DIALYPETALANTHUS FUSCESCENS KUHLM. (DIALYPETALANTHACEAE): THE PROBLEMATIC TAXONOMIC POSITION OF AN AMAZONIAN ENDEMIC[1]

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ABSTRACT

The neotropical rainforest tree *Dialypetalanthus fuscescens* Kuhlm. is the only species of the Dialypetalanthaceae. In-depth morphological and anatomical documentation is presented, including newly recorded features such as indeterminate inflorescences, anthers with calcium oxalate packages, silica bodies in the wood, U-shaped placentas and dendritic hairs, and corrections of erroneous literature observations, e.g., on supposed stipular dimorphism. The genus is heterobathmic, combining advanced gynoecial characters with such primitive features as free petals, dimery, stipules, and (here postulated) cantharophily. In the past, *Dialypetalanthus* was most frequently suggested to be related to Myrtales or Gentianales. However, because of the lack of bicollateral vascular bundles, presence of well-developed stipules, paracytic stomata, obvious endosperm and unitegmic ovules, seed-coat structure, and gynoecial origin of the disk, a close relationship with the Myrtales is unlikely. An affinity with the Gentianales, the Rubiaceae in particular, is accepted instead. It is concluded that ontogenetic and micro- and macromolecular data are much needed for a further elucidation of the relationships of *Dialypetalanthus*.

The monospecific Amazonian genus *Dialypetalanthus* is enigmatic as regards its systematic position. Characters such as the opposite, entire leaves with sheathing stipules and the dry fruits with winged seeds obviously point to a position in (or near) the Rubiaceae. However, a close relationship with the Rubiaceae must be questioned because of the presence of certain deviant floral characters (e.g., free petals and numerous stamens in two whorls with their filaments fused into a basal ring). As for the classification of *Dialypetalanthus*, all present authors accept its familial status, but they do not agree about the relatives of the Dialypetalanthaceae. While some prefer a position in the Myrtales or Rosales, others assign the family to Gentianales or Rubiales. In the present paper we aim (1) to document knowledge of *Dialypetalanthus fuscescens* Kuhlm. as broadly as possible and (2) to clarify its systematic position.

HISTORICAL SURVEY

In October 1874, Ferreira was the first to collect some flowering branches of a yet unknown tree from the Amazonian region. The specimen (*Ferreira 438*) was filed in the herbaria of K and LISU as an unidentified taxon of the Rubiaceae. In 1925 the tree was re-collected and described by Kuhlmann as the new genus and species *Dialypetalanthus fuscescens* Kuhlm.

According to Kuhlmann (1925, 1942), the ascending imbricate ovules, winged seeds, and embryo "formando núcleo central" (1942: 25) clearly indicate a relationship between *Dialypetalanthus* and Rubiaceae, more specifically with the tribe Cinchoneae of the subfamily Cinchonoideae sensu Schumann (1891). Kuhlmann established a monogeneric tribe Dialypetalantheae in the Rubiaceae, characterized by free petals and anisomery.

After a reinvestigation, mainly of wood and leaf anatomical characters, Rizzini and Occhioni (1949) established the monotypic family Dialypetalanthaceae. They concluded that the Dialypetalanthaceae are to be placed in the Myrtales, somewhere near the Myrtaceae (*Eugenia*), Melastomataceae (*Huberia*), or Hydrocaryaceae (= Trapaceae). Note that

Kuhlmann (1925) had already mentioned that the copious flowering of *Dialypetalanthus* reminded him of certain Myrtaceae. In addition, Rizzini and Occhioni sent samples of *Dialypetalanthus* to some "eminent botanists" (Burkart, Erdtman, Lam, Janssonius, and Bremekamp), asking for their opinion. In 1952, Occhioni and Rizzini assembled their answers into a publication. All the taxonomists consulted accepted the establishment of a new family, which probably explains why it is generally accepted today. They disagreed, however, about its possible relatives. Burkart stated that relatives of *Dialypetalanthus* should be looked for somewhere in his Myrtiflorae; Erdtman concluded that the pollen of *Dialypetalanthus* resembles that of certain Rhizophoraceae (see also Erdtman, 1971); Lam, while admitting some resemblances to the Rubiaceae, suspected a relationship with Lythraceae or Melastomataceae; Janssonius found similarities between the wood of *Dialypetalanthus* and that of the genus *Psychotria* of the Rubiaceae; finally, Bremekamp agreed with Rizzini and Occhioni (1949) that relatives of *Dialypetalanthus* should be sought near the Myrtaceae and Melastomataceae, notwithstanding the large leaf-like stipules and lack of intraxylary phloem (see also Bremekamp 1966: 3, 8).

Emberger (1960), Melchior (1964), Cronquist (1968), Stebbins (1974), and Dahlgren (1975) followed Rizzini and Occhioni (1949) and placed the Dialypetalanthaceae in the Myrtales. Cronquist (1981), however, reconsidered his opinion, placing *Dialypetalanthus* in "the rather amorphous Rosales" (p. 551), where it was kept in his system of 1988. He refused to associate the family either with Myrtaceae (because of the stipules and the lack of internal phloem) or with Rubiaceae (because of the free petals and numerous stamens on top of the ovary).

Dahlgren also changed his view on the systematic position of *Dialypetalanthus*. At first, he transferred the Dialypetalanthaceae from Myrtales to Cornales (Dahlgren, 1980); later he moved the family to Gentianales (Dahlgren, 1983; no arguments were provided for this transfer, but are presumably the same as given in Dahlgren & Thorne, 1984; discussed further).

According to Hutchinson (1959), free petals and polyandry occur in Dialypetalanthaceae, as well as in some genera of the Rubiaceae, and should not be considered as distinctive characters (but his argument does not hold; see Discussion). He placed the Rubiaceae and Dialypetalanthaceae in a separate order Rubiales, closely related to the Loganiaceae (Gentianales).

In a study of the Myrtales, Dahlgren and Thorne (1984) concluded that *Dialypetalanthus* should be excluded from the order. Stressing inter alia the paracytic stomata, they considered the Dialypetalanthaceae as an "early off-shoot of the Rubiaceae or a relict family closely related to the Rubiaceae in the Gentianales" (p. 690).

Robbrecht (1994), in a review of the delimitation of the Rubiaceae, added a few new characters that are in common between Dialypetalanthaceae and Rubiaceae, namely the thickening pattern of the inner tangential walls of the exotestal cells and the occurrence of colleters on the adaxial surface of the stipules. He concluded that a profound study of the Dialypetalanthaceae is needed to shed more light on the possible relationships.

In their consensus classification of the Gentianales, Nicholas and Baijnath (1994) suggested that *Dialypetalanthus* represents an archaic group without any close living relatives. They excluded the genus from the Gentianales and placed it near the order Cornales and its allies, concluding that it needs much closer analysis.

MATERIAL AND METHODS

This study is based on herbarium material from NY, US, and K (herbarium abbreviations following Holmgren et al., 1990). Numerous attempts to obtain fixed material were unsuccessful. The distribution map was completed with locality data from specimens from the Museu Goeldi (MG) (data provided by L. Macias, Belém).

Both for scanning electron microscopy (SEM) and light microscopy (LM) observations, the herbarium material was prepared by simple boiling or by the method described by Peterson et al. (1978), using a mixture (6:1) of 10% aqueous di-(2-ethylhexyl) sodium sulfosuccinate, and 98% acetone for 24 hours (see also Erbar, 1995). For LM, the material was dehydrated in an alcohol series and embedded in paraffin, using a Histokinette 2000. Sections (10–14 μm) were made with an M1R Shandon rotation microtome, and subsequently colored with safranin (10 min) and fastgreen (4 min) in a Varistain 24-3, Shandon. After staining, the sections were mounted in Eukitt. Observations were made with a Dialux 20 Leitz microscope.

For SEM, the material was dehydrated in an alcohol series and FDA (formaldehydedimethylacetal). After critical-point drying (CPD 030 Critical Point Dryer, Balzers), the material was mounted on stubs with Leit-C Conductive Carbon Cement and sputter-coated with gold (± 180 nm) in a Spi-module® Sputter Coater (Spi Supplies). Observations were made with a JEOL JSM-6400 electron micro-
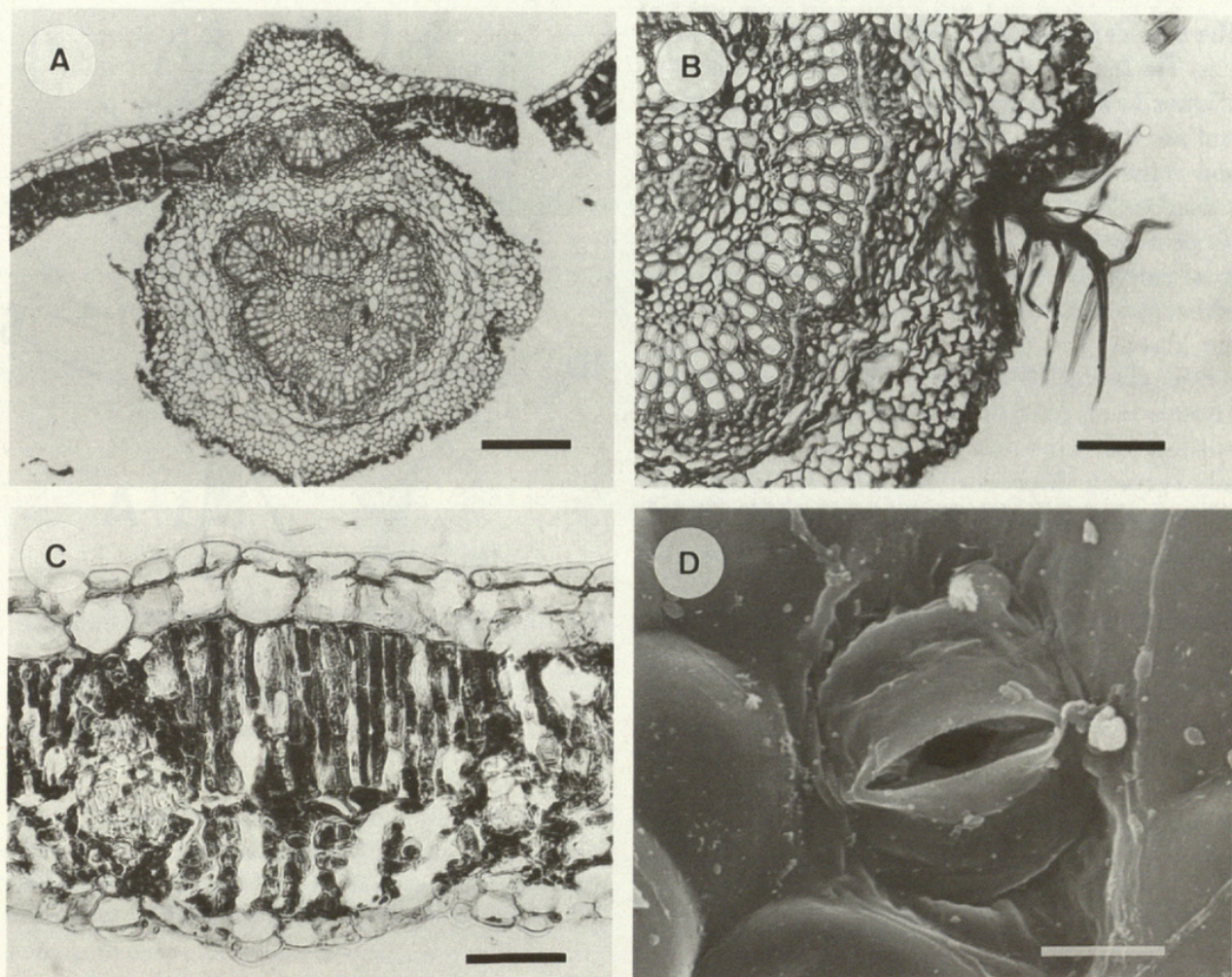
Figure 1.   Leaf structure of *Dialypetalanthus fuscescens*. (A–C LM; D SEM.)—A. Transverse section of the main vein; bar = 0.25 mm.—B. Dendritic hair on the main vein; bar = 0.1 mm.—C. Transverse section of the lamina; bar = 50 μm.—D. Paracytic stoma in surface view; bar = 10 μm. After *Cid Ferreira 9018* (A–C) and *Lobo et al. 328* (D).

scope. In order to show the thickenings of the inner tangential walls of the exotestal cells, the outer tangential walls had to be removed. Therefore, boiled seeds were transferred to a 3:1 mixture of alcohol 96% and acetic acid 99% for 24 hours. Afterward they were put in a 3% aqueous mixture of sulphuric acid at 50°C for at least 10 hours (modified from Braune et al., 1967). Remaining specks of dirt were removed by ultrasonication.

The methods used for acetolysis and breaking pollen grains are discussed in detail by Huysmans et al. (1994). Wood anatomical sections were prepared as described by Jansen et al. (in prep.).

RESULTS

VEGETATIVE STRUCTURES

Habit.   *Dialypetalanthus fuscescens* is a large, slender rainforest tree reaching up to 30 m (but usually smaller). It has a soft, fibrous (because of the formation of several concentric phellogen layers), red to cinnamon-colored bark. The trunk is

fluted toward the base. The wood is light but extremely hard. It is used locally for house construction (Rizzini & Occhioni, 1949), but as far as we know it has little economic value.

