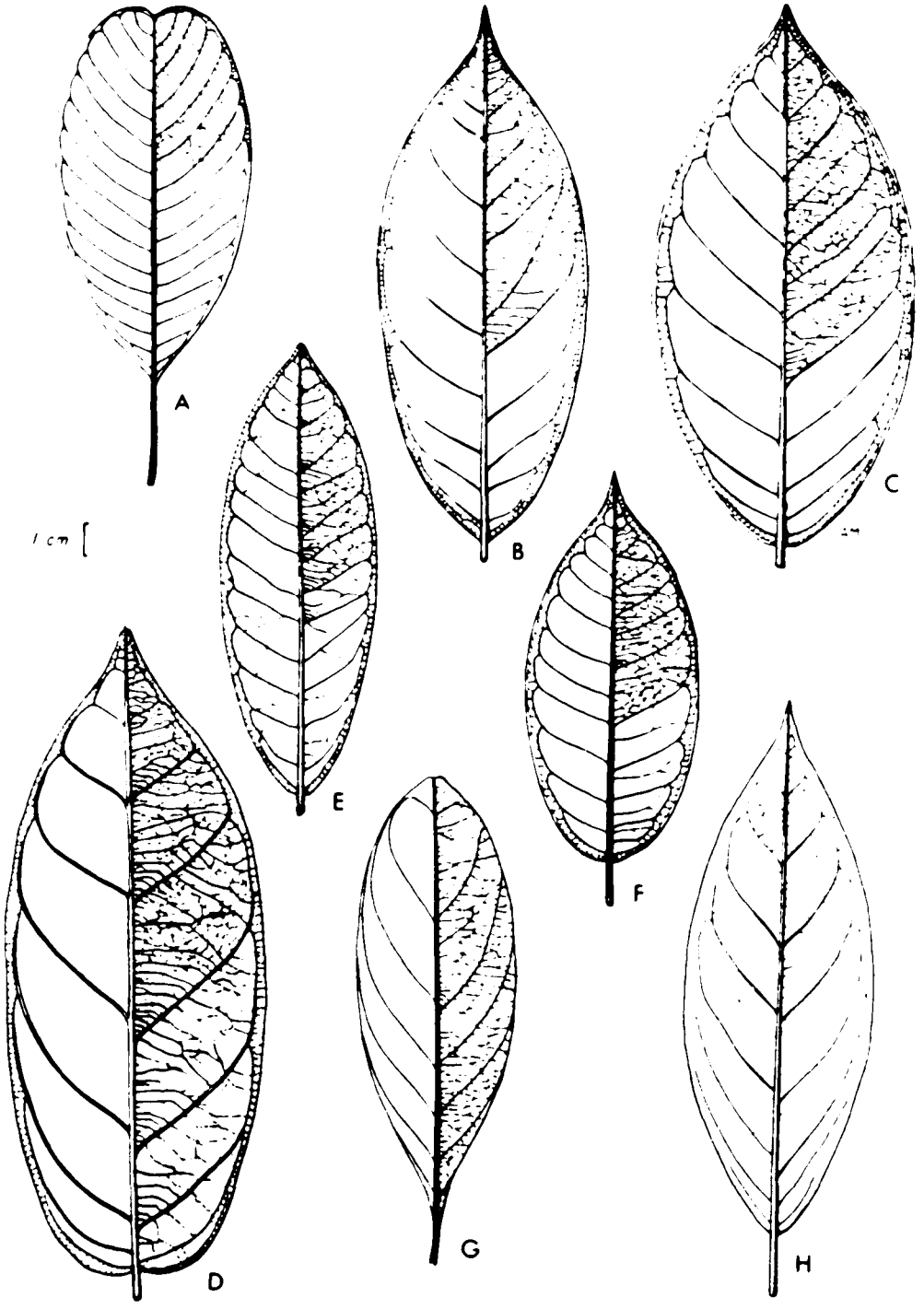

A
B
C
1 cm
E
F
D
G
H

FIGURE 05. Inflorescences and flowers of Erisma. A. E. bicolor (Daly 5756). Photo D. Daly. B. E. floribundum (collector unknown). Photo B. Boom. C. E. calcaratum (Mori & Gracie 19262). Photo S. Mori. D. E. uncinatum (Mori et al. 21585). Photo C. Gracie.

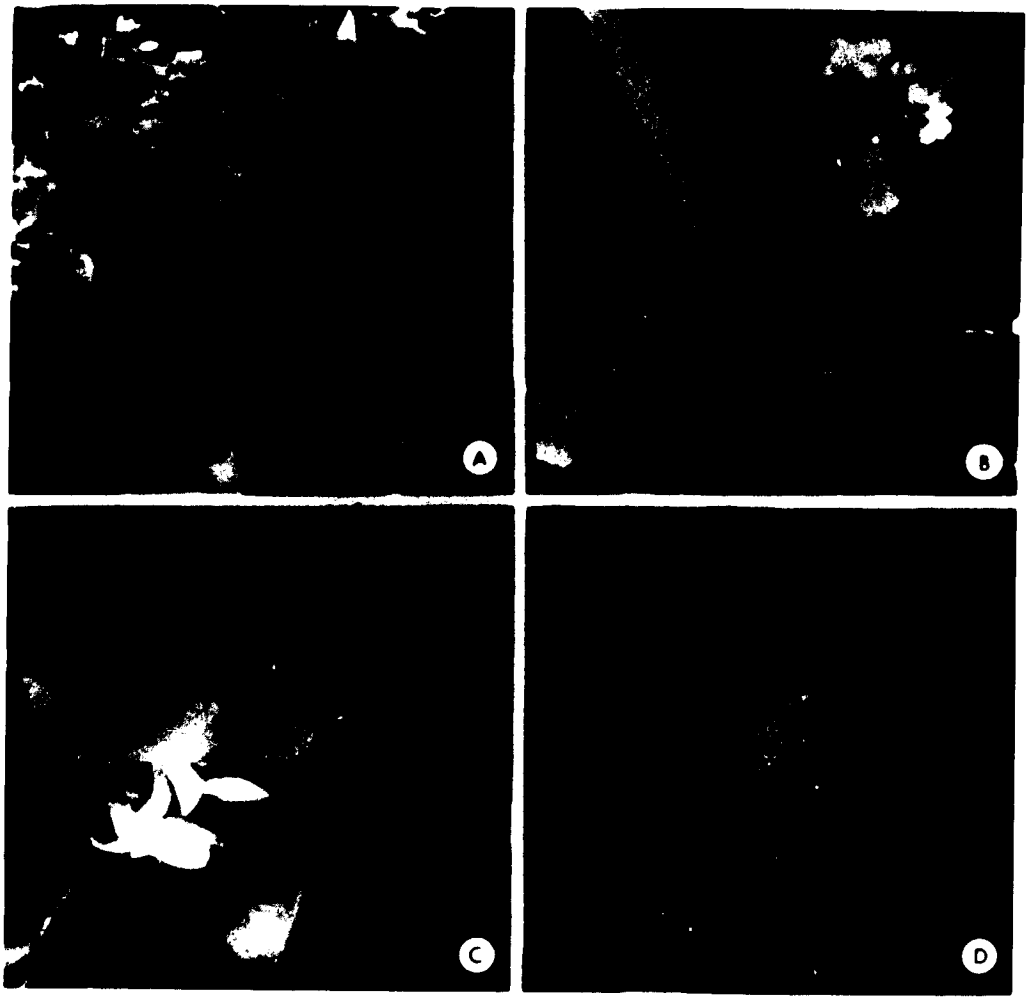
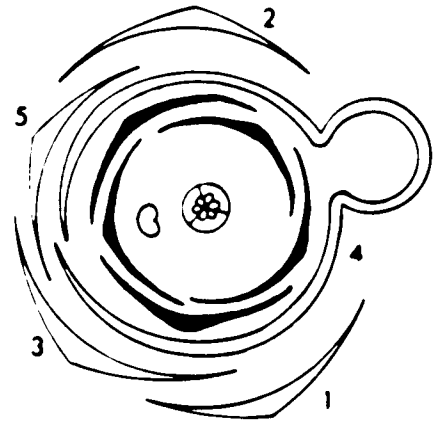
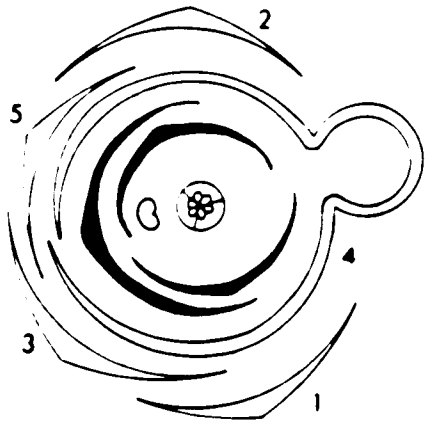

