



A Revision of *Philodendron* Subgenus *Meconostigma* (Araceae)

S. J. Mayo

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A revision of *Philodendron* subgenus *Meconostigma* (*Araceae*)

S. J. MAYO

Summary. *Philodendron* subgenus *Meconostigma* is defined and described taxonomically and a revision of the 15 recognized species is presented; two new species, *P. dardanianum* and *P. uliginosum*, are described. *P. selloum* is reduced to the synonymy of *P. bipinnatifidum*. Keys to the three subgenera of *Philodendron* and to the species of subgen. *Meconostigma* are presented. Brief reviews are given of vegetative and inflorescence morphology and anatomy, floral biology, geography, ecology and the fossil record.

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1. INTRODUCTION

Philodendron subgenus *Meconostigma*, with fifteen species recognized in the present revision, is the smallest of the three subgenera of *Philodendron* Schott (Mayo 1989b). It consists mainly of robust, arborescent plants with handsome foliage, making them desirable horticultural subjects.

In one form or another the taxon has been recognized as distinct for almost as long as the genus itself (Mayo 1990) because of the characteristic habit and the style and stigma morphology (Mayo 1989b) from which its name is derived ('mekonos' – Greek for 'poppy' – the stigma of *Papaver* is somewhat similar). Better understanding of the group has further emphasized its distinctive character. The inflorescence, shoot morphology and geographical range all differ in important respects from those of the other two subgenera *Philodendron* and *Pteromischum*.

The extent of these differences poses the question of whether the genus *Philodendron* is a natural (monophyletic) group. Unpublished phenetic and cladistic analyses of the three subgenera and related genera of subfamily *Philodendroideae* (sensu Bogner 1979) tend to confirm the integrity of the genus, though it remains unclear which characters can be reliably regarded as generic synapomorphies (Mayo 1986). Unique characters for the genus have not been found, but inflorescence resin secretion and separate stylar canals in the gynoeceum are almost always present (Mayo 1989b). For now there is no sensible alternative to the continued recognition of the genus *Philodendron* as a putatively monophyletic taxon. Future investigation of this problem might profitably be directed at the possible relationships of *Homalomena* to subgen. *Philodendron* and of *Cercestis* to subgen. *Meconostigma*.

The material presented here is based on an unpublished dissertation (Mayo 1986) which provided material for three other papers on the systematics of the genus *Philodendron*; Mayo (1989a) on evolution and biogeography, Mayo (1989b) on gynoeceal characters and Mayo (1990) on history and nomenclature.

Cultivation

Philodendron is a genus of outstanding horticultural importance and subgen. *Meconostigma* includes some very well known ornamental species. *P. bipinnatifidum* (syn. *P. selloum*), one of the world's most ubiquitous houseplants, has provided a rich source of variation for the breeding of different foliage forms. Most of the species popularly known as 'self-headers' belong to this subgenus. These are arborescent species which are free-standing and produce a terminal crown of leaves, in contrast to the predominantly climbing habit of other philodendrons. They are highly valued as landscape plants in tropical and subtropical countries and in indoor landscaping and displays in temperate countries (Birdsey 1951, Kramer 1974, Graf 1985, Everett 1981). These plants have been used to splendid artistic effect in the work of the Brazilian landscape architect Roberto Burle Marx.

No attempt is made here to give a detailed treatment of cultivated forms, which lies beyond the scope of this study. However, two notable hybrids should be mentioned: –

***Philodendron* × *evansii* (*P. bipinnatifidum* × *P. speciosum*)**

A commonly cultivated taxon with a stout trunk-like stem which can sprawl and scramble as in *P. bipinnatifidum*. The large shallowly lobed leaves resemble those of *P. undulatum*.

Philodendron speciosum* × *P. goeldii

Karl Wendlinger and Roberto Burle Marx created this extraordinary hybrid, which can be seen in the Parque del Este, Caracas and in Burle Marx's own collection near Rio de Janeiro. The leaves are deeply pedatifid with relatively few lobes rather than pedately compound with more numerous leaflets as in *P. goeldii*.