Leaves.   The simple leaves are decussately arranged and have blades with entire margins. The petiole is well developed (0.6–3.5 cm) and shallowly sulcate above. The blades are broadly elliptic (L/W-ratio 1.5:1), elliptic (2:1), suborbiculate (1.2:1), to narrowly (2:1) or widely obovate (1.2:1) (sometimes slightly asymmetric), with a shortly acuminate to rounded tip, and an obtuse, acute or cuneate to slightly decurrent base (terminology following Hickey, 1988); they are (2–)6–17(–20) × (1–)4–11(–14) cm. The leaf venation is pinnate and camptodromous. The veins, especially the midvein (Fig. 1A), are prominent on the abaxial side of the blade. The divergence angle between primary and secondary veins is about 35° in the center of the blade and gradually rises toward the base of the leaf. The veins are detectable up to the fifth order.

The areoles have a more or less constant shape and size. The leaves become gradually smaller and have a lower L/W-ratio toward the inflorescence region, and are eventually replaced by bracts. The petiole and veins are densely covered with unicellular to uniseriate hairs on the abaxial side. Dendritic hairs occur as well very sporadically (Fig. 1B). The adaxial side of the leaf is almost completely glabrous or bears few hairs along the main veins. Domatia are absent. The upper epidermis consists of flat, rectangular cells (Fig. 1C) that occasionally contain crystals of an unknown nature. The strongly developed cuticle runs over the leaf margin and gradually becomes thinner on the lower epidermis. The outer tangential wall of the epidermal cells is straight, except above the veins, where it is rounded. Beneath the upper epidermis, a well-developed hypodermis occurs with clearly larger cells. The palisade tissue is well developed and consists of a maximum of 6 cell layers (often less). It is interrupted only by the main veins. At the leaf margin, the palisade tissue is replaced by angular collenchyma. According to Rizzini and Occhioni (1949), the spongy mesophyll and palisade tissue are separated by a layer of isodiametric cells (not seen by us). The lower epidermis (inclusive of the hypodermis) is much thinner and more irregular than the upper epidermis. The difference in cell size between epi- and hypodermis is much less pronounced. Stomata are paracytic, randomly oriented, more or less sunken, and found only in the lower epidermis (Fig. 1D). The vascular configuration of the petiole and midvein is complex and rather variable in successive sections (Fig. 1A). In the center, short radial vessel rows are arranged in an arc, open toward the adaxial side. The main leaf anatomical characters were described by Rizzini and Occhioni (1949). Most of their observations were confirmed in our preparations.

Stipules. At each node, two large leaf-like stipular lobes—the most conspicuous vegetative character of *Dialypetalanthus*—occur on either side between the two petioles (Fig. 2). Rizzini and Occhioni (1949), Hutchinson (1959), and Cronquist (1981) considered them to be intrapetiolar, while Dahlgren and Thorne (1984) described them as interpetiolar. We observed that the four stipular lobes are connected at their base to form a low sheath around the stem, i.e., they are intra- as well as interpetiolar. This sheath is covered adaxially with a basal row of long silvery hairs and colleters of the standard Rubiaceae type (that is, consisting of an axis of elongated cells, covered by a palisade-like epidermis; Robbrecht, 1988). The abaxial sur-
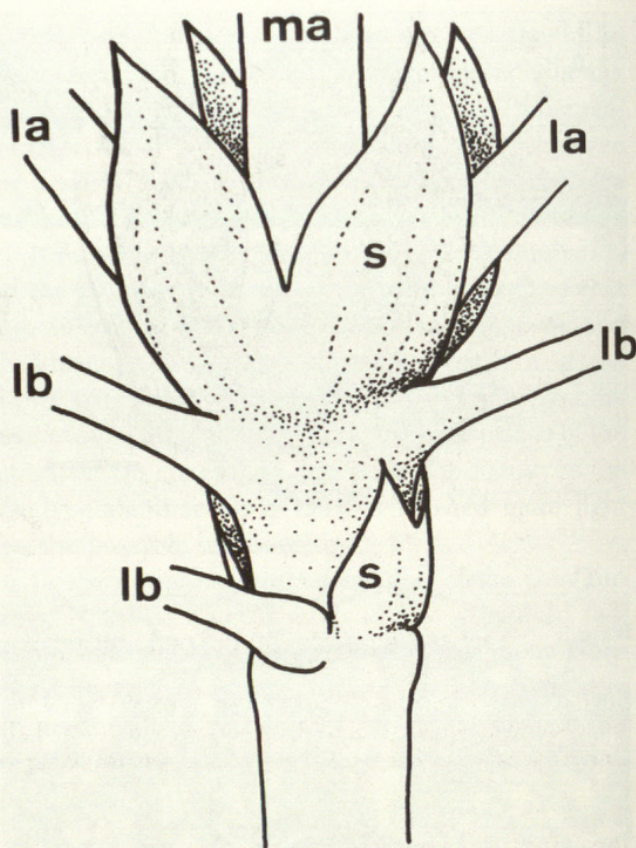

Figure 2. Stipular dimorphism at the base of an inflorescence; lb = leaf base, s = stipule, la = lateral inflorescence axis, ma = main inflorescence axis.

face is densely covered with unicellular to uniseriate trichomes. Rizzini and Occhioni (1949) claimed that *Dialypetalanthus* has two types of stipules, namely normal and "bud stem covering" ones ("bud stipules" as we will call them in the following discussion). They considered this so-called "stipular duality" to be unique in the dicotyledons. The bud stipules would bear a "remarkable pilose scale at the base" and fall off when the "gemma" (apical bud) increases. We have dissected several intact terminal buds (Fig. 3A), looking for possible scars of former structures, but could not confirm the findings of Rizzini and Occhioni. After we had removed the outer stipules (these are the bud stipules of Rizzini and Occhioni) of a terminal bud, two structures, densely covered with hairs, indeed appeared (Fig. 3B, C). However, their position (alternating with the last normal pair of leaves and alternating with the hairy structures of the next node; Fig. 3D), and their clearly pinnate venation pattern, proves that these "pilose scales" are reduced leaves. Therefore, there is no essential difference between bud stipules and the other stipules. The only genuine stipular dimorphism we noticed is in the transition zone between vegetative and generative parts, i.e., at the base of the inflorescence. Here consecutive nodes bear stipules that differ strongly, mainly
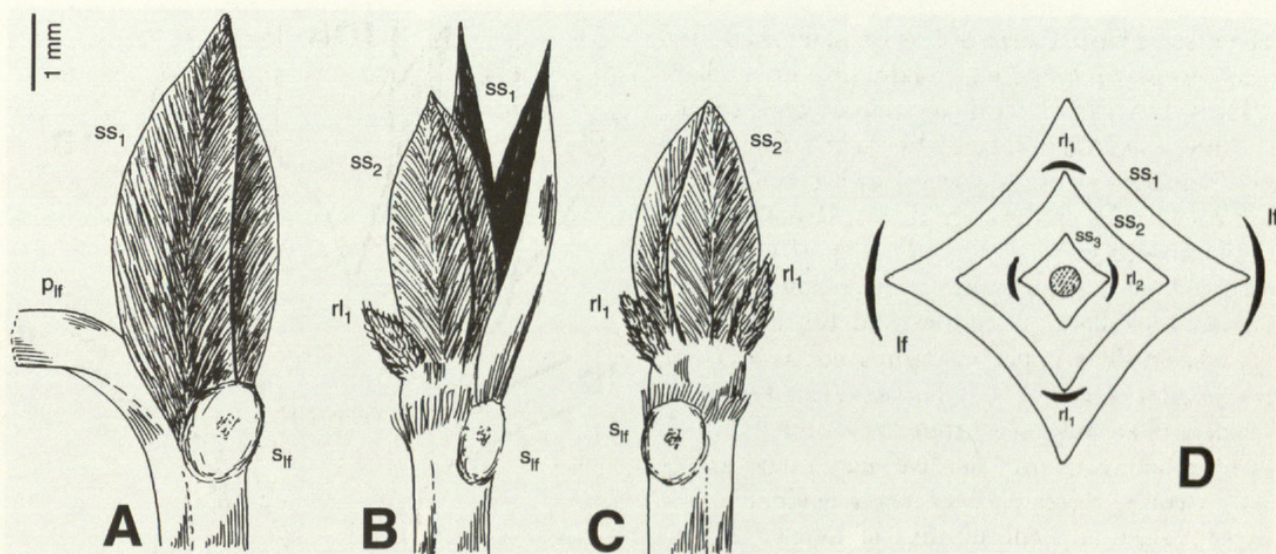
lf: leaf (s$_{lf}$, scar of leaf; p$_{lf}$, petiole); rl$_1$, rl$_2$: reduced leaves; ss$_1$, ss$_2$, ss$_3$: stipular sheaths

Figure 3.   Dissection of a terminal vegetative bud of *Dialypetalanthus fuscescens.*—A. Intact bud.—B. Half of the outer stipular sheath removed, revealing a reduced hairy leaf and the stipular sheath of the next node.—C. Outer stipular sheath removed completely.—D. Schematic representation of a vegetative bud. After *Nee 34472.*

in size (upper ones much larger than the short, triangular lower ones; Fig. 2). Anatomically, the stipules have a characteristic adaxial epidermis, consisting of thickened cells. Scattered through the homogeneous chlorenchyma are numerous small vascular traces that are surrounded by fibers. Rizzini and Occhioni (1949) recorded occasional paracytic stomata in the abaxial epidermis.

Wood anatomy.   The wood of *Dialypetalanthus* shows indistinct growth rings (probably reflecting the precipitation cycle), marked by a transition from thin- to thick-walled fibers. The fibers are septate (Fig. 4C) and have simple pits in vertical rows (Fig. 5D) (libriform fibers sensu Baas, 1986). The wood is diffuse-porous. The vessels are solitary or arranged in short radial rows (2–8 cells) (Fig. 4D, E). In young wood, close to the pith, the radial vessel rows are often longer. The outline of the solitary vessels is rounded (Fig. 4E), although the smaller vessels are often compressed between the larger ones. Axial parenchyma is present and occurs as scanty, paratracheal strands (Fig. 4B). The width of the rays varies from (1–)2 to 6 cells (Fig. 4A); their height may exceed 100 cells. In radial sections, the procumbent body-ray cells have a margin of one or often several layers of square cells (Fig. 4F). Sometimes a mixture of procumbent and more or less square cells occurs. The rays are visible to the naked eye as clear, narrow, parallel lines. The pith and the rays contain very small cubic to prismatic crystals; navicular crystals occur as well. The septate fibers as well as the rays con-

tain silica-bodies (Fig. 4G, H). The perforation plates of the vessels are simple, bearing a single elliptical to almost circular opening (Fig. 5A). The vessel-ray pits are simple (Fig. 5B). The intervessel pits are alternately arranged and vestured (Fig. 5C). Internal phloem is absent.

REPRODUCTIVE STRUCTURES

Inflorescence.   The bloom of *Dialypetalanthus* is copious, with numerous white, fragant flowers in large inflorescences. The inflorescence of *Dialypetalanthus* (Figs. 6–8) was described by Kuhlmann (1925) as paniculate and racemose. Rizzini and Occhioni (1949) and Hutchinson (1959) also indicated it was a panicle. According to Weberling (1992), a panicle is characterized by terminal flowers on its main axis and side branches. Thus, a panicle is a determinate inflorescence. *Dialypetalanthus,* however, does not have a terminal flower but a terminal bud that at first sight may be confused with a single terminal flower. Dissection of the terminal bud reveals a floral meristem where acropetal inception of lateral flowers occurs (the flowers in the most terminal zone seem to be poorly developed) (Fig. 7). The inflorescence of *Dialypetalanthus* is thus indeterminate, contrary to a panicle. Dahlgren and Thorne (1984) provided the first correct illustration of the inflorescence but did not describe it. Cronquist (1981) was the first to correctly call the *Dialypetalanthus* inflorescence a thyrse. More specifically, it is a frondobracteose, heterothetic, indeterminate thyrse with opposite branches (Fig.
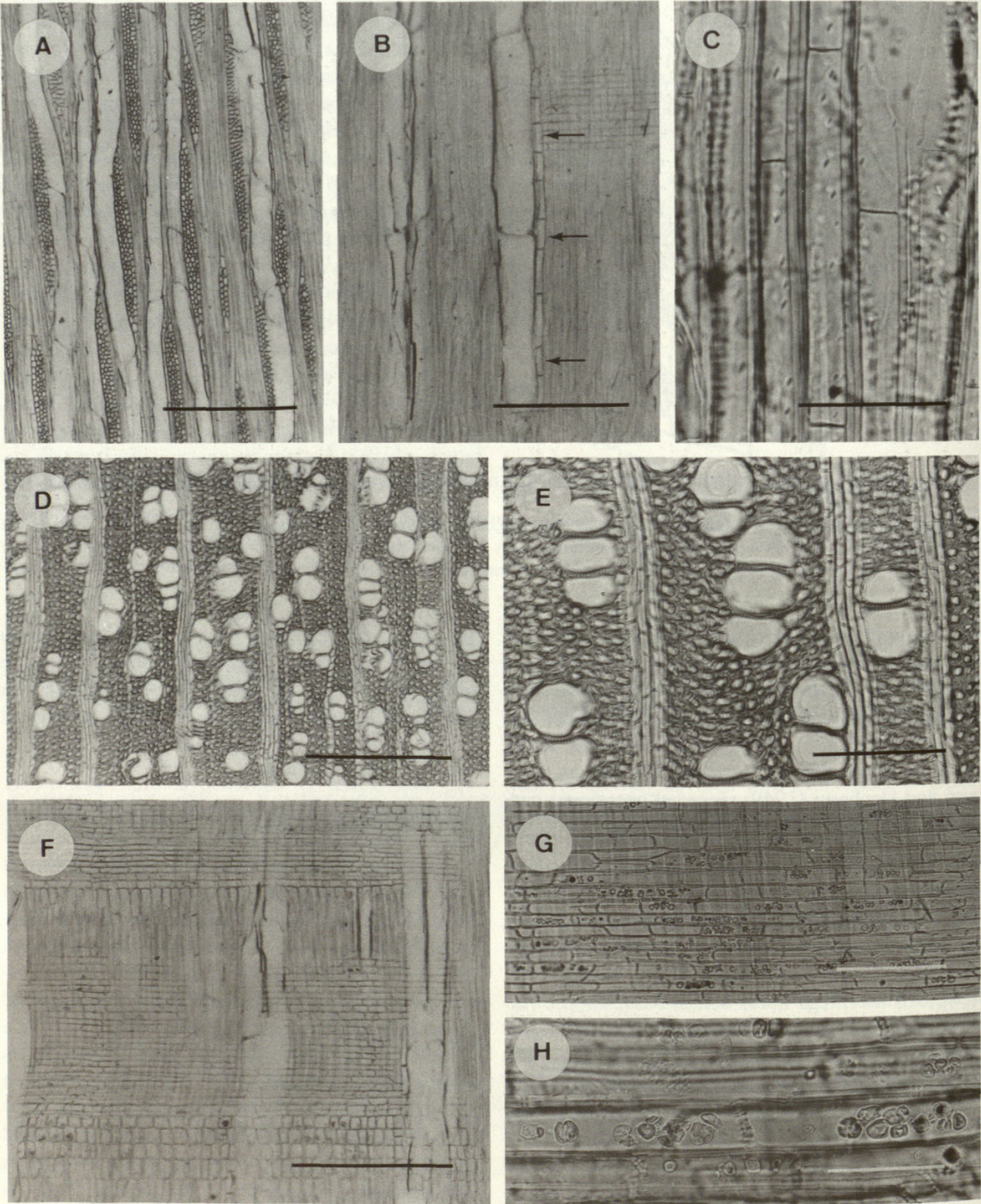
Figure 4. Wood anatomy of *Dialypetalanthus fuscescens* (LM).—A. Tangential section; bar = 0.5 mm.—B. Radial section showing paratracheal parenchyma (arrows); bar = 0.35 mm.—C. Tangential section of septate fibers; bar = 50 μm.—D, E. Transverse sections with short radial vessel rows and 4-cellular rays; bars: D = 0.5 mm, E = 0.2 mm.—F. Radial section of a ray with several layers of square marginal cells; bar = 0.5 mm.—G. Radial section showing silica bodies in a ray; bar = 0.2 mm.—H. Radial section with detail of silica bodies; bar = 50 μm.