A
B
C
D

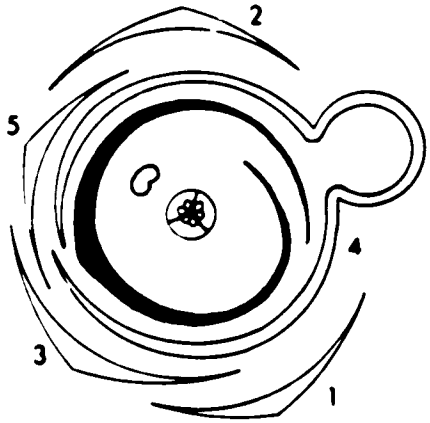
FIGURE 06. Floral diagrams of the genera of Vochysiaceae. A. Salvertia. B. Vochysia. C. Callisthene. D. Qualea and Ruizterania. E. Erismadelphus. F. Erisma.



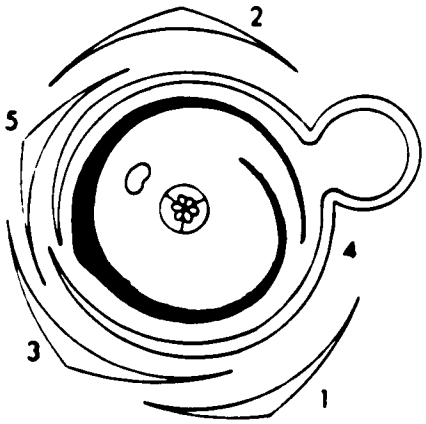
A.



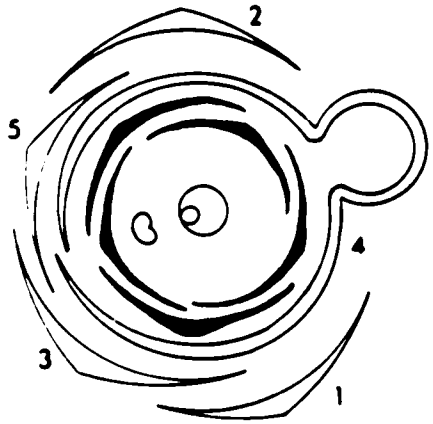
B.



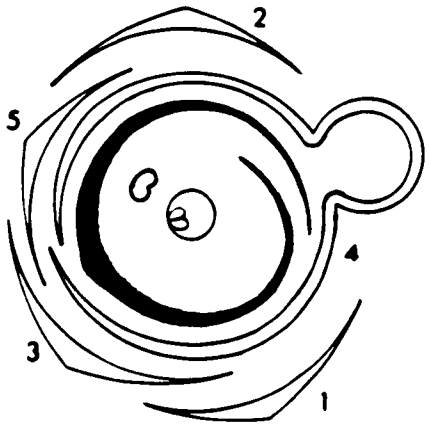
C.



D.



E.



F.

FIGURE 07. Floral buds of Erisma. A. E. bracteosum (W. Rodrigues 8672); B. E. floribundum (Ducke RB 32144); C. E. bicolor (Daly 5756); D. E. gracile (Ducke 371); E. E. laurifolium (Spruce 2889); F. E. micranthum (Ducke RB 34684); G. E. uncinatum (M. Silva s.n.); H. E. fuscum (Ducke RB 17745); I. E. calcaratum (N. T. Silva 2608); J. E. japura (Ducke RB 23798); K. E. splendens (L. Coêlho INPA 3054); L. E. nitidum (Jenman 7439); M. E. silvae (N. T. Silva & Brazão 60790); N. E. arietinum (Polli 8/78).

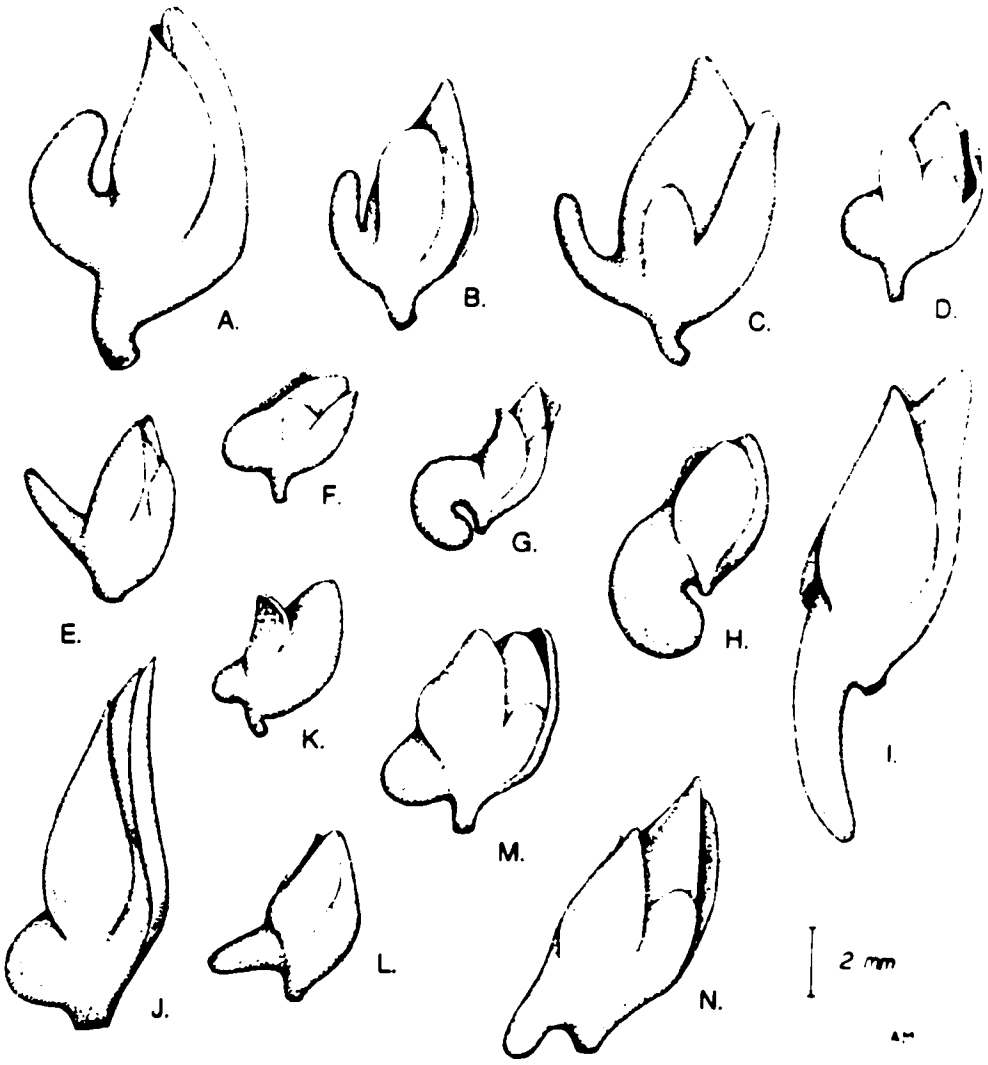

A.
B.
C.
D.
E.
F.
G.
H.
I.
J.
K.
L.
M.
N.
2 mm

FIGURE 08. SEM of pollen grains of Erisma. A: E. arietinum (Folli 8/78); B, E, F: E. floribundum (Oliveira 3913); C. E. calcaratum (Mori & Gracie 19262); D: E. splendens (Acero & Rodriguez 192); E: Striate exine; F: Exine in section showing tectum and columellae. Bars= 5 um (A-B); 0.5 um (C-F).