2. TAXONOMIC DEFINITION

The diagnostic or otherwise important characters of the subgenus are given in Table 1 and many are discussed further below (see also Mayo 1986, 1989b). The three subgenera of *Philodendron* may be distinguished conveniently as follows: –

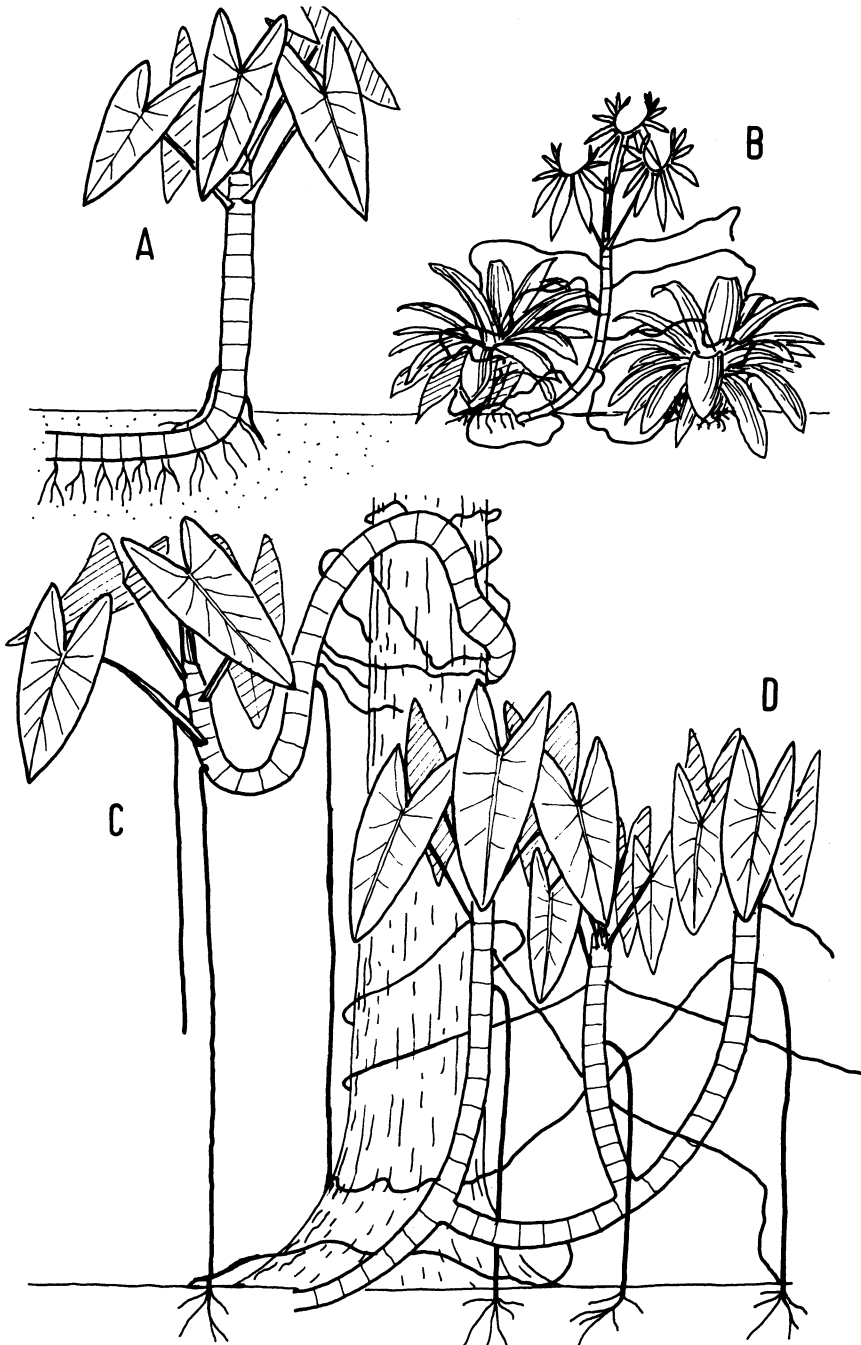


FIG. 1. Habit types in *Philodendron* subgen. *Meconostigma*. **A** Erect aerial stem lacking widely spreading adventitious roots, older stem portion prostrate or rhizomatous; e.g. *P. speciosum*, *P. tweedianum*; **B** Erect terrestrial aerial stem with widely spreading and rapidly growing adventitious roots seeking moisture in bromeliad leaf sheaths; only known in *P. leal-costae*; **C** Pendent hemiepiphyte with erect stem tip and anchor roots attaching plant to tree support and feeder roots growing to ground level; e.g. *P. solimoesense*, *P. goeldii*; **D** Scrambling, branching terrestrial or hemiepiphytic plants with erect distal stem portions, anchor roots are widely spreading and cling to support, feeder roots descend vertically to ground; e.g. *P. corcovadense*, *P. bipinnatifidum*.

KEY TO THE SUBGENERA OF *Philodendron*

1. Mature flowering shoots consisting of a succession of many foliage leaves with long petiole sheaths, terminated by solitary, or rarely several, inflorescences subgen. **Pteromischum**
1. Mature flowering shoots consisting of a succession of short sympodial articles each bearing a bladeless bicarinate prophyll and a single foliage leaf with a short or very reduced petiole sheath; inflorescences solitary to numerous, appearing as if axillary to foliage leaves:
 2. Staminal zone between fertile male and female zones of spadix always much shorter than fertile male zone; stamens less than 3 times longer than broad subgen. **Philodendron**
 2. Staminal zone between fertile male and female zones of spadix subequal to or longer than fertile male zone; stamens at least 3 times longer than broad (except *P. leal-costae*) .. subgen. **Meconostigma**

3. VEGETATIVE MORPHOLOGY

Habit