8) (all terms sensu Weberling, 1992). The inflorescences are (usually) terminal. Normally, two side branches occur at each node (three branches in the type specimen, *Kuhlmann 1514*; observed nowhere else). Bracteoles are situated somewhere near the middle of the pedicel. The bracts, bracteoles, and true leaves of the inflorescence are all deciduous. As mentioned earlier, the transition zone from
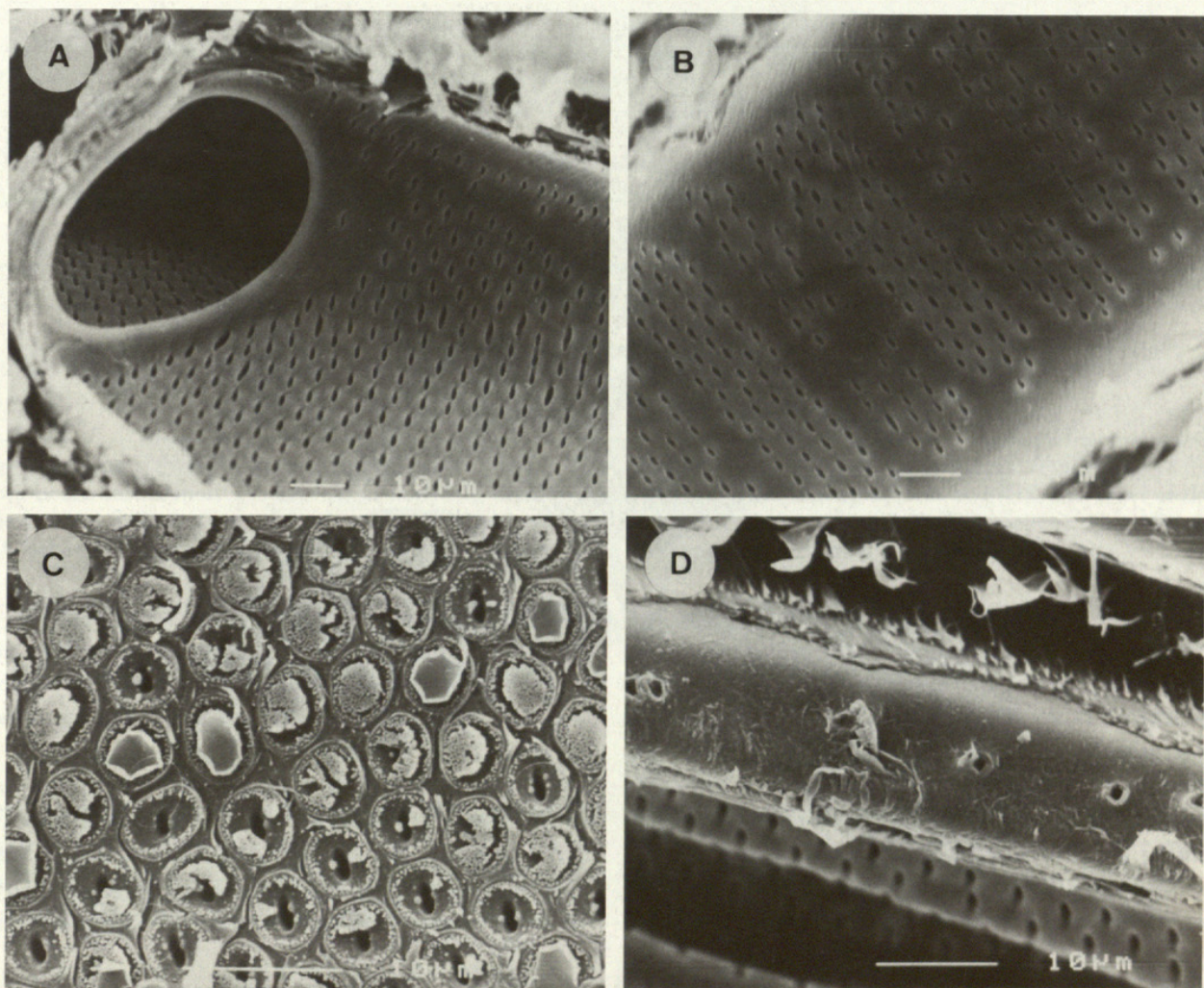
Figure 5.   Wood anatomy of *Dialypetalanthus fuscescens* (SEM).—A. Simple perforation of a vessel.—B. Simple pits between a vessel and underlying ray parenchyma.—C. Vestured pits.—D. Simple fiber pits.

woody to herbaceous parts at the base of the inflorescence is characterized by a short stem portion with different-sized stipules.

Calyx.   The calyx of *Dialypetalanthus* consists of four green, semicircular lobes. These lobes arise as two decussate whorls of two primordia (Fig. 9G). In early ontogenetic stages, the sepals cover the other floral structures completely (cryptopetaly sensu Sprague, 1940). Later, they are pushed apart by the developing petals, stamens, and style. The abaxial side of the sepals as well as that of the petals is covered with a typical, velvet-like indumentum, consisting of long uniseriate hairs, with the exception of a rather broad (1 to 2 mm) hairless border. The margins are fringed. Apart from the base, the adaxial side of the sepals is glabrous. As in the other floral structures, the sepal lobes are thick and fleshy. In the center, they usually consist of about 20 cell layers. The cells of the epidermis are clearly smaller than the cells of the underlying parenchyma. Numerous vascular traces occur in the center of the parenchyma. The sepal lobes are persistent.

During maturation and dehiscence of the fruit, they are split in two (Fig. 15A).

Corolla.   The corolla is composed of four free, white petals. Just like the calyx lobes, they arise as two decussate whorls of two primordia each (Figs. 9G, 10). This dimerous origin of calyx and corolla (sometimes noted in the literature: Cronquist, 1988; Maas & Westra, 1993) should be represented on a floral diagram with petals opposite to sepals (Fig. 10), instead of alternating with them. In very young buds, all petals are globular and cover almost completely the interior floral parts. In older stages, petals enclose the interior floral parts in pairs. During anthesis, the petals unfold into broadly elliptic (2 to 2.5 cm long and 1.5 cm wide), shortly ungulate structures. The innermost petal is distinguished from the other petals because of an apical prolongation with transparent hairs at the margin in the bud stage. The inner petals are often more or less wrinkled, thus allowing rapid expansion during anthesis. Aestivation is imbricate, but with variations. Sometimes a petal will overlap an-

Figure 6. Flowering specimen of *Dialypetalanthus fuscescens* with flowers in late bud stage (*Fernández Casas & Susanna 8188*, NY); bar = 5 cm.

other on both sides, as is always the case with the inner petal whorl (and the sepals); sometimes the overlapping will occur only on one side (this has only been observed in the outer petal whorl). As mentioned above, the abaxial indumentum of the petals is comparable to that of the calyx lobes. The adaxial side is glabrous. The corolla is shed shortly after anthesis (Fig. 9D). It is not clear whether pollination has already occurred at that stage or if the yellow-colored stamens take over the attractive function of the corolla. Anatomically, the corolla is very similar to the calyx. The fleshy petals have a distinct epidermis with relatively small cells. Beneath the epidermis there is a poorly differentiated, many-layered parenchyma enclosing numerous,

parallel vascular bundles. Crystal sand occurs scattered through the parenchyma.

Androecium. The androecium of *Dialypetalanthus* consists of 16 to 25 (usually less than 20; commonly 16 or 17) stamens that are united at their base into a short androecial ring atop the ovary, free from the corolla. Two whorls can be distinguished within the androecium, the outer whorl always having more stamens than the inner. A slight dimorphism can be seen between stamens of the two whorls: the inner ones have slightly longer anthers and a shorter filament than the outer ones (Fig. 9A). The stamens are closely packed together in bud stage and tightly enclose the developing style. They
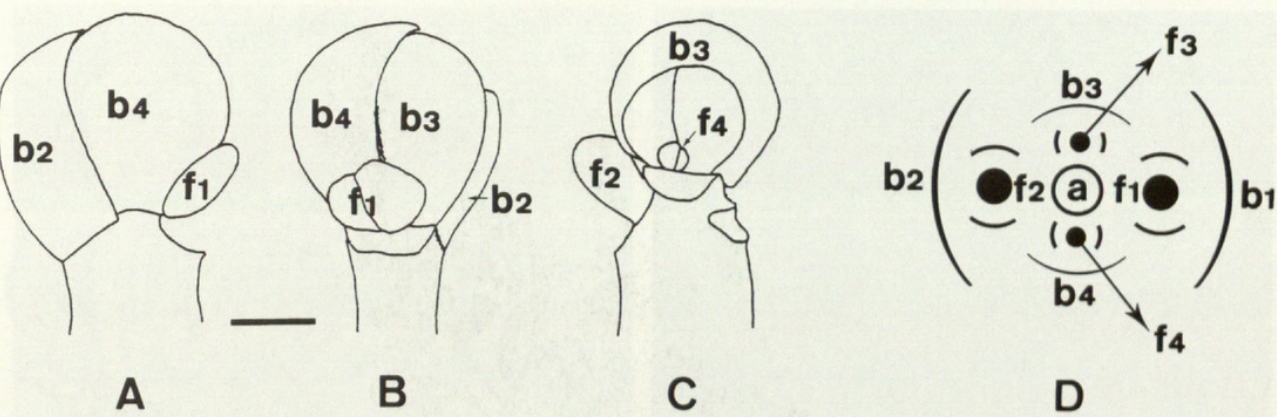
Figure 7.   Dissection of a terminal bud of the inflorescence of *Dialypetalanthus fuscescens*.—A. Right bract removed, revealing the right floral bud surrounded by two bracteoles (f1).—B. The same dissection showing a frontal view of the two bracteoles around the right floral bud.—C. Same view as A; left bract (b2), right floral bud (f1), and bract of the next whorl (b4) also removed, showing left floral bud of the first whorl (f2) and floral bud of the second whorl (f4).—D. Schematic representation of a terminal inflorescence bud; a = axis; bar = 1 mm. After *Ducke 22816.*

are yellow-green and remain after the corolla has fallen off. Later, the androecium falls off as a whole, leaving only the style.