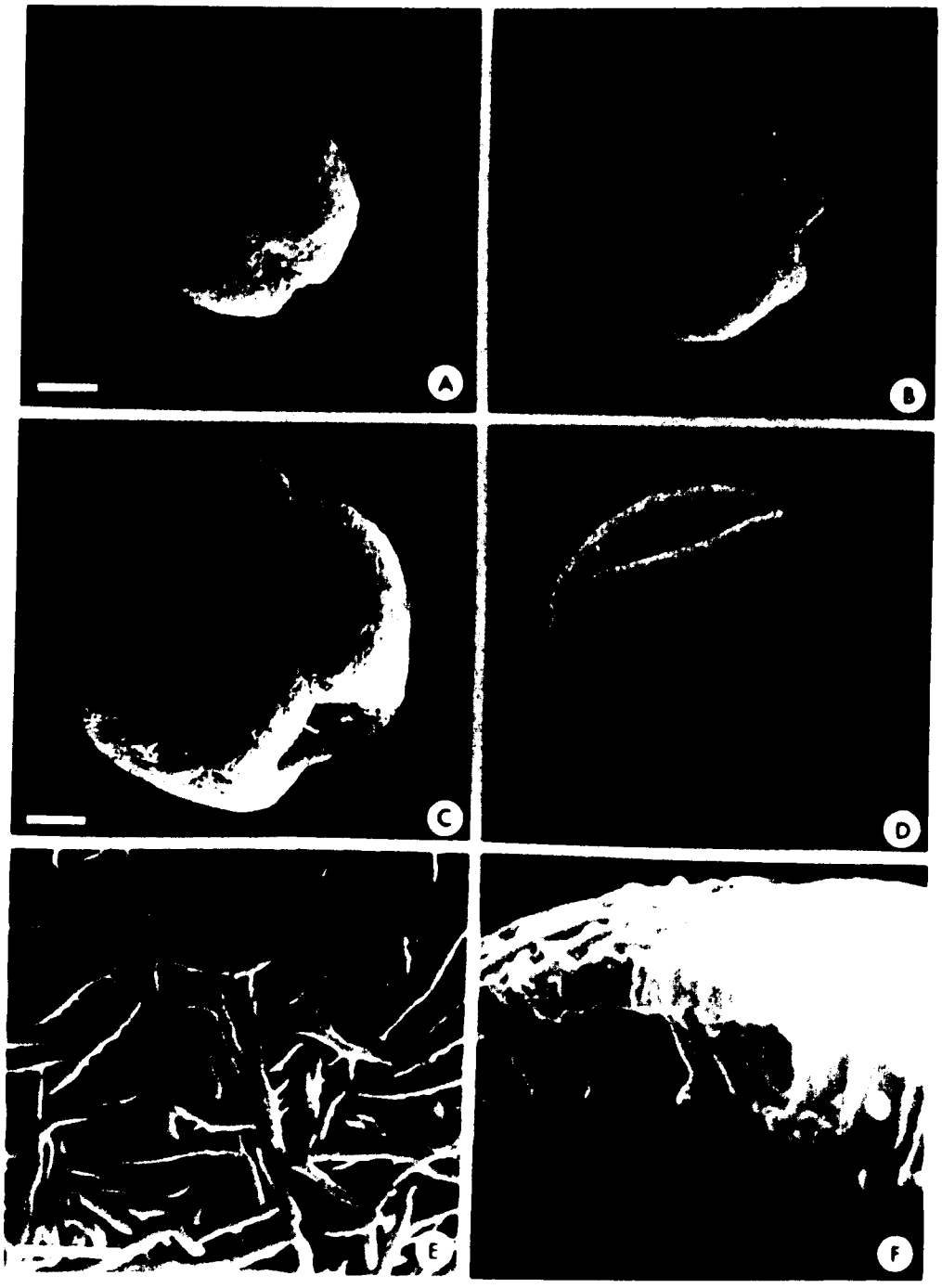

A
B
C
D
E
F

FIGURE 09. Erisma arietinum (A-F: Folli 8/78; G: Kawasaki 400). A. Habit; B. Stipules; C. Floral bud; D. Stellate hairs; E. Flower; F. Longitudinal section showing the two apical ovules; G. Spurred sepal; H. Petal; I. Unilocular ovary in cross section; G. Fruit.