In subgenus *Meconostigma* the leaves are crowded together at the shoot apex into a distinct crown. The aerial stem may be erect, unbranched and lack conspicuous adventitious roots (Figs. 1A, 4C) the habit usually found in aquatic species (e.g. *P. uliginosum*, *P. tweedianum*). In other species the stem is scrambling, frequently branched and produces numerous adventitious roots (Fig. 1B–D). In hemi-epiphytic plants of *P. bipinnatifidum* and *P. corcovadense* the roots act as a system of stays to suspend the often heavy stem from adjacent tree boles (Fig. 1D). In the terrestrial *P. leal-costae*, a root system of similar general appearance allows the plant to tap water and nutrients from neighbouring bromeliad plants (Fig. 1B). In some aquatic species the arborescent habit may alternate with a rhizomatous to decumbent habit, according to prevailing ecological conditions (e.g. *P. tweedianum*). Hemi-epiphytic plants may also be pendent, as in *P. goeldii* and *P. solimoesense*, but their growth remains orthotropous (Blanc 1980) – the shoot tip is constantly erect, even though the older stem becomes pendent under the influence of its own weight (Fig. 1C).

All the hemi-epiphytic species seem able to grow as arborescent terrestrial plants and then have shorter internodes. *P. goeldii* is characteristically a hemi-epiphyte of riverine forests but also occurs along roadsides as an arborescent terrestrial plant (Madison, pers. comm.). Crisci & Gancedo (1971) describe comparable variability in *P. bipinnatifidum*.

Shoot morphology

Stem architecture in subgen. *Meconostigma* is superficially similar to that of subgen. *Philodendron*, since the mature stems of both are sympodia composed of diphyllous articles (terminology after Ray 1987). However, in those species of subgen. *Meconostigma* which have appreciably elongated internodes (*P. goeldii*, *P. leal-costae*, *P. corcovadense*) the pattern of elongation appears to be different from that of subgen. *Philodendron*. This does not seem to have been previously observed, probably because most species of subgen. *Meconostigma* have very short internodes.