Each locule consists of two clearly separated pollen sacs (Fig. 9B). The locules are large, elongate (7 to 8 mm long and 2 mm wide), and pointed to the lateral-adaxial side. The short filament (Fig. 9A) is basifixed and continues in a massive, essentially abaxial connective (Fig. 9B). A peculiarity of

the stamens of *Dialypetalanthus* is the (very) sporadic occurrence of stellate trichomes on the anthers (Fig. 9E). In most cases, however, the stamens are completely glabrous. The locules possess two horn-like appendages at their apex (Fig. 9C). These locular appendages are curved toward each other and have two basal branches, one to each pollen sac (Fig. 11A). Kuhlmann (1925) did not mention these structures at first, but later he called them, rather unfortunately, "little valves" (Kuhlmann, 1942). Neither Rizzini and Occhioni (1949), Hutchinson (1959), nor Cronquist (1981) paid any attention to these appendages; Dahlgren and Thorne (1984) illustrated them but did not refer to them. The locular appendages are clearly visible in bud stage (Fig. 11A). Just before anthesis the anthers tear open between the basal branches of the appendages (Fig. 11B), leaving small, more or less round pores at the top of the locules (Fig. 11C) through which the pollen is released. Anther dehiscence therefore is porate (as stated by Kuhlmann, 1925; Rizzini & Occhioni, 1949; Cronquist, 1981; Dahlgren & Thorne, 1984). It has to be mentioned, however, that in some cases the pollen sacs are split open over their entire length, probably explaining why Hutchinson (1959) stated that dehiscence is longitudinal. The locular appendages consist of parenchymatic tissue filled with crystal sand, surrounded by a more or less sclerified zone (Fig. 9C). A similar kind of calcium oxalate accumulation in anthers was described for Solanaceae and some other families by D'Arcy et al. (1996). They reported a special type of hypodermal tissue in the stamens, the so-called resorption tissue, filled with calcium oxalate crystals and situated at the stomium, running lengthwise around the anther. During maturation of the stamens, the tissue surrounding the
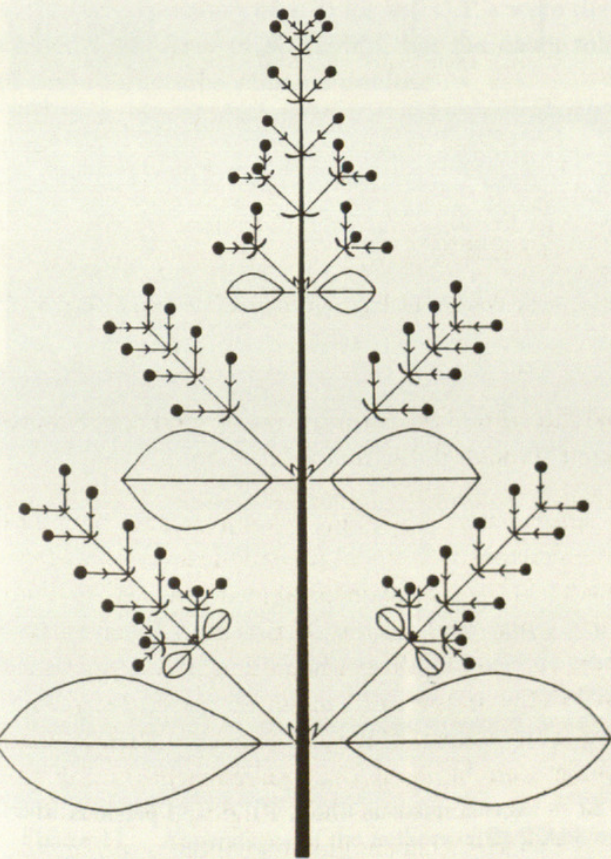

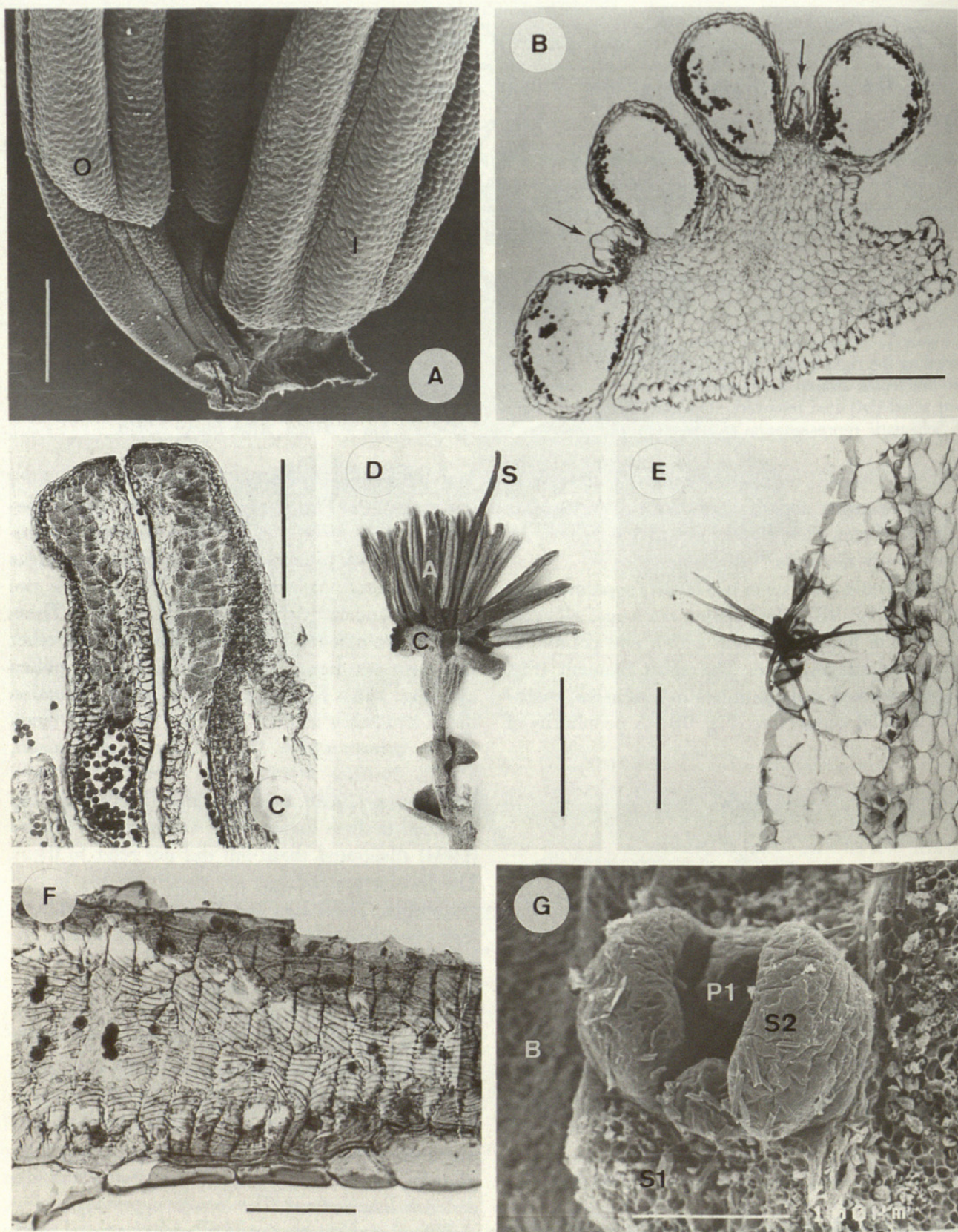Figure 8.   Schematic representation of the inflorescence of *Dialypetalanthus fuscescens.*

Figure 9.   Androecial structure (A–F) and floral ontogeny (G) of *Dialypetalanthus fuscescens*. (A and G SEM; B, C, E, and F LM; D macro photograph.)—A. View of the fused base of the outer (O) and inner (I) androecial whorls; bar = 1 mm.—B. Transverse section of a stamen; note the epidermal protuberance between the pollen sacs (arrows); bar = 0.5 mm.—C. Longitudinal section of the crystalline appendix of a locule; bar = 0.25 mm.—D. Appearance of a flower after the petals have fallen off; S = style, A = androecium, C = calyx; bar = 1 cm.—E. Stellate hair on stamen; bar = 0.25 mm.—F. Endothecial thickenings; bar = 0.1 mm.—G. Young flower showing the dimerous origin of calyx and corolla; B = whorl of bracts, S1 = first sepalous whorl, S2 = second sepalous whorl, P1 = first petalous whorl. After *Ducke 22816* (B, C, E, F, G), *Ducke 21684* (A), and *Nee 34472* (D).
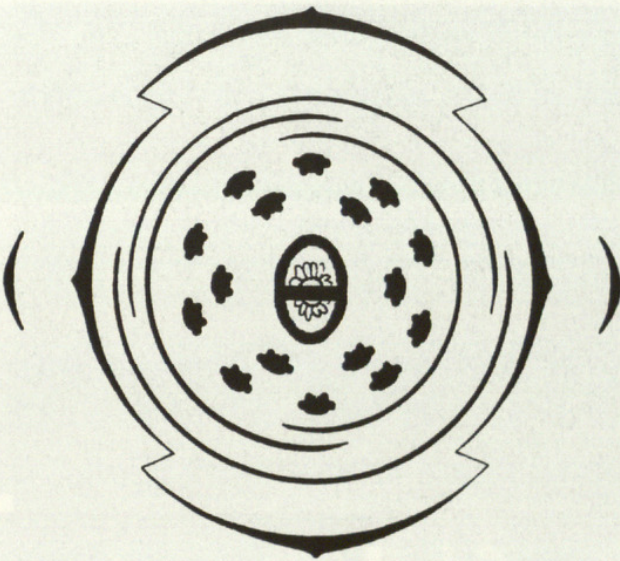
Figure 10.   Floral diagram of *Dialypetalanthus fuscescens*. Note the alternation of dimerous whorls. The stamens are united at their base into a short androecial ring.

resorption tissue disintegrates and a mass of crystals, the "oxalate packages" (O.P.'s), is set free. It appears that the situation in *Dialypetalanthus* is very similar, although the location of the crystals (at the top of the anthers instead of the stomium) is somewhat different (see also the section on Pollination Biology). Various possible functions (e.g., in anther dehiscence, discouragement of herbivores, as pollinator reward) for the O.P.'s were discussed by D'Arcy et al. (1996), but the exact role of these structures remains unclear.

The inside of the pollen sacs is covered with small (< 1 μm), globular, smooth orbicules. Huysmans et al. (1997) have recently drawn attention to these easily overlooked structures in Rubiaceae. Between the pollen sacs of each locule, a clear epidermal protuberance with remarkably enlarged epidermal cells occurs (Fig. 9B). The same epidermal configuration is found in between the locules, at the adaxial side of the connective. In transverse sections, the cortex cells of the connective are isodiametric with large intercellular cavities. Longitudinally, the cells are elongated and clearly smaller than the epidermal cells. They become smaller in the proximity of the pollen sacs. The cortex zone beneath the epidermal protuberances is strongly lignified, often with off-shoots into the endothecium (Fig. 9B). A one-layered endothecium occurs, except at the dorsal side of the pollen sacs. The endothecial thickenings are mostly spiral, seldom circular or U-shaped, or may even be absent (Fig. 9F). In longitudinal sections the endothecial cells have the polygonal appearance of cambial cells, with their longitudinal axis perpendicular to that of the cortical cells. The well-developed connective is triangular in cross section (Fig. 9B). It contains one central vascular bundle that seldom splits into two smaller bundles at the apex of the stamens. In the filament, at the adaxial side of the vascular bundle, one can find a half circle of dark-staining cells, possibly with high metabolic activity. A transverse section of the androecial ring shows a ring of dark-colored cells connecting the vascular bundles of all stamens. The function of these cells is unclear.

It is not yet clear how the androecium is initiated. Most probably it is not an example of primitive polyandry (that is, each stamen arising as a separate primordium; Ronse-Decraene & Smets, 1992), but a case of complex polyandry. In view of the dimerous origin of calyx and corolla, we expect the existence of two alternating whorls of two complex primordia each, giving rise to numerous stamens by "dédoublement." This would also be in
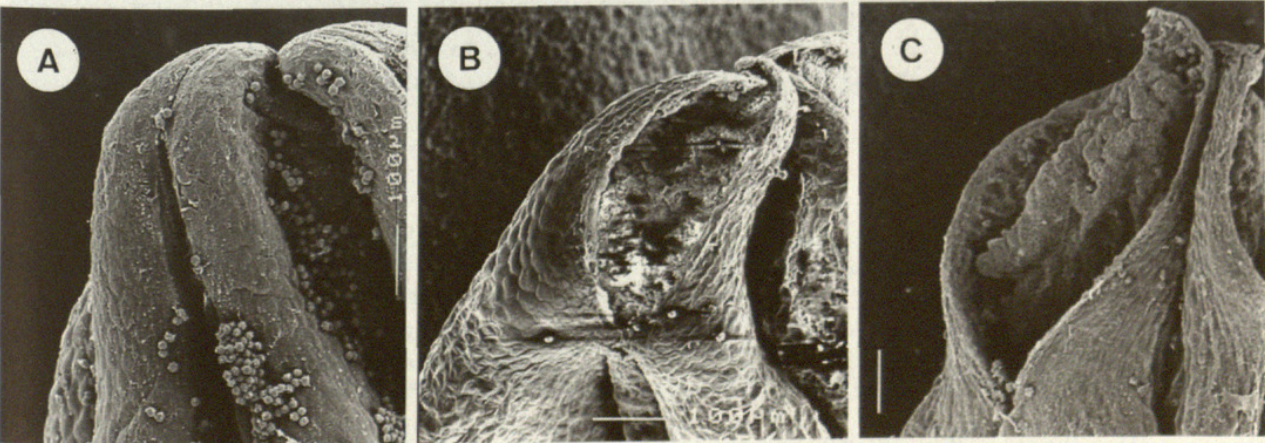