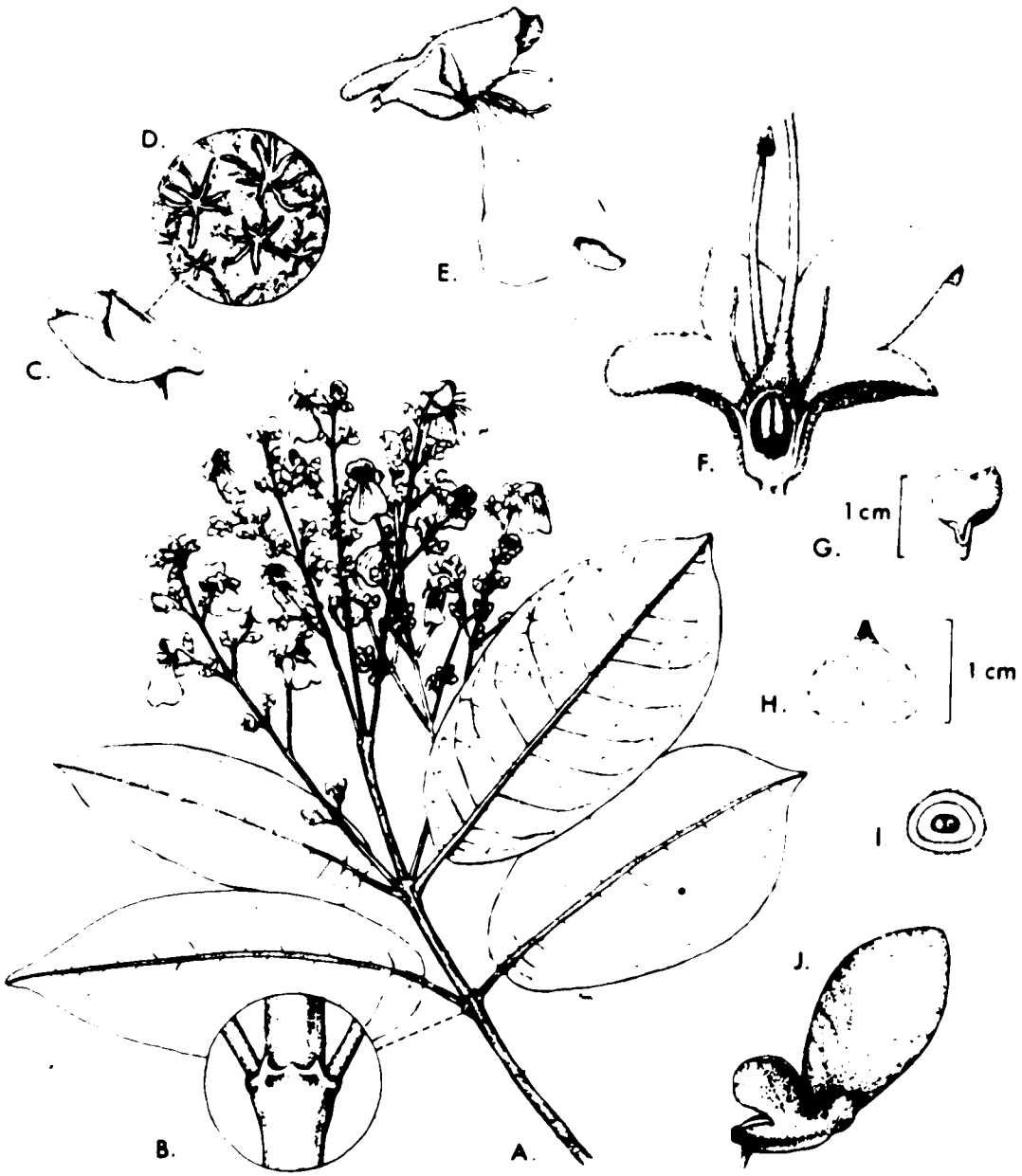
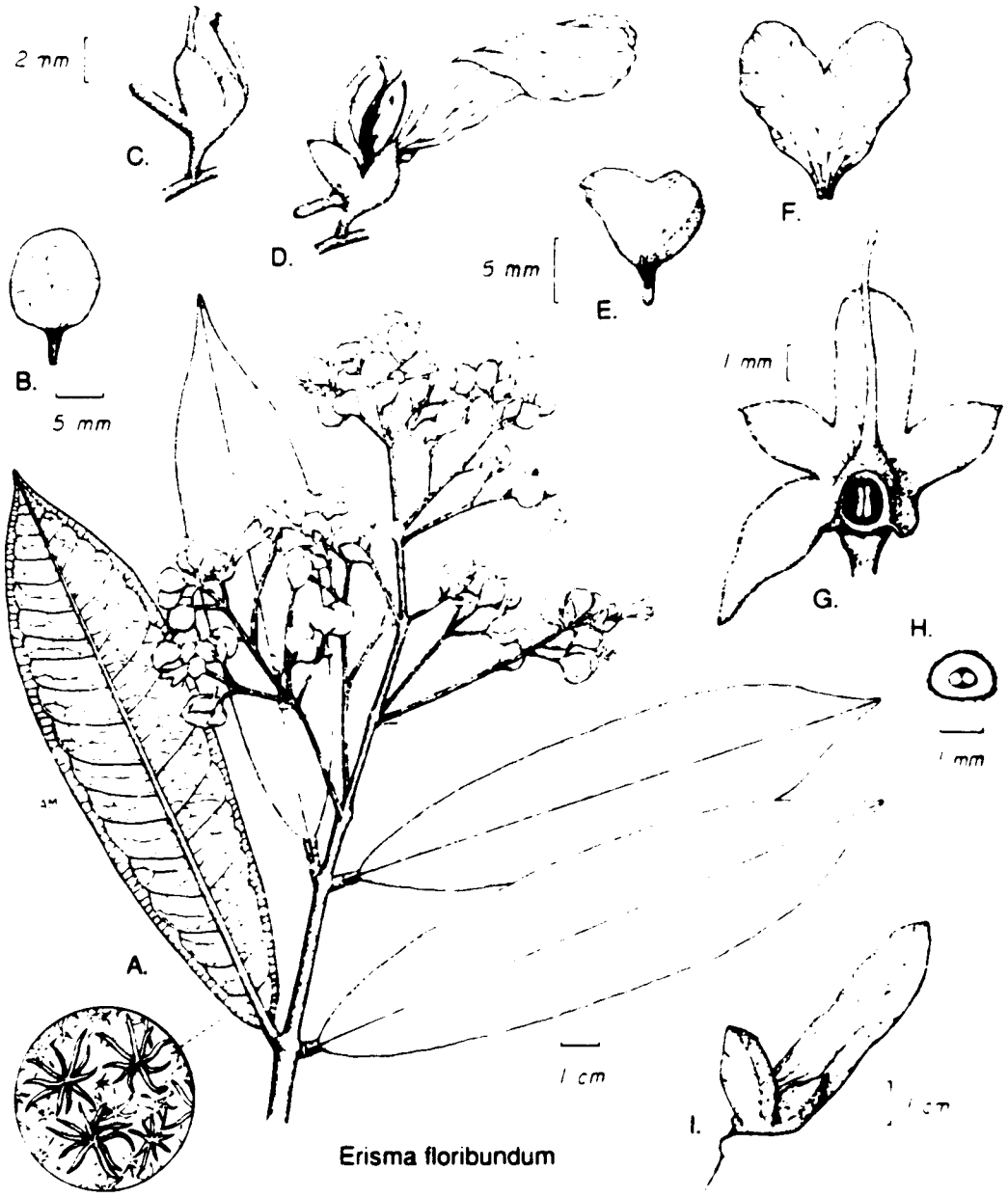

D.
E.
C.
F.
1 cm
G.
A
H.
1 cm
I
J.
B.
A.

FIGURE 10. Erisma floribundum (A-H: Oliveira 3913; I: Krukoff 1679). A. Habit; B. External bract; C. Floral bud; D. Flower; E. Spurred sepal; F. Petal; G. Longitudinal section showing the two apical ovules; H. Unilocular ovary in cross section; I. Fruit.



Erisma floribundum

FIGURE 11. Erisma uncinatum (A-H: Mori et al. 20890; I: Kawasaki 396). A. Habit; B. Stipules; C. Stellate hairs; D. Floral bud; E. Flower; F. Petal; G. Longitudinal section showing the two apical ovules; H. unilocular ovary in cross section; G. Fruit.