In *P. leal-costae* and *P. corcovadense* (subgen. *Meconostigma*) the elongated internode of each article is that between the prophyll and the succeeding

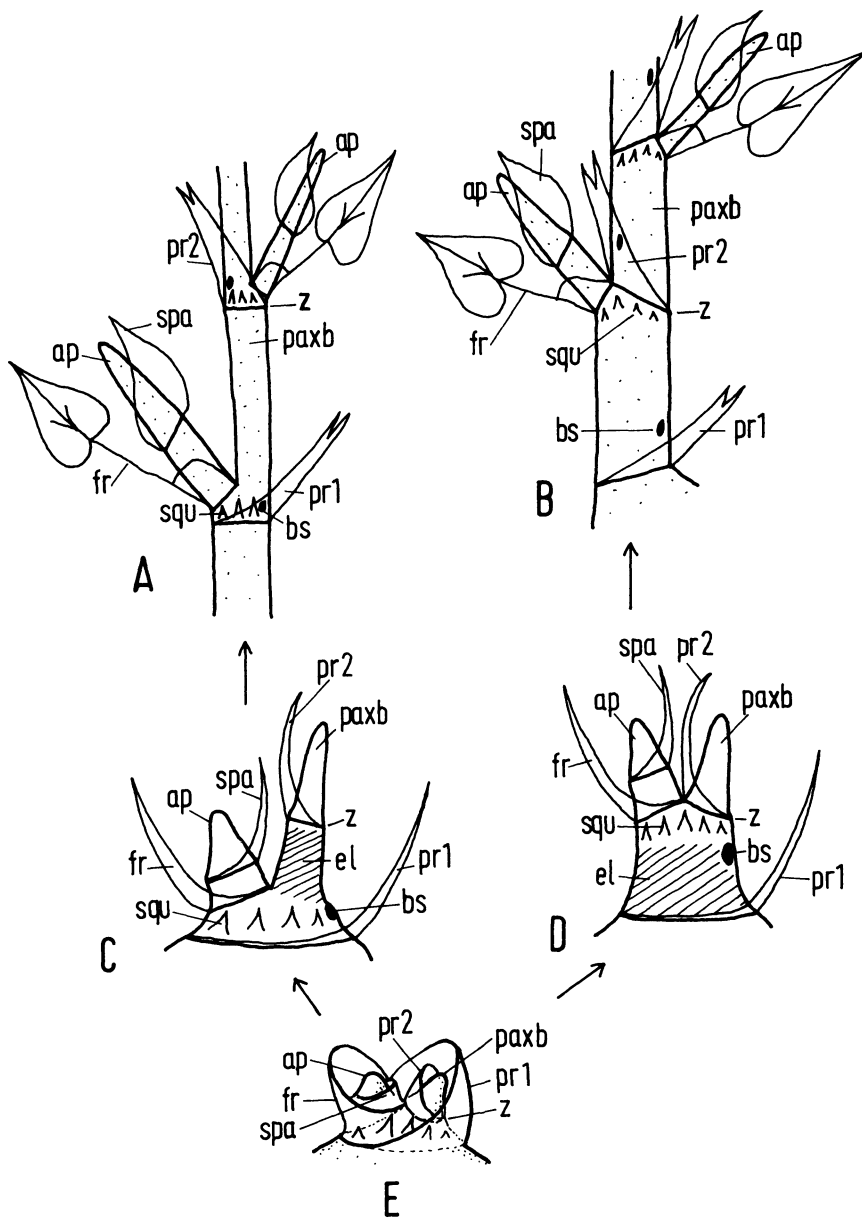


FIG. 2. Internode elongation in *Philodendron*. **A** Morphology of adult shoot of *P.* subgen. *Philodendron*; elongated internode (paxb) corresponds to the hypopodium of each sympodial unit, so that the first node (z) of the succeeding unit is distant from the node of the foliage leaf (fr) of the preceding unit; intravaginal squamules (squ) are located immediately above node z; **B** Morphology of adult shoot of *P.* subgen. *Meconostigma* in a species with developed internodes, e.g. *P. corcovadense*; elongated internode (paxb) lies between prophyll (pr) and foliage leaf (fr) of each sympodial unit, so that the first node (z) of the succeeding unit is adjacent to the node of the foliage leaf (fr) of the preceding unit; intravaginal squamules (squ) are located immediately below the foliage leaf insertion and node z; **C–E** Hypothesized model of internode development from early stage of differentiation of floral organs; **C** Mode of elongation in *P.* subgen. *Philodendron* leading to adult morphology shown in **A**; **D** Mode of elongation in *P.* subgen. *Meconostigma* leading to adult morphology shown in **B**; **E** Early stage of differentiation of primary axillary branch (paxb) in axil of prophyll (pr1) of preceding sympodial unit (ap); note position of node z of prophyll (pr2) of primary axillary branch (after Blanc 1978); ap: apex of sympodial unit; bs: secondary (adventive) axillary bud; el: zone of main elongation; fr: foliage leaf with reduced sheath; paxb: primary axillary branch; pr: prophyll (prophyllar cataphyll); spa: spathe; squ: intravaginal squamules; z: prophyll node (i.e. 1st node) of primary axillary branch.