Figure 11.   Appendages of the anthers of *Dialypetalanthus fuscescens* (SEM).—A. Locular appendage before anthesis.—B. Stage between A and C: appendage tears open between its basal branches.—C. Locules after anthesis; the appendages are completely torn open. After *de Albuquerque et al. 1295* (A), *Ducke 22816* (B), and *Anderson 11865* (C).
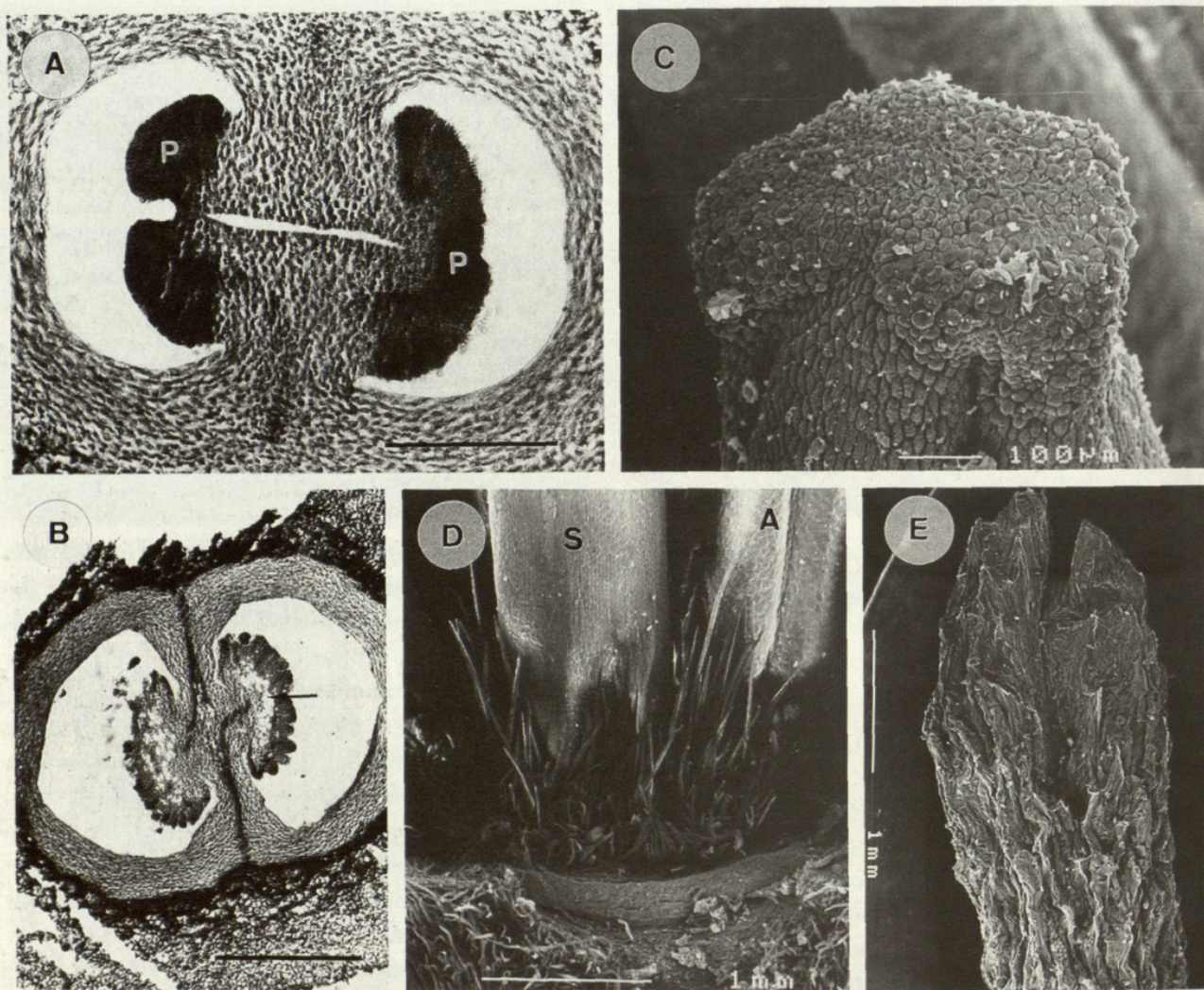
Figure 12. Gynoecial structure of *Dialypetalanthus fuscescens.* (A, B LM; C–E SEM.)—A. Transverse section at the top of a young gynoecium; P = placental zone; bar = 0.2 mm.—B. Transverse section of mature gynoecium, seen with polarized light; note the uplighting oxalate crystals in the placenta (arrow); bar = 0.5 mm.—C. Slightly bilobed, papillose stigmatic surface.—D. Long hairy disk at the base of the style (S); A = anther.—E. Apical split of the placenta in fruit stage. After *Vilhena et al. 1003* (A), *Nee 34518* (B), *de Albuquerque et al. 1295* (C), *Ducke 21684* (D), and *Thomas et al. 5205* (E).

accordance with the alternation pattern of dimerous whorls in the flower as a whole.

Pollen. The pollen of *Dialypetalanthus* is trizonocolporate (Fig. 13A). The grains are oblate-spheroidal in equatorial view (P/E-ratio 0.88–1) and rounded to triangular in polar view. The polar diameter (P) varies from 17 to 21 μm, the equatorial diameter (E) from 19 to 24 μm. The margins of the ectocolpus are irregular, but form sharp angles at the end (Fig. 13B). The mesoaperture is a porus or colpus (2 to 3 μm long and mostly less than 1 μm wide), often provided with a clear margo or annulus (Fig. 13B). The endocolpus (Fig. 13E) is oriented perpendicular to the exocolpus; it has the same dimensions as the exocolpus but is more regularly bordered. The ends of the endocolpi are sometimes bifurcate (Fig. 13F). The apocolpium is well-developed (apocolpium-index 0.35–0.45; Fig.

13A, C). The sexine is tectate perforate (perforations < 1 μm; muri larger than lumina but still < 1 μm; Fig. 13C, D). Muri are smooth to warty. The inside surface of the pollen grains is granular between the margins of the endocolpi (Fig. 13F, white star). At the top of the endocolpi, the endexine is characterized by a weak-looking zone with many irregular grooves that connects the endocolpi (Fig. 13F, black star). Sexine is as thick as or slightly thinner than the nexine (Erdtman, 1971). The columellae are short and thick.

Gynoecium. The inferior ovary of *Dialypetalanthus* is composed of two fused carpels. It is more or less flattened, grooved, and densely covered with uniseriate hairs (white in the living state; Rizzini & Occhioni, 1949). The septum is oriented perpendicular to the widest part of the ovary, parallel to the outer sepal whorl (wrongly illustrated by Rizzini
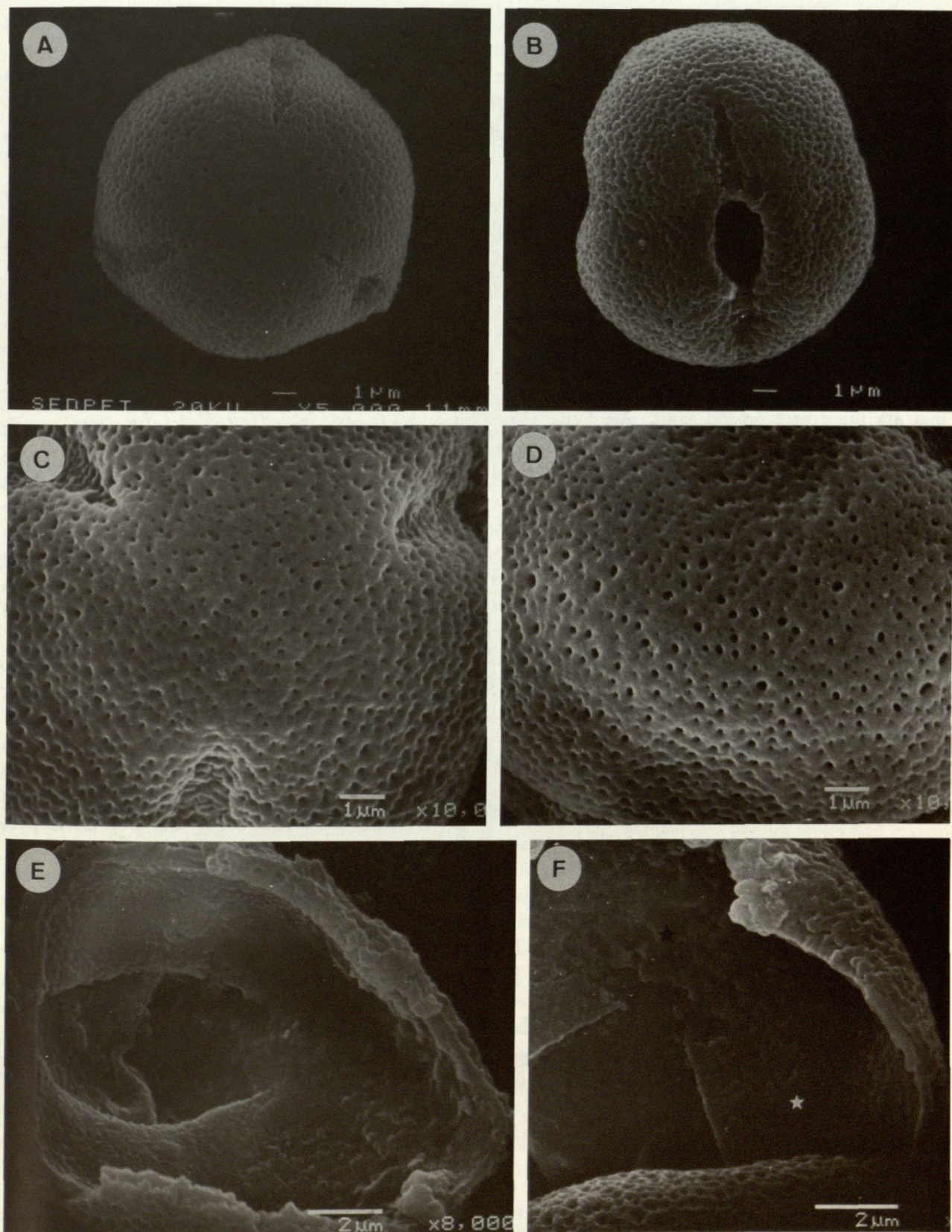
Figure 13. Pollen morphology of *Dialypetalanthus fuscescens* (SEM). A–D. Entire pollen. E, F. Broken pollen.—A. Polar view with well-developed apocolpium.—B. Equatorial view of ecto- and mesoaperture.—C. Detail of the apocolpium.—D. Detail of the mesocolpium.—E. Endocolpus.—F. Endexine ornamentation; note the difference between the warty (white star) and weaker looking zone at the top of the endocolpus (black star). After *de Albuquerque et al. 1295*.

& Occhioni, 1949). In very young buds, the two halves of the septum[4] are fused in the lower part of the ovary. In the upper part, however, they are distinct (Fig. 12A). In mature flowers, the septum is continuous throughout the ovary (Fig. 12B). As a consequence of this septal development, the placenta is U-shaped. This can be seen mainly in young flowers, where septal development is still incomplete, but even in mature fruits the apical split of the placenta is often clearly visible (Fig. 12E). Placentation is therefore axile in the lower part of the ovary and parietal in the upper part. This is often obscured by the fact that the ovules and seeds are closely packed together. Anatomically, the placenta is characterized by the occurrence of cells that are filled with crystal sand (Fig. 12B). Each locule contains numerous ascending, imbricate ovules. Even before anthesis they have the sigmoid shape that is characteristic of the seeds. Most authors (Kuhlmann, 1925; Rizzini & Occhioni, 1949; Cronquist, 1981) have described the ovules as bitegmic. However, we believe that the exotestal seed-coat structure (described later) indicates that the ovules are in fact unitegmic, as was already mentioned by Dahlgren and Thorne (1984). The style is long (up to 12 mm) and glabrous. The papillose stigma is shortly bilobed (Fig. 12C). In stained sections, the papillae are very dark, indicating that the stigma probably secretes a sticky substance in vivo. In bud stage the style is tightly enclosed by the stamens. After anthesis it elongates and rises above the androecium. The style persists even after the other floral parts (with the exception of the calyx lobes) have fallen off. In mature fruits, it falls off as well. The epidermal cells of the style are somewhat smaller than the cortical cells. The latter are more or less arranged in radial rows. The center of the cortex is formed by the transmission tissue. On each side of the transmission tissue there is a small vascular bundle. Cells containing crystal sand occur scattered through the style. Very occasionally, prismatic crystals occur as well. At the base of the style, on top of the ovary, there is a low annular disk, covered with long unicellular trichomes (Fig. 12D). Based on its position (inside the androecial whorls), the origin of the disk is most probably gynoecial and not receptacular. The nature of the secretion, if any, is not known. Just as the style, the disk is characterized by the presence of cells containing crystal sand. The ovary wall shows few striking characters. In the subepidermal

zone, numerous tannin idioblasts occur. A clear zone of flattened cells forms the wall of the locules. This zone transforms into a sclerified endocarp in the fruit stage.

Fruit and seeds. *Dialypetalanthus* bears fruits starting from the end of March or beginning of April (immature fruits are green). The fruit (Figs. 14, 15) is an elongated to more or less round (1.2–1.8 × 0.5–0.9 cm), bilocular capsule with persistent calyx lobes. In old capsules these calyx lobes may break off. The bracts and bracteoles are deciduous. The top of the fruit often protrudes above the calyx lobes. The hairy disk as well as the scars of the other floral structures remain visible (Fig. 15A). The fruit is sparsely covered with hairs (more densely so at the base of the calyx lobes), becoming almost completely glabrous when the fruit grows older. After maturation, the fruit splits at first along the septum (from the top downward), by which the outer calyx lobes are split in two. Afterward the locules are split (equally from the top downward) and the seeds set free (Fig. 15A, B). The four parts of the fruit wall remain attached together at the base.

Anatomically, the fruit consists of a thin exocarp, a "fleshy," fibrous mesocarp (due to the vascular bundles that are situated here), and a strongly sclerified endocarp. The exocarp and mesocarp can be easily removed, leaving two coffee-bean-like halves (i.e., endocarp and seeds). When a locule is opened, the numerous seeds and well-developed, U-shaped placenta are visible (Fig. 15B).

The seeds are rather small (up to 7 mm long, but usually smaller and about 1 mm wide at the widest part). Their sigmoid shape (Fig. 16A) causes a rotation when they fall out of the fruit and probably allows further dispersal by wind. The seeds have a wing that is well developed basally and apically, and extremely narrow in the central endosperm-bearing part (Fig. 16E). They are attached to the placenta with the basal part of the wing. The apical part of the wing differs from the basal in that it is wider and not twisted. The endosperm and embryo, visible as a distinct swelling in the center of the seed, are present in only a minority of the seeds. The majority of the seeds are devoid of embryos; some of the examined fruiting specimens seemed to lack embryos almost completely. The seeds are exotestal (sensu Corner, 1976). The endotesta consists of a few layers of crushed cells. Only in the wings is a clear cellular structure visible (Fig. 16D). The inner tangential walls of the exotestal cells have a reticulate thickening pattern (lumina mostly about 10 μm, wider than the muri and often in two rows); their radial walls are also thickened

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[4] Each septal half is formed by fusion and subsequent inward growth of the two carpels; finally, the septal halves meet in the center of the ovary.