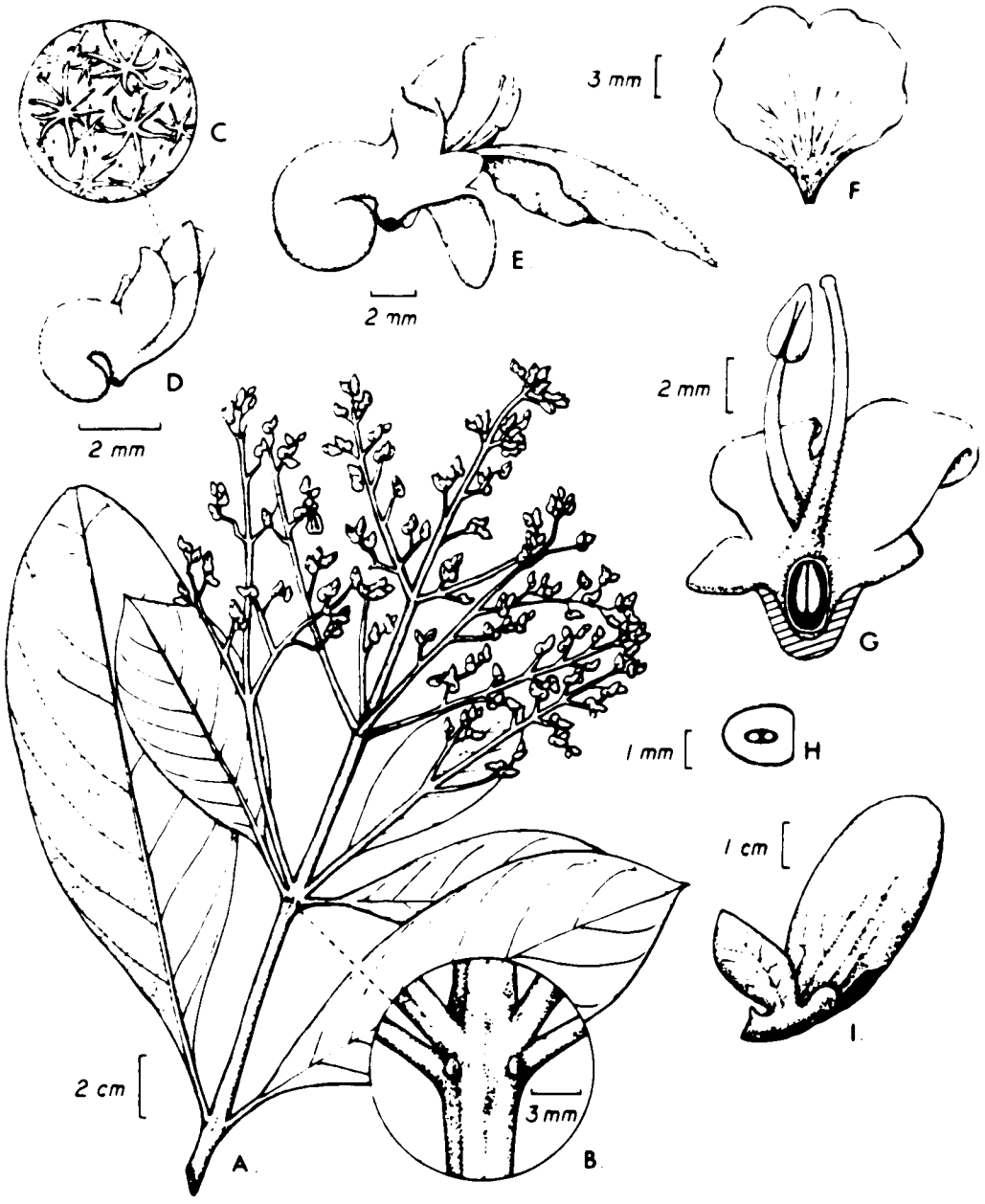

C
D
2 mm
E
2 mm
3 mm
F
2 mm
G
1 mm
H
1 cm
I
2 cm
A
3 mm
B

FIGURE 12. Distributions of Erisma arietinum and E. bicolor.

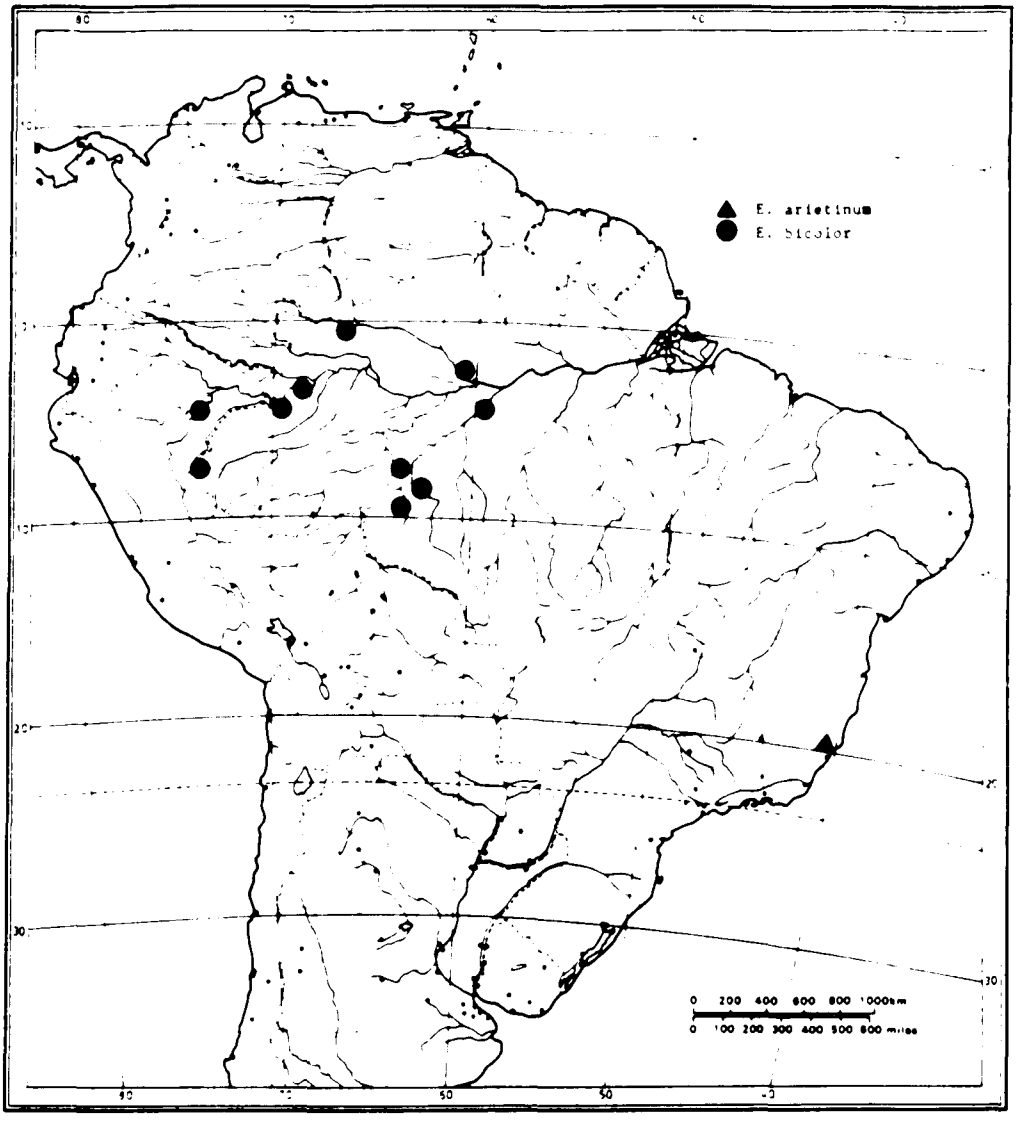

E. arietinum
E. bicolor
0 200 400 600 800 1000km
0 100 200 300 400 500 600 miles

FIGURE 13. Distributions of *Erisma floribundum*, *E. laurifolium*, *E. gracile*, *E. lanceolatum*, and *E. nitidum*.