foliage leaf (Fig. 2B), while the hypopodial internode ('hypopodium' of Ritterbusch 1971, French & Tomlinson 1984) is very abbreviated. The converse is found in subgen. *Philodendron*, where the hypopodial internode is elongated and that between prophyll and foliage leaf is abbreviated (Fig. 2A). A schematic comparison of the two patterns is given in Fig. 2, in which a speculative model for internode elongation is proposed, based mainly on the observations of Engler (1912), Ritterbusch (1971) and Blanc (1977). Two developmental paths are hypothesized here, differing in the position of the zone of internode elongation; Figs. 2E-C-A correspond to subgen. *Philodendron* and Figs. 2E-D-B to subgen. *Meconostigma*. The position of the so-called 'intravaginal squamules' (Dahlgren & Clifford 1982) is also different in the two subgenera and is evidence of the two contrasting patterns of internode elongation. The squamules are always found immediately above the prophyll scar in mature internodes of subgen. *Philodendron* (Fig. 2A). However, in subgen. *Meconostigma* the squamules occur immediately below the prophyll scar and often surround the foliage leaf scar as well (Fig. 2B). In *P. corcovadense* they are frequently scattered over the distal part of the internode.

Intravaginal squamules (scale-like appendages) also occur in the aroid genera *Cryptocoryne* and *Lagenandra*, in *Acorus* (Acoraceae) and in *Lemnaceae* and families of the *Alismatiflorae* (Dahlgren & Rasmussen 1983). It is not clear that they are homologous in these families, nor has any function clearly been assigned to them, although their anatomy has been reported as glandular in appearance (French in press). In subgen. *Meconostigma* the squamules frequently persist on the adult stem and are normally spinose or aculeate projections (Fig. 3A, B, D); their number, size, shape and persistence are taxonomically useful. In subgen. *Philodendron*, by contrast, they are not usually persistent and wither on older internodes to form inconspicuous brown or black remnants. Squamules have not yet been reported in subgen. *Pteromischum*.

Mature articles in subgen. *Meconostigma* normally end in a single inflorescence, but occasionally a floral sympodium of two inflorescences is formed, the second inflorescence being subtended by a prophyll; this has been observed in *P. bipinnatifidum* and *P. goeldii*.

Prophyll scars

The relative length of internodes and prophyll scars varies considerably in subgen. *Meconostigma*, even within a single species. In most, the internodes are extremely short (1 mm long or less), and are discernible only because they bear rows of intravaginal squamules. The interval between the internodes is often considerably longer than the true internode and externally corresponds to the scar left by the abscission of the prophyll. Abscission normally occurs as the succeeding foliage leaf unfolds and with subsequent expansion of the new article to the mature stem width, the scar expands until it resembles an internode. Thus the stem surface of most species is almost entirely composed of prophyll and leaf base scars, separated by very narrow, sinuous internodes. In species with elongated internodes the prophyll scars are short and annular, resembling those of subgen. *Philodendron*.

Foliage leaf scars

Foliage leaf scars are normally very conspicuous on the stem and vary in shape from elliptic to circular or transverse-elliptic. The phyllotaxy is very distinctly shown by the spirals of scars (Fig. 3C), except in those few species

(*P. leal-costae*, *P. goeldii* and *P. corcovadense*) which have internodes