Figure 14. Fruiting specimen of *Dialypetalanthus fuscescens* (*Silva & Morio 3238*, NY); bar = 5 cm.

(Fig. 16B, C). The seeds have a thin but very obvious, oil-containing endosperm (Fig. 16E). The embryo is large, straight, and has two short cotyledons; in cross section it is round.

POLLINATION BIOLOGY

Rizzini and Occhioni (1949) are the only authors who postulated a pollination strategy for *Dialypetalanthus*. They claimed that *Dialypetalanthus* shows "obvious adaptations for anemogamy," namely many light, dry and small pollen grains. However, Juncosa and Tomlinson (1987: 1315) pointed out that "the existence of light powdery pollen in the taxa with animal pollination is an example of the way in which pollen characteristics may be mis-

leading about the method of pollination." In our opinion, Rizzini and Occhioni's (1949) hypothesis is wrong. The pollen characteristics mentioned as well as the exposed stamens and stigma of *Dialypetalanthus* are indeed often found in wind-pollinated taxa, but the following facts are hardly brought in line with anemogamy: bisexual flowers, unexposed inflorescences, a large attractive corolla (although it falls off soon after anthesis), fragrant flowers (described by Rizzini and Occhioni as "jasmine"), a disk that may secrete nectar (or oil), locular appendages that may have a reward function for pollinators, numerous ovules (indicating the need of successful pollination, contrary to wind-pollinated species, which mostly have few ovules
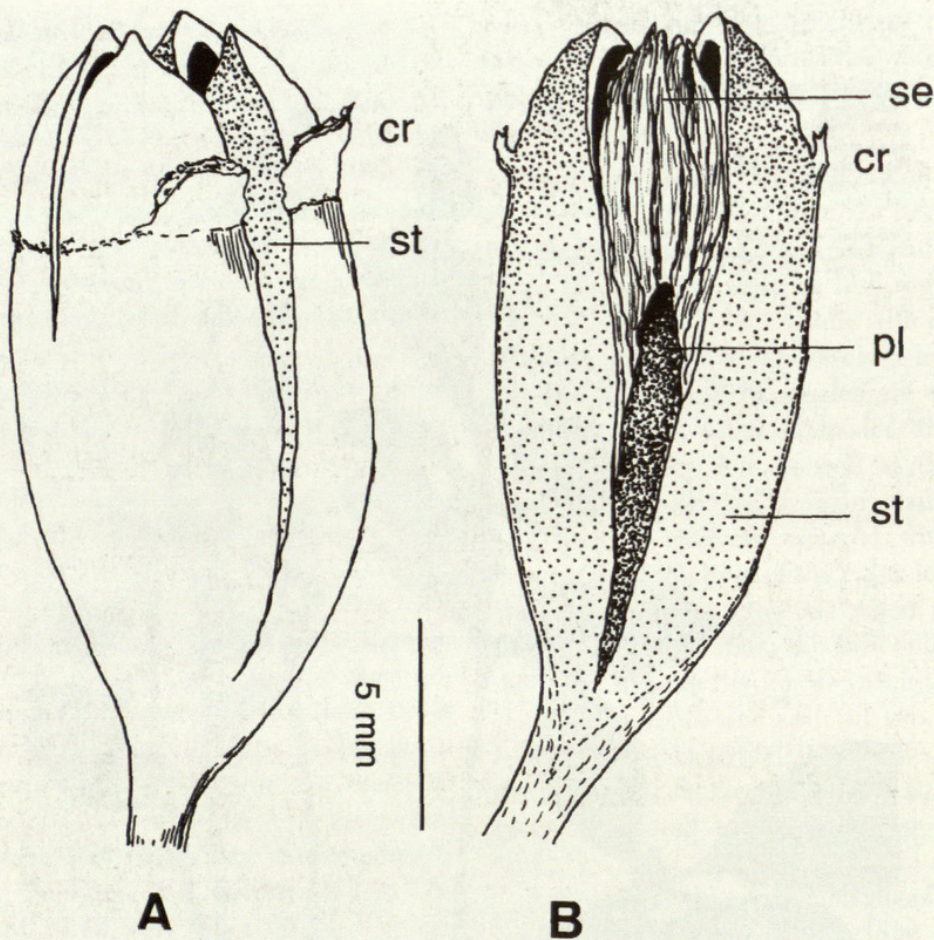
Figure 15. Fruit structure of *Dialypetalanthus fuscescens*.—A. Fruit in late stage of opening, showing deep septicidal and more shallow loculicidal slits.—B. Septal view of a half fruit in the same stage after artificial separation; cr = calyx remnants and scars, st = septum, se = seeds, pl = placenta. After *Silva & Morio 3238* (A) and *Silva 740* (B).

per style) and pollen sacs closely associated with the filament instead of the versatile anthers that are typical of wind-pollinated species. Moreover, one should bear in mind that *Dialypetalanthus* is a rainforest tree. The dense vegetation of mostly evergreen species in rainforests, the large amount of precipitation, and the low turbulence due to the closed canopy, by which pollen cannot stay in the air long enough to cause successful pollination, make wind pollination unlikely. All of these morphological and ecological data strongly suggest animal pollination. A plausible type of pollination is cantharophily. Beetles are especially attracted to white, fragrant flowers with abundant and easily attainable pollen (Willemstein, 1987). All of this is offered by *Dialypetalanthus*. Grant (1950) stated that an inferior ovary may be an adaptation to destructive pollinators (in this case beetles) as a protection for the vulnerable ovules. Cantharophily would be a good explanation for the simultaneous occurrence of numerous stamens and an inferior ovary in *Dialypetalanthus*. The rough flower treatment that is so typical for beetles would also explain the earlier-mentioned lignified zones in the stamens and the overall firm, fleshy structure of the flower.

On the other hand, pollination by bees seems to be an acceptable alternative, because the poricidal anthers may point to buzz-pollination. Moreover, D'Arcy et al. (1996) stated that the occurrence of oxalate packages is rather typical for bee-pollinated species. The pollen becomes mixed with the calcium oxalate crystals when the anthers are vibrated by the insect, although it is still unclear what the crystals are used for. Field observations are needed to establish the pollination strategy of *Dialypetalanthus*.

DISTRIBUTION AND ECOLOGY

In the past it was assumed that *Dialypetalanthus* occurs mainly in the eastern part of Brazil, around Belém (Robbrecht, 1994; Nicholas & Baijnath, 1994). This was probably due to the fact that the first collections (*Kuhlmann 1514*; *Ducke 17921, 23660,* and *21684*) were from this region. The specimens presently available reveal, however, that the center of distribution is in the northern border
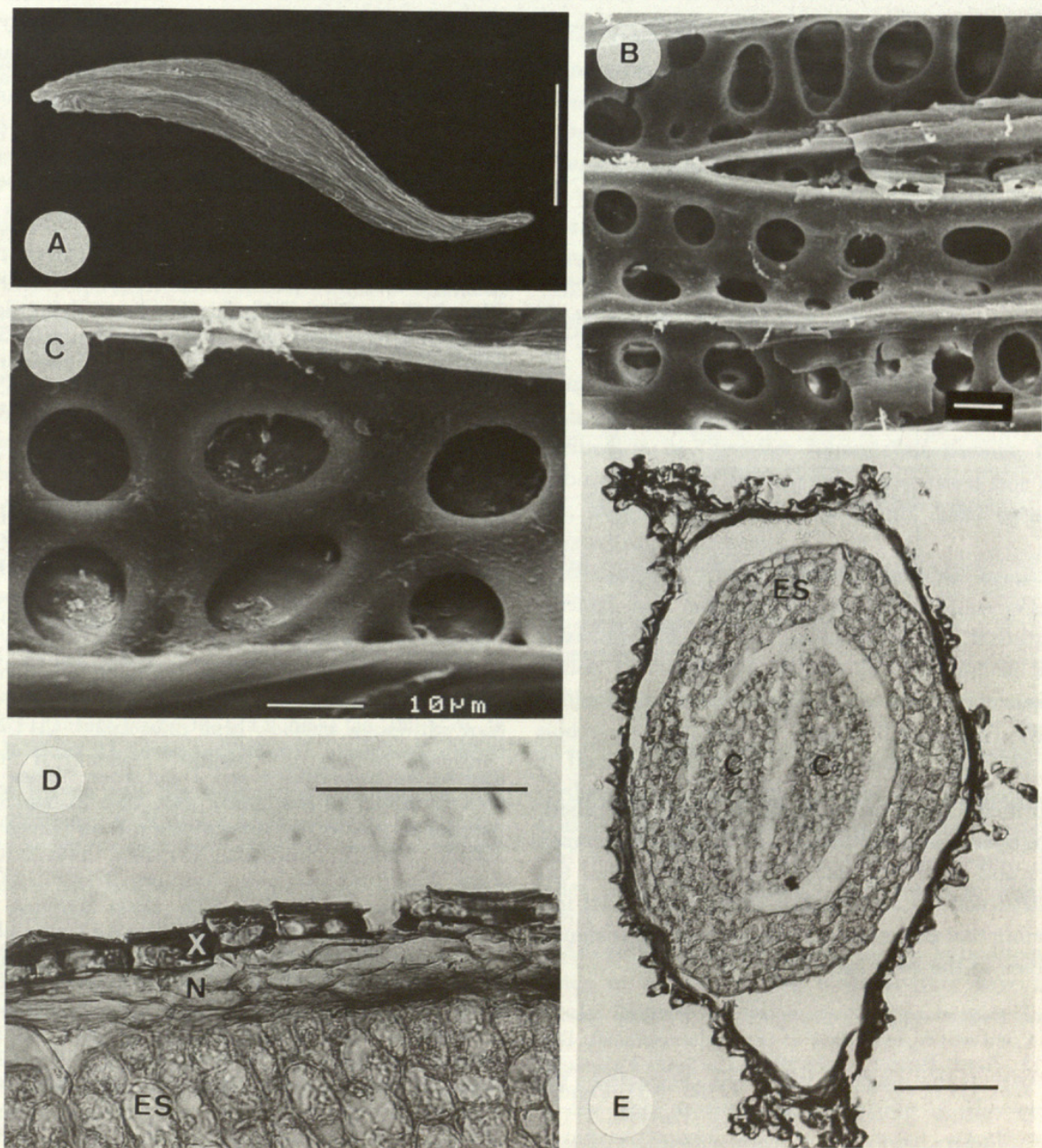
Figure 16.   Seed morphology and anatomy of *Dialypetalanthus fuscescens*. (A–C SEM; D, E LM.)—A. Entire seed with typical sigmoid shape (base of seed is at the right); bar = 1 mm.—B. Pitted thickened inner tangential walls of the exotestal cells; bar = 10μm.—C. Detail of the thickening pattern shown in B.—D. Tangential section of the seed coat showing the thickened exotestal cells (X), crushed endotestal cells (N), and endosperm (ES); bar = 0.1 mm.—E. Transverse section of seed; note the cotyledons (C) and well-developed endosperm (ES); bar = 0.1 mm. After *Thomas et al. 5205* (A, D, E) and *Silva 740* (B, C).

region between Bolivia and Brazil (Guajará-Mirim, Costa Marques, Pôrto Velho, Rondônia, Rio Branco) (Fig. 17). The distribution area of *Dialypetalanthus* is situated in Takhtajan's (1986) Amazonian Province, i.e., the southern half of his Amazonian region. In the phytogeographic division of Andersson (1992), *Dialypetalanthus* occurs in the (i) western Amazon of Colombia, Peru, and Brazil; (ii) central Amazon of Brazil; and (iii) eastern Amazon of Brazil.

Although the tree inhabits the terra firme forest (information derived from herbarium labels), it seems to be linked to the rivers in one way or another. This could of course be due to the fact that rivers are avenues for collectors to reach the collecting localities. *Dialypetalanthus* mostly grows on sandy or gravelly soils, schist outcrops (where it occurs together with such taxa as *Orbignya phalerata* Mart., *Hevea*, and *Bertholletia*), or granite outcrops. *Dialypetalanthus* has been found only south of the Amazon River. No collections are known from the region between the Amazon and the Orinoco.

According to Prance (pers. comm.), *Dialypetalanthus* is a rather common tree in Brazil, occurring

Figure 17. Distribution map of *Dialypetalanthus fuscescens*.

in primary forest as well as in partly disturbed, more open regions. However, as the forest becomes more and more devastated due to agricultural expansion and the construction of dams, it is not impossible that *D. fuscescens* will become a threatened species in the near future.