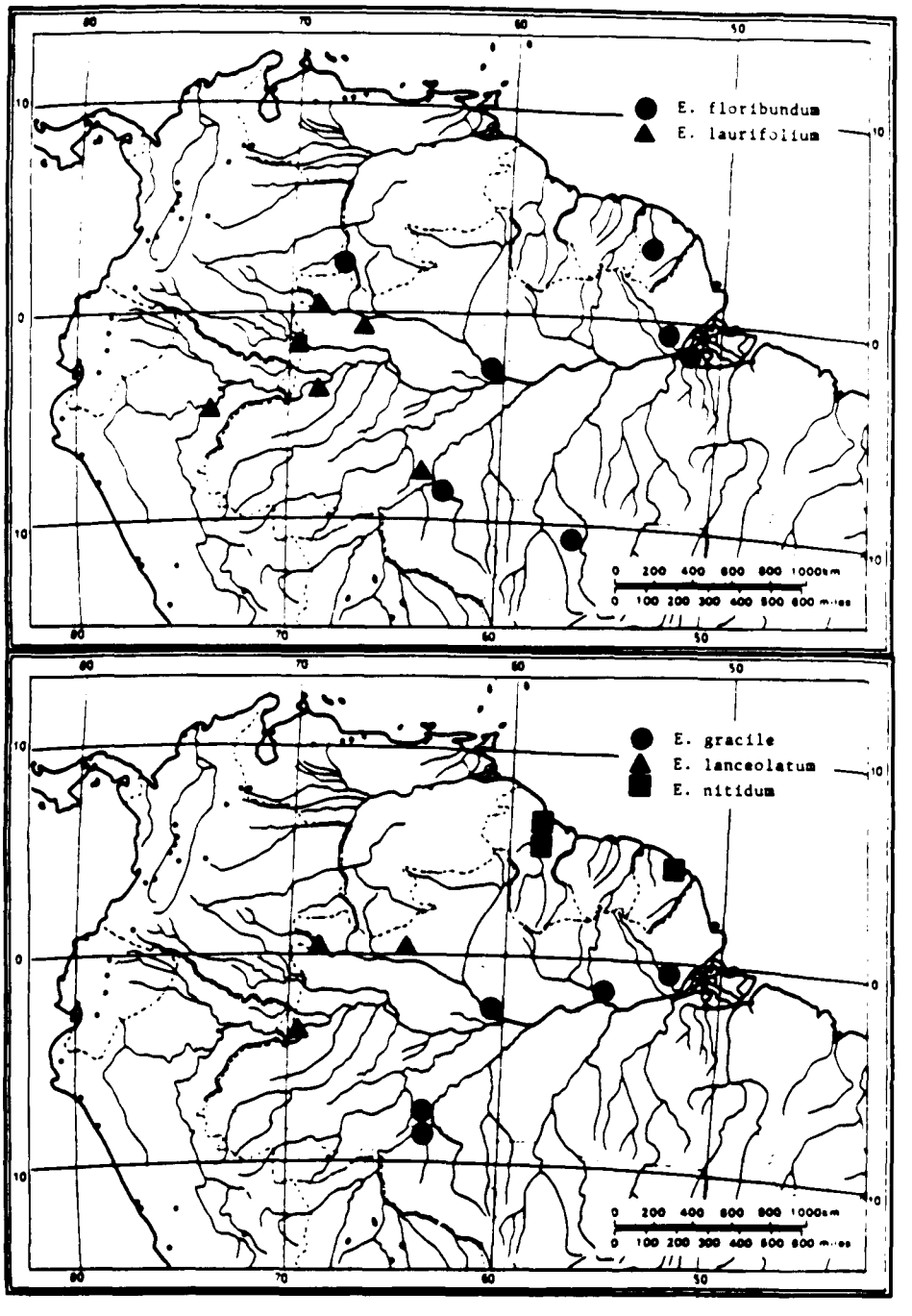

E. floribundum
E. laurifolium
E. gracile
E. lanceolatum
E. nitidum

FIGURE 14. Distributions of *Erisma calcaratum*, *E. blancoa*, *E. bracteosum*, and *E. micranthum*.

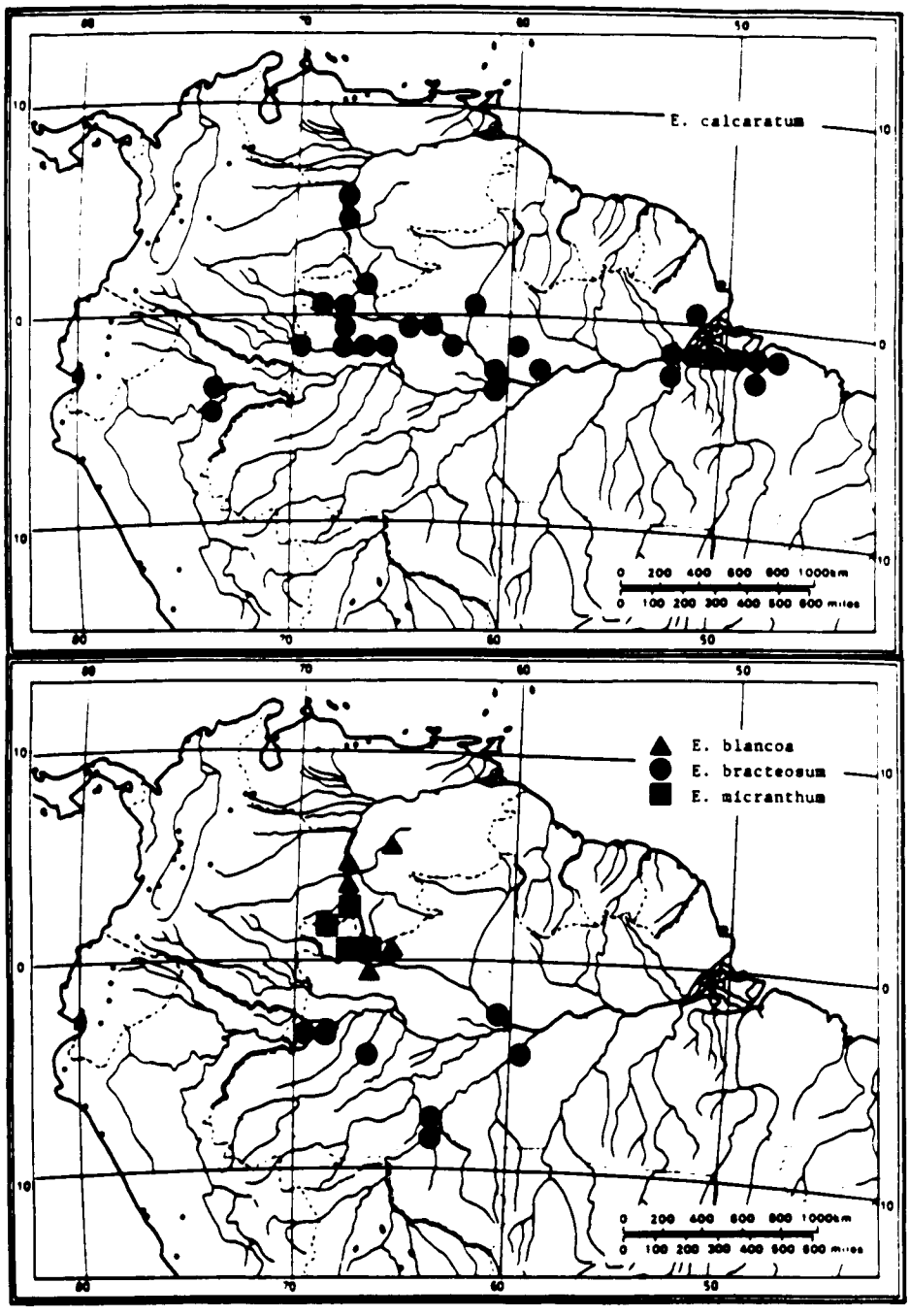

E. calcaratum
0 200 400 600 800 1000km
0 100 200 300 400 500 600 miles
E. blancoa
E. bracteosum
E. micranthum
0 200 400 600 800 1000km
0 100 200 300 400 500 600 miles

FIGURE 15. Distributions of *Erisma japura*, *E. splendens*, *E. fuscum*, *E. uncinatum*, and *E. silvae*.

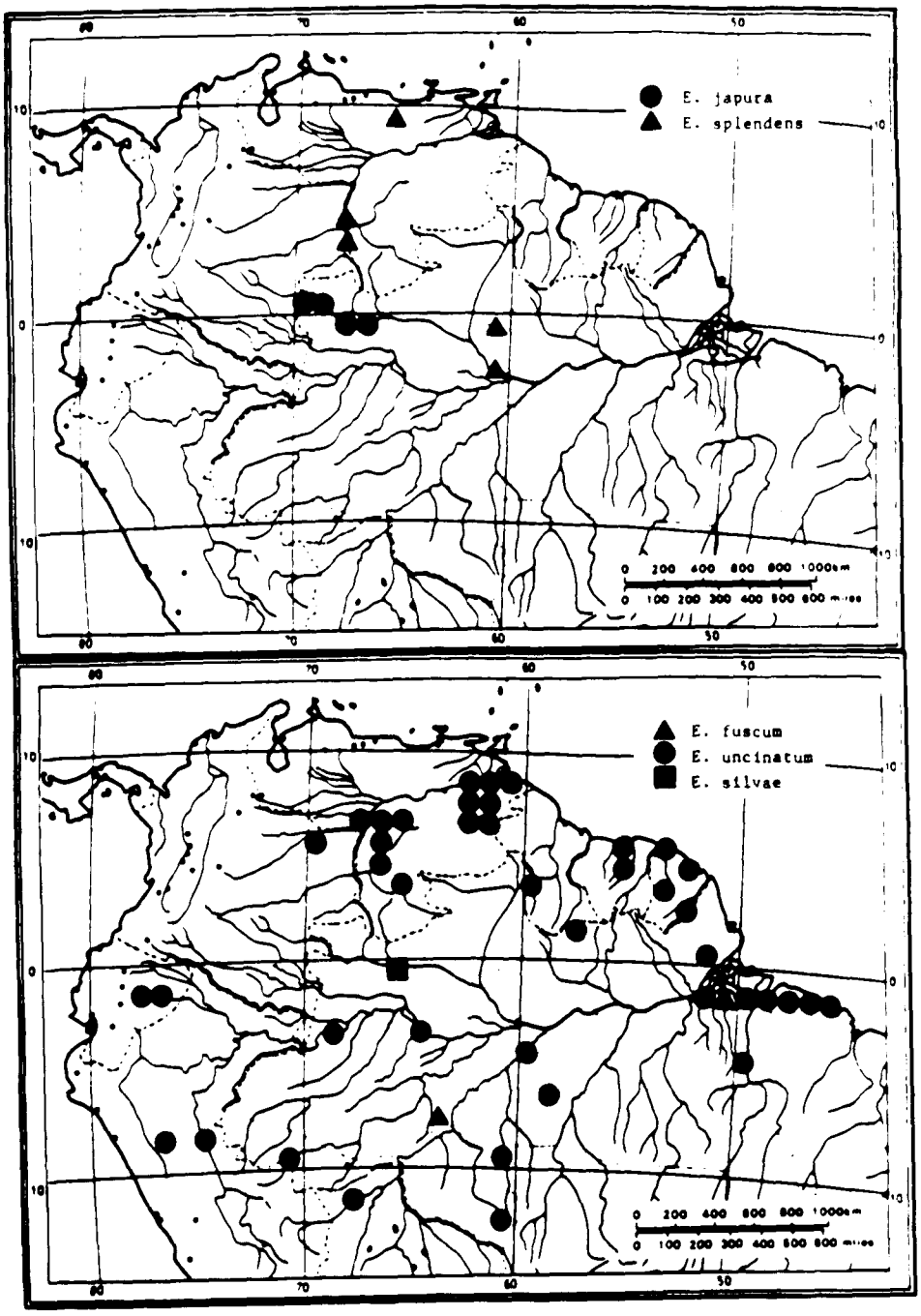

E. japura
E. splendens
E. fuscum
E. uncinatum
E. silvae

FIGURE 16. Species density map of Erisma.
Dots represent number of species collected in each degree grid square. ●:1; ●:2; ●:3; ●:4; ●:5.

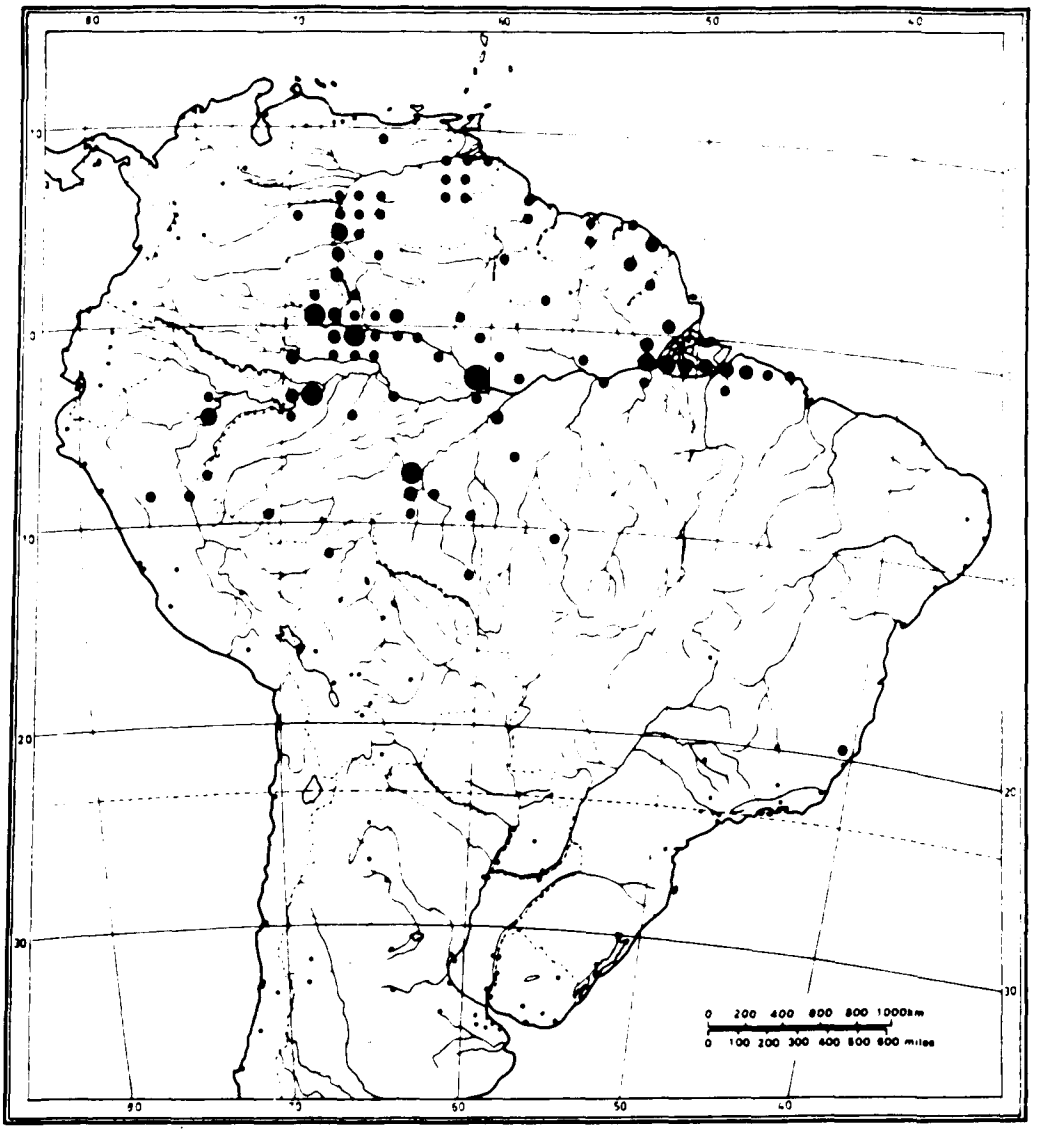

80
70
60
50
40
10
0
10
20
30
90
70
60
50
40
0 200 400 600 800 1000km
0 100 200 300 400 500 600 miles

FIGURE 17. Cladogram of the genera of Vochysiaceae. *: polymorphism; -: synapomorphy; =: reversal; ●: parallelism.