Specimens examined (square brackets indicate coordinates determined by means of place descriptions). BOLIVIA. **Beni:** Road Guajará-Mirim-Cachuela Esperanza, Rio Yata, [11°S, 66°W], *Anderson 11865* (NY). **Pando:** Nicolás Suárez, between Cobija and Porvenir, [11°S, 68°30′W], *Fernández Casas & Susanna 8188* (NY); Puerto Oro, 74 km SW of Cobija, 11°25′S, 69°05′W, *Pennington et al. 143* (K). BRAZIL. **Acre:** Mun. Sena Madureira, basin of Rio Purus, Rio Macauã, Colocacão Apui, 09°48′S, 69°11′W, *Daly et al. 8068* (NY not seen); Mun. Sena Madureira, basin of Rio Purus, Rio Macauã, Fazenda São José, 09°46′S, 69°09′W, *Daly et al. 8095* (NY not seen); Mun. Rio Branco, road Rio Branco-Pôrto Velho, km 22, Quinoá, [10°S, 67°30′W], *de Albuquerque et al. 1295* (NY, US); Mun. Sena Madureira, Rio Macauã, Seringal Santa Luzia, 09°39′S, 69°01′W, *de Lima et al. 575* (NY not seen). **Amazonas:** Rio Madeira, Humaitá, [07°30′S, 63°W], *Ducke 35428* (K, US). **Goiás:** Xambioa, 06°26′S, 48°27′W, *Edison Mileski 397* (MG not seen); Rio Araguia, região de Araguatins, Ilha Santa Isabel, [06°30′S, 49°W], *Oliveira 1572* (NY). **Maranhão:** Mun. Santa Luzia, Fazenda Agripec da Varig, Rio Pindaré, [04°S, 45°30′W], *Lobo et al. 328* (K, NY, US); Funai, 40 km from Arame, *Vilhena et al. 1003* (NY). **Mato Grosso:** Dardanelos, Sta. Elena, *Cordeiro 175* (NY); Fazenda Cachimbo, [09°30′S, 55°W], *Cordeiro 1085* (NY); Rio Madeira, Salto Theotônio, [15°S, 59°30′W], *Ducke 22816* (K, US); Rio Tapajós, Salto Augusto, *Kuhlmann 1514* (NY) SYNTYPE; Rio Juruena, Aripuanã, Fontanilha, [10°30′S, 58°W], *Silva & Morio*

3238 (NY). **Pará:** Rio Tapajós, Itaituba, [04°S, 55°30′W], *Ducke 17921* (K, US) SYNTYPE; Serra de Santarém, [02°30′S, 55°W], *Ducke 21684* (K, NY); Serra de Santarém, [02°30′S, 55°W], *Ducke 23660* (US); Igarapé Fernando do Noronha, Rio São Manuel, Caldeirao, [9°S, 64°30′W], *Pires 3853* (NY, US); Rio Itacaiuna-Rio Tocantins, 05°30′S, 50°15′W, *Pires et al. 12531* (MG not seen); Região Gorotire, Rio Xingu, 06°38′S, 52°00′W, *Silva 740* (NY); Cabeça, 09°45′S, 51°20′W, *Silva 740* (NY); Tucuruí, Breu Branco, [03°45′S, 49°45′W], *Silva 5457* (MG not seen); Rio Tocantins, Tucuruí, Breu Branco, [04°S, 49°W], *Silva & Bahia 3514* (NY); Rio Itacaiuna, 2 km downstream from ferry crossing to AMZA camp3-alfa, 05°53′S, 50°30′W, *Sperling et al. 6167* (NY). **Rio de Janeiro:** Rio de Janeiro, cultivated plant in the Botanical Garden, *Occhioni et al. 57941* (K). **Rondônia:** Mun. de Presidente Medici, BR364, road Cuiaba-PôrtoVelho, km 300, 11°12′S, 61°62′W, *Cid et al. 4801* (NY); Mun. Costa Marques, BR429, near Rio Cautarinho at 5 km of BR, 12°10′S, 63°25′W, *Cid Ferreira 8649* (NY); Mun. Pôrto Velho, Estrada da Serra do Balateiro a 3 km da Vila Campo Novo, 10°35′S, 63°39′W, *Cid Ferreira 8895* (NY); Mun. Alvorada do Oeste, BR429, estrada para Costa Marques, Serra da Onça a 35 km da cidade de Alvorada do Oeste, 11°30′S, 62°30′W, *Cid Ferreira 9018* (NY); Guajará-Mirim, border region with Bolivia, [11°S, 65°W], *Cordeiro 1007* (MG not seen); Pôrto Velho, [10°S, 63°W], *Maciel et al. 1674* (MG not seen); 2 km of Guajará-Mirim, [11°30′S, 65°W], *Nascimento 316* (MG not seen); 15 km N of Ariquemes, on hwy. BR364 and 1 km E on "Linea 75," 09°47′S, 63°05′W, *Nee 34357* (NY, US); 21 km SE of Ariquemes, on hwy. BR364 and 1 km E on "Linea 45," 10°07′S, 62°56′W, *Nee 34426* (NY); Mun. Costa Marques, 2 km W of Rio Cautarinho, along hwy. BR429, 12°04′S, 63°28′W, *Nee 34472* (NY); Mun. Costa Marques, road Costa Marques-Forte Príncipe da Beira, 9.5 km E of Forte Príncipe da Beira, 12°26′S, 64°20′W, *Nee 34518* (NY); road Abuña-Guajará-Mirim, 1 km N of Riberão, [10°30′S, 65°W], *Prance et al. 6526* (NY, US); vicinity of São Lorenco Mines, basin of Rio Madeira, 09°33′S, 65°06′W, *Prance et al. 8967* (NY, US); Rio Urupa, [11°S, 62°W], *Rosa 428* (MG not seen); Pôrto Velho, [08°45′S, 64°W], *Rosa 485* (MG not seen); Mun. de Ariquemes, Mineração Mibrasa, Setor Alto Candeias, km 128, 10°35′S, 63°35′W, *Teixeira et al. 562* (NY); Pôrto Velho, Represa Samuel, 09°04′S, 63°15′W, *Thomas et al. 5205* (NY, US). PERU. **Madre de Dios:** Tambopata, 12°49′S, 69°18′W, *Gentry et al. 45957* (NY). LOCALITY UNCERTAIN. *Ferreira 438* (K).

DISCUSSION

Because of its polyandrous androecium, most authors (Cronquist, 1968; Dahlgren, 1975; Emberger, 1960; Melchior, 1964; Rizzini & Occhioni, 1949; Stebbins, 1974) have placed *Dialypetalanthus* near the Myrtales (more precisely near the Myrtaceae and Melastomataceae) rather than near the Gentianales. However, a relationship between *Dialypetalanthus* and the Myrtales is unlikely because Myrtales have internal phloem, leaves typically covered with glandular dots, and seldom have paracytic stomata, unlike *Dialypetalanthus*. Moreover, Myrtaceae lack septate fibers and their wood is of-

ten characterized by well-developed axial paren-
chyma. Melastomataceae have an acrodromous ve-
nation pattern, a synapomorphy for this family
according to Renner (1993); this venation pattern
does not occur in the Dialypetalanthaceae. The
only vegetative resemblances between *Dialypeta-
lantus* and Myrtales are the simple, opposite, entire
leaves and the vestured intervessel pits of the wood,
but these characters are common in the Gentianales
as well and are by themselves insufficient to sup-
port a close relationship. The stipules of *Dialype-
talanthus* give no more indication of relationship.
Myrtales are exstipulate (e.g., in Melastomataceae)
or possess rudimentary stipules (e.g., Myrtaceae,
Trapaceae; Dahlgren & Thorne, 1984). Gentianales
s.l. often have well-developed (Rubiaceae, Loga-
niaceae) or rudimentary stipules (Apocynaceae).

In vegetative (and also fruiting) stage, *Dialype-
talanthus* is hard to distinguish from certain Cin-
chonoideae (Rubiaceae). Robbrecht (1994: 23) not-
ed that "the habitual resemblance of vegetative or
fruiting material to Rubiaceae is impressive, and
almost all Amazonian field workers assign the tree
to the Rubiaceae." Indeed, the simple, opposite,
entire leaves and the well-developed stipules are
characteristic of Rubiaceae as well as *Dialypeta-
lanthus*. The paracytic stomata, colleters of the
standard Rubiaceae-type at the inside of the stip-
ules, the lack of internal phloem, the vestured pits,
and septate libriform fibers are shared as well.

The following features are in our opinion critical
to assess the relationship of *Dialypetalanthus*, and
need to be discussed in detail:

Dendritic hairs. Dendritic hairs have a rather
restricted taxonomic distribution in the angio-
sperms (Theobald et al., 1988). Our observation of
the occasional occurrence of dendritic and stellate
hairs on the petioles and stamens of *Dialypetalan-
thus* is new. Rubiaceae generally have simple or
uniseriate trichomes (Robbrecht, 1988), although
Theobald et al. (1988) mentioned the occurrence of
non-glandular stellate hairs in this family (they did
not specify species or genera, however). Stellate
hairs were not mentioned in Verdcourt's (1958) and
Robbrecht's (1988) survey of Rubiaceae trichomes.
Since stellate and dendritic hairs each were ob-
served only once in *Dialypetalanthus*, it remains
unclear whether any systematic value should be at-
tached to it.

Choripetaly. *Dialypetalanthus* is characterized
by the occurrence of four free petals. According to
Hutchinson (1959), the free petals of *Dialypetalan-
thus* are no reason to exclude it from the Rubi-
aceae, because "the corolla is divided to the base

in at least three genera" (p. 386) [*Molopanthera*
(Rondeletieae; Delprete, 1996), *Synaptanthera*
(Hedyotideae; note that the correct name is *Syn-
aptantha*; Robbrecht, 1994), and *Aulacodiscus* (=
Pleiocarpidia; Urophylleae; Robbrecht, 1994)].
However, the three genera cited by Hutchinson are
characterized by a deeply to very deeply divided
corolla tube instead of free petals. Schumann
(1891) described the corolla of *Molopanthera* as
"sehr tief geteilt" (p. 54) and that of *Synaptantha*
as "fast bis zum Gründe geteilt" (p. 24). Breme-
kamp (1940a) paid no special attention to the co-
rolla in his monograph of *Pleiocarpidia*. He de-
scribed it as "breviter hyperocrateriformis, tubo
suburceolato." If *Pleiocarpidia* possessed free pet-
als, this most probably would not have escaped
Bremekamp's attention.

Hedstromia (Psychotrieae) has also been de-
scribed as "having five essentially free petals"
(Darwin, 1979) or "polypetalous" (Smith & Darwin,
1988), but again we assume that the utmost base
of the corolla lobes is fused, as the stamens are
said to be "attached at base of the corolla" (Smith
& Darwin, 1988). The same authors (p. 239) de-
scribed *Mastixiodendron* as having "semisuperior
ovaries and polypetalous corollas, characteristics
that occur in a number of rubiaceous tribes." The
latter statement apparently only refers to semisu-
perior ovaries.

Altogether, *Mastixiodendron* seems to be the only
genus in Rubiaceae that may possibly have free
petals. Note that this genus has previously been
placed in the Cornaceae because of its "choripe-
taly" (Melchior, 1925, fide Darwin, 1977). Howev-
er, the only modern documentation of *Mastixiod-
endron* (Darwin, 1977) contains insufficient
information to judge its choripetaly. It states that
"at anthesis, the corolla lobes are always entirely
free," but gives no information on early ontogenetic
stages or the state of immature corollas. We have
looked at flowers of *Mastixiodendron* (*M. pachycla-
dos* (Schum.) Melch., *Schodde & Craven 4245*, L)
in order to verify the true nature of the corolla. At
anthesis, the corolla lobes are indeed entirely free.
In bud stage, however, they are fused; when the
flower opens they split down to the base along the
fusion margins. The mature stamens are completely
free from the corolla (and alternating with the lobes)
and are inserted below the intrastaminal disk.
Thus, all reports of true choripetaly within the Ru-
biaceae seem to be based on inadequate observa-
tions.

Free petals are, however, not the major problem
in postulating a relationship between Rubiaceae
and *Dialypetalanthus*, since both taxa could have

developed from a common ancestor with free petals. In this context, it is interesting to recall that the Gentianales are included in the Cornidae in some modern angiosperm classifications (Frohne & Jensen, 1992; Smets, 1988 unpublished Ph.D. thesis). Here, the basal family Cornaceae (Cornales) does have free petals. Whereas Lee and Fairbrothers (1978) demonstrated serological links between Rubiaceae (a derived family of the Cornidae) and Cornaceae, *Dialypetalanthus* seems to add a morphological dimension to this connection.

Polyandry. The major problem in postulating a close relationship between *Dialypetalanthus* and Rubiaceae, and at the same time the strongest argument of Rizzini and Occhioni (1949) for the inclusion of *Dialypetalanthus* in Myrtales, is the polyandrous androecium. Rizzini and Occhioni stressed the fact that Rubiaceae are isomerous: "Ora, sabemos serem as Rubiaceae notáveis pela fixidêz de seu número estaminal: este é sempro igual ao de segmentos da corola, a tal ponto de, mesmo em formas anômalas por cultivo, persistir essa característica" (p. 249). As an extreme example, they mentioned *Gardenia thunbergii* L.f., which sometimes has up to 11 petals and 11 corresponding stamens. Note that pleiomery is a rather common feature within the Rubiaceae–Gardenieae, and that it is not restricted to cultivated species (Robbrecht & Puff, 1986).

Polyandrous androecia are, according to Hutchinson (1959), also known in the genus *Praravinia* (Rubiaceae–Urophylleae). Bremekamp (1940b) attributed the notion of polyandry in *Praravinia* to Korthals's protologue of the genus, but doubted its correctness, because all the specimens he examined were isomerous.

Whereas the polyandry of *Praravinia* is probably based upon wrong observations, this cannot be said of *Coprosma* (Anthospermeae); some species have a secondarily increased stamen number [e.g., *C. nephelephila* Florence, corolla 5–6-merous, stamens 5–8(–12); Florence, 1986]. *Theligonum*, now generally accepted as being a rubiaceous genus (Robbrecht, 1994; Rutishauser et al., 1997), is polyandrous as well. In *Coprosma* and *Theligonum*, polyandry seems to be an adaptation to anemophily.

Oxalate packages. Our study revealed the occurrence of oxalate packages (O.P.'s) in the anthers of *Dialypetalanthus* at a moment when these peculiar structures were receiving renewed attention (D'Arcy et al., 1996). According to D'Arcy et al., the only positive reports of O.P.'s are from the Solanaceae, Ericaceae, Theophrastaceae, Balsaminaceae, Bromeliaceae, Araceae, Lemnaceae, Areca-

ceae, Liliaceae, Onagraceae, and Tiliaceae. In the Dialypetalanthaceae, the O.P.'s are different from the common or Solanaceae type described by these authors, since they are not located in the stomium but in apical, sterile appendages of the anthers.

O.P.'s are not recorded from the candidate relatives Myrtaceae, Melastomataceae, or Rubiaceae. We have observed, however, very obvious O.P.'s in *Cinchona pubescens* M. Vahl. (unpublished); here they occur as crystal sand and belong to the type described in Solanaceae (D'Arcy et al., 1996), i.e., situated at the stomium and running the length of the anther. Since the Rubiaceae are characterized by the common occurrence of several types of calcium oxalate crystals, one may expect that O.P.'s occur much more generally in this family but remain overlooked.

Rubiaceae and Dialypetalanthaceae both have O.P.'s, but these belong to a different morphological type. It seems that the taxonomic distribution of these anther structures is insufficiently known at present to draw further systematic conclusions.

Dimery. The calyx and corolla of *Dialypetalanthus* are initiated as dimerous whorls. Dimery has a rather restricted occurrence within the dicotyledons. As far as we know, it is only reported for the Begoniaceae, Berberidaceae, Cecropiaceae, Brassicaceae, Capparidaceae, Ebenaceae, Elatinaceae, Fumariaceae, Gunneraceae, Lauraceae, Nepenthaceae, Nymphaeaceae, Oleaceae, Onagraceae, Phytolaccaceae, Polygonaceae, Portulacaceae (Ronse Decraene & Smets, 1991: 95), Ranunculaceae, and Winteraceae (Watson & Dallwitz, 1991; Ronse-Decraene, 1992 unpublished Ph.D. thesis). Almost all Myrtales and Gentianales having four sepals and petals are truly tetramerous instead of dimerous, as can be derived from their floral diagram. Therefore, the dimery of *Dialypetalanthus* more or less isolates the genus. It should be noted, however, that *Theligonum* (Rubiaceae) may be dimerous as well (Rutishauser et al., 1997).

Anther dehiscence and monadelphy. Rizzini and Occhioni (1949) considered the united filaments and porate dehiscence of the anthers as strong arguments to exclude *Dialypetalanthus* from the Rubiaceae. However, porate anthers occur in the rubiaceous genera *Rustia* (apically porate; Delprete, 1995), *Tresanthera* (laterally porate; Delprete, pers. comm.), and *Argostemma* (Robbrecht, 1988). The character is definitely without value to corroborate or exclude a possible rubiaceous relationship.

Monadelphy is not especially rare in Rubiaceae. It occurs, for example, in *Capirona*, *Bikkia*, *Coutarea*, and *Exostema* (Robbrecht, 1988) and is even

considered to be a synapomorphy of the Chiococceae (Bremer & Struwe, 1992). In all these cases, however, the ring formed by the filament bases is attached to the corolla tube. In this feature Rubiaceae differ from *Dialypetalanthus*. However, in a few genera of the Chiococceae sensu Delprete the stamens are not attached to the corolla tube, but on top of the ovary (Delprete, pers. comm.).

Gynoecial structure.   Whereas the corolla and androecium of *Dialypetalanthus* and Rubiaceae show fundamental differences, their gynoecial structure is completely similar. Both *Dialypetalanthus* and many Rubiaceae are characterized by an inferior, bilocular gynoecium with numerous ovules in each locule and a disk on top of the ovary, surrounding the base of the style. The supposedly primitive (Leinfellner, 1951), U-shaped placentas of *Dialypetalanthus* occur in numerous genera of the Rubiaceae as well (De Block & Robbrecht, 1997).

The numerous, ascending, imbricate ovules of *Dialypetalanthus* offer a strong argument for exclusion of this genus from the Myrtales. As Dahlgren and Thorne (1984) already concluded from observations of the seed-coat structure, these ovules are unitegmic. This character is typical for Gentianales and Cornales, but is lacking in Myrtales (except for *Syzygium*; Dahlgren & Thorne, 1984).

With the exception of Melastomataceae and Memecylaceae, both Myrtales and Gentianales are provided with a more or less well-developed disk. Smets (1988) stated, however, that these disks may not be homologous, because the disk of Myrtales has a receptacular origin, whereas that of Gentianales is gynoecial. The disk of *Dialypetalanthus* arises late in the floral ontogeny as a swelling, situated at the inside of the androecial ring, surrounding the base of the style. Its origin is therefore most probably gynoecial, as in Gentianales.

Pollen.   Erdtman (1971) considered the pollen of *Dialypetalanthus* to be more similar to pollen of Rhizophoraceae than to that of Myrtaceae, Melastomataceae, and Rubiaceae. We do not deny the resemblances between the pollen of *Dialypetalanthus* and certain Rhizophoraceae, nor the differences from that of Myrtaceae (often synaperturate pollen) and Melastomataceae (usually with pseudocolpi); however, the pollen fits perfectly within the pollen morphological variation of the Rubiaceae. At the time Erdtman wrote his book, this variation was insufficiently known, as is demonstrated by his limited treatment (only ± 5 % of the genera) of this huge family. The tricolporate, tectate-perforate pollen of *Dialypetalanthus* is now

known to be the most common type encountered in Rubiaceae (Robbrecht, 1988).

Fruit and seeds.   The capsules with numerous winged seeds of *Dialypetalanthus* are hardly distinguishable from those of certain Rubiaceae–Cinchonoideae. For example, capsules that split into four parts and seeds with basally attached seed wings (as in *Dialypetalanthus*) are very common in several genera of the Rondeletieae s.l. (Delprete, 1996). Winged seeds occur in many Rubiaceae tribes. Seed wings are extremely diverse; the condition found in *Dialypetalanthus* (wing mainly restricted to base and apex) occurs, e.g., in *Mitragyna* (Coptosapelteae; Stoffelen et al., 1996: fig. 2I). Although Rizzini and Occhioni (1949) thought that winged seeds are not very useful for classification purposes, they add another resemblance between the fruit and the seeds of *Dialypetalanthus* and the Cinchonoideae.

The seed-coat structure of *Dialypetalanthus* cannot be classified as one of the three seed-coat types that Corner (1976) distinguished for the Myrtales, and therefore presents another argument for excluding *Dialypetalanthus* from this order. On the contrary, the pitted thickenings of the inner tangential walls of the exotestal cells and the crushed endotestal cells of the seed coat of *Dialypetalanthus* are considered to be typical of the Cinchonoideae (Bremekamp, 1966; Robbrecht, 1988).

Myrtales (with the exception of some rare cases in Myrtaceae, where scanty endosperm may be formed) are characterized by the lack of endosperm (Dahlgren, 1991). This again argues against inclusion of *Dialypetalanthus* in the Myrtales. With its well-developed endosperm, it fits far better in the Gentianales (and Rubiaceae).

CONCLUSION

Summarizing the evidence obtained from floral and fruit structure, a close relationship between *Dialypetalanthus* and Myrtales is unlikely because of the following character states of *Dialypetalanthus*: unitegmic ovules, gynoecial disk covered by unicellular trichomes, exotestal seed coat, and well-developed endosperm. Gynoecial structure, fruit, and seeds show remarkable resemblances with the Rubiaceae (more specifically the subfamily Cinchonoideae), whereas pollen morphology does not exclude a relationship with that family. The dimerous origin of calyx and corolla, the free corolla lobes, and the supposed cantharophily are unique, possibly primitive, features of *Dialypetalanthus*, giving it a somewhat isolated position. The interpretation of the polyandrous androecium remains

problematic as long as its origin is not elucidated by ontogenetic studies. We consider *Dialypetalanthus* to be a textbook case of heterobathmy, combining primitive features (the presence of stipules and U-shaped placentas may be added to the characters enumerated above) with derived gynoecial features. Our observations consequently corroborate a *Dialypetalanthus*–Rubiaceae relationship, but the genus can clearly not be included in that family. The translation of this conclusion into a proposal for a classification above the family level (i.e., should the Dialypetalanthaceae be placed in the order Gentianales s.l. or in the Rubiales) is not easy. Since the delimitation of the Gentianales, and more specifically the position of the Rubiaceae, is still problematic and subject to frequent change (Nicholas & Baijnath, 1994; De Laet & Smets, 1996), it seems best to maintain at present a widely conceived order Gentianales, including the Dialypetalanthaceae and Rubiaceae and arising from a cornalean stock. In order to gain a better understanding of the position of the Dialypetalanthaceae within this gentianalean complex (e.g., should Dialypetalanthaceae and Rubiaceae be put together in the Rubiales s.l., closely related to the Gentianales s. str.?), a cladistic analysis including Gentianales, Cornales, and other members of the Cornidae alliance most certainly would be very useful. In the latter context, however, it is regrettable that phytochemical (Darnley-Gibbs, 1974; Hegnauer, 1990), floral ontogenetic, and macromolecular data of *Dialypetalanthus* are still very poorly or not at all known. Consequently, future research should mainly concentrate on these and other missing characters of *Dialypetalanthus* to further elucidate its systematic position.

Literature Cited

Andersson, L. 1992. A provisional checklist of neotropical Rubiaceae. Scripta Bot. Belg. 1: 7–9.

Baas, P. 1986. Terminology of imperforate tracheary elements—In defence of libriform fibres with minutely bordered pits. I. A. W. A. Bull., N.S. 7: 82–86.

Braune, W., A. Leman & H. Taubert. 1967. Pflanzenanatomisches Praktikum: zur Einführung in die Anatomie der Vegetationsorgane der höheren Pflanzen (Spermatophyta). VEB Gustav Fischer Verlag, Jena.

Bremekamp, C. E. B. 1940a. A monograph of the genus *Pleiocarpidia* K.Sch. (Rubiaceae). Recueil Trav. Bot. Néerl. 37: 198–236.

———. 1940b. The genus *Praravinia* Korth. (Rubiaceae) in Borneo and Celebes. Recueil Trav. Bot. Néerl. 37: 237–278.

———. 1966. Remarks on the position, the delimitation and the subdivision of the Rubiaceae. Acta Bot. Neerl. 15: 1–33.

Bremer, B. & L. Struwe. 1992. Phylogeny of the Rubiaceae and the Loganiaceae: Congruence or conflict between morphological and molecular data? Amer. J. Bot. 79: 1171–1184.

Corner, E. J. H. 1976. The Seeds of Dicotyledons, Vol. 1. Cambridge Univ. Press, Cambridge.

Cronquist, A. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin, Boston.

———. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.

———. 1988. The Evolution and Classification of Flowering Plants, 2nd ed. The New York Botanical Garden, New York.

Dahlgren, G. 1991. Steps toward a natural system of the dicotyledons: Embryological characters. Aliso 13: 107–165.

Dahlgren, R. 1975. A system of classification of the angiosperms to be used to demonstrate the distribution of characters. Bot. Not. 128: 119–147.

———. 1980. A revised system of classification of the angiosperms. Bot. J. Linn. Soc. 80: 91–124.

———. 1983. General aspects of angiosperm evolution and macrosystematics. Nordic J. Bot. 3: 119–149.

——— & R. F. Thorne. 1984. The order Myrtales: Circumscription, variation and relationships. Ann. Missouri Bot. Gard. 71: 633–699.

D'Arcy, W. G., R. C. Keating & S. L. Buchmann. 1996. The calcium oxalate package or so-called resorption tissue in some angiosperm anthers. Pp. 159–191 *in* W. G. D'Arcy & R. C. Keating (editors), The Anther. Form, Function and Phylogeny. Cambridge Univ. Press, Cambridge.

Darnley-Gibbs, R. 1974. Chemotaxonomy of Flowering Plants. Vol. III. McGill. Queens Univ. Press, Montreal.

Darwin, S. P. 1977. The genus *Mastixiodendron* (Rubiaceae). J. Arnold Arbor. 58: 349–381.

———. 1979. A synopsis of the indigenous genera of Pacific Rubiaceae. Allertonia 2: 1–44.

De Block, P. & E. Robbrecht. 1997. On the ovary structure of *Dictyandra* and *Leptactina* compared with other Pavetteae (Rubiaceae–Ixoroideae), or evolution from multiovulate to uniovulate placentas. Bot. Jahrb. Syst. 119: 1–15.

De Laet, J. & E. Smets. 1996. A commentary on the circumscription and evolution of the order Gentianales, with special emphasis on the position of the Rubiaceae. Opera Bot. Belg. 7: 11–18.

Delprete, P. G. 1995. Three new species of *Rustia* (Rubiaceae, Condamineeae) from Panama and Ecuador. Novon 5: 133–139.

———. 1996. Evaluation of the tribes Chiococceae, Condamineeae and Catesbeeae (Rubiaceae) based on morphological characters. Opera Bot. Belg. 7: 165–192.

Emberger, L. 1960. Les végétaux vasculaires. Pp. 754–1539 *in* M. Chadefaud & L. Emberger (editors), Traité de botanique (systématique), tome II. Masson et Cie éditeurs, Paris.

Erbar, C. 1995. On the floral development of *Sphenoclea zeylanica* (Sphenocleaceae, Campanulales)—SEM investigations on herbarium material. Bot. Jahrb. Syst. 117: 469–483.

Erdtman, G. 1971. Pollen Morphology and Plant Taxonomy—Angiosperms (An introduction to palynology), Vol. I. Hafner Publishing, New York.

Florence, J. 1986. Sertum Polynesicum II. Rubiaceae nouvelles des îles Marquises (Polynésie Française). Bull. Mus. Nat. Hist. Nat., 4e sér., B, Adansonia 8: 3–11.

Frohne, D. & U. Jensen. 1992. Systematik des Pflanzen-