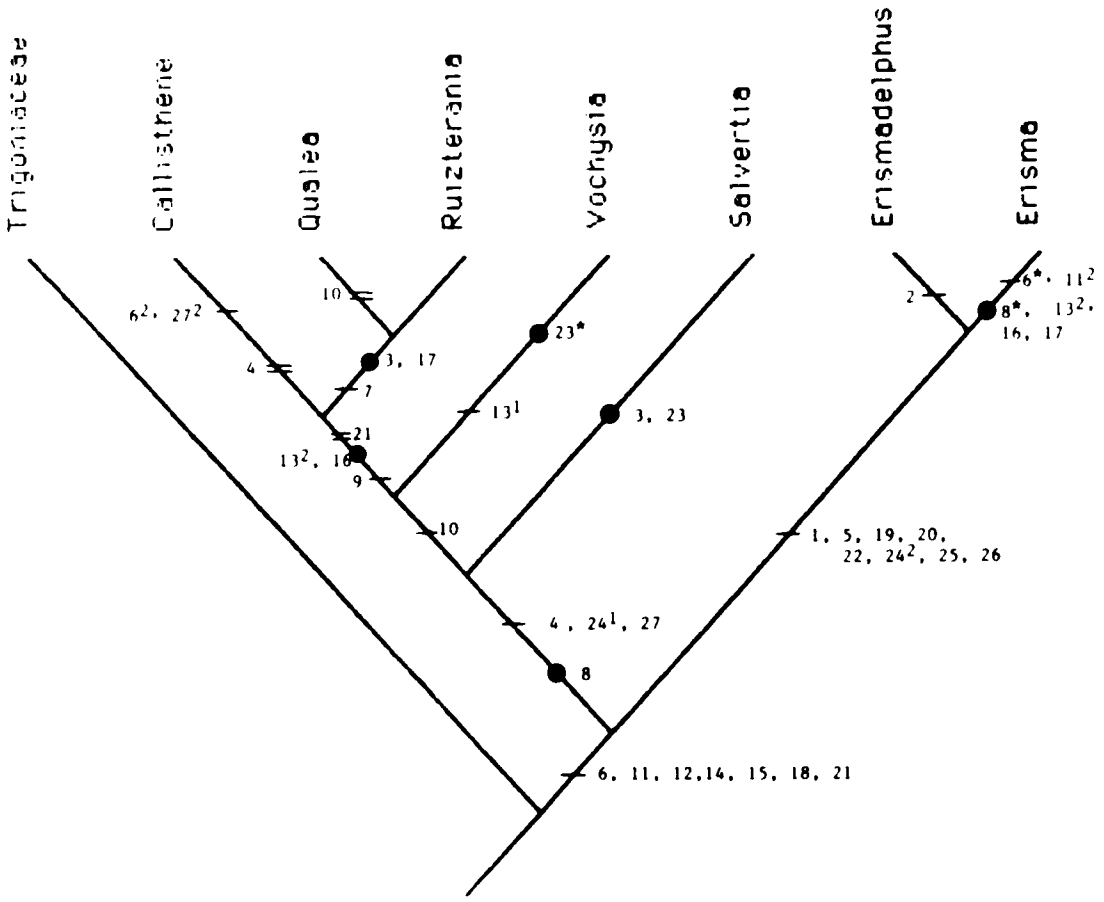
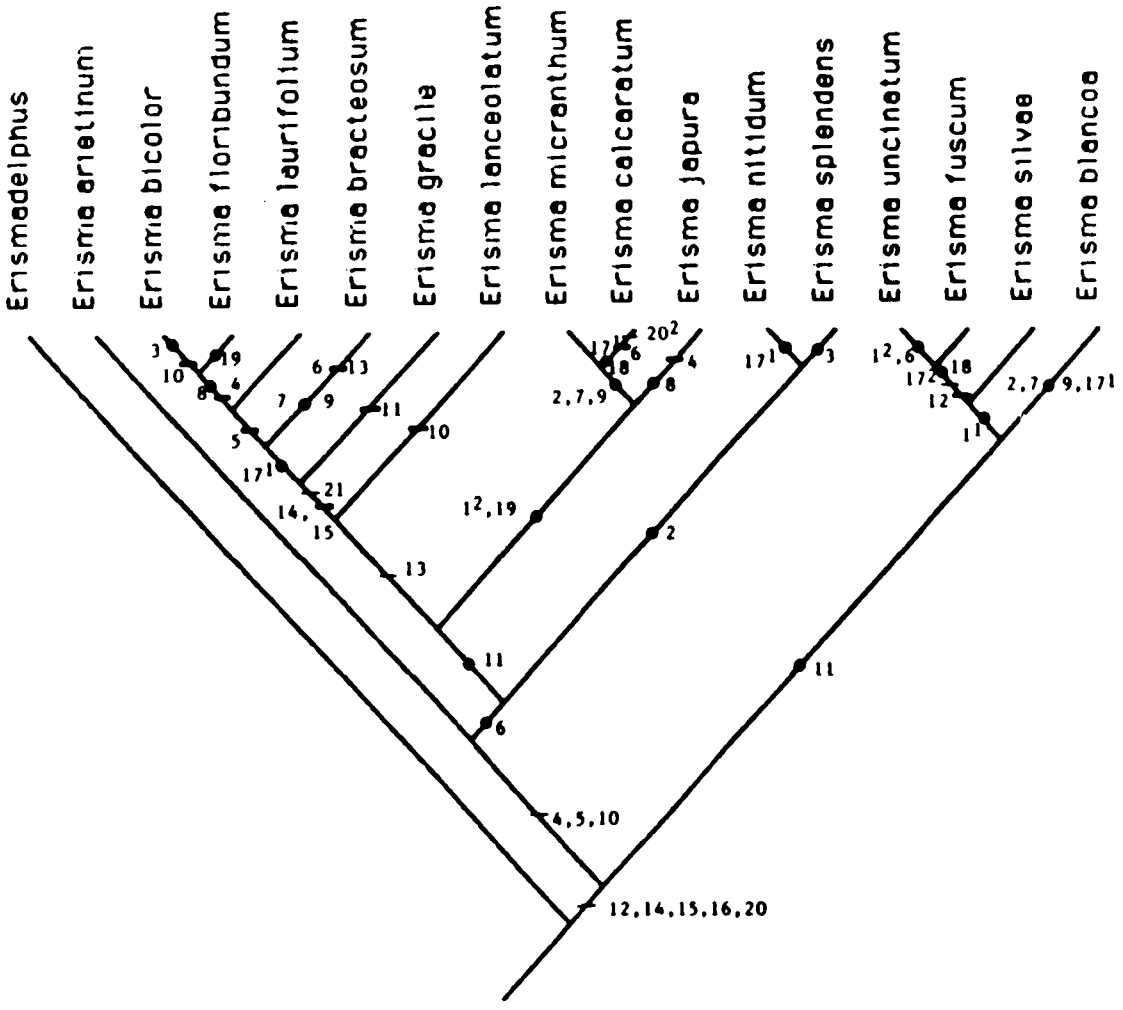

Trigoniaceae
Callisthene
Qualea
Ruizterania
Vochysia
Salvertia
Erismadelphus
Erisma
6², 27²
10
4
3, 17
7
21
13², 16
9
10
23*
13¹
3, 23
2
6*, 11²
8*, 13², 16, 17
1, 5, 19, 20, 22, 24², 25, 26
4, 24¹, 27
8
6, 11, 12, 14, 15, 18, 21

FIGURE 18. Cladogram of the species of Erisma.
-: synapomorphy; ▬: reversal; ●: parallelism.


Erismadelphus
Erisma arietinum
Erisma bicolor
Erisma floribundum
Erisma laurifolium
Erisma bracteosum
Erisma gracile
Erisma lanceolatum
Erisma micranthum
Erisma calcaratum
Erisma japura
Erisma nitidum
Erisma splendens
Erisma uncinatum
Erisma fuscum
Erisma silvae
Erisma blancoa
12,14,15,16,20
4,5,10
6
11
13
12,19
2
11
2,7,9
2,7
9,17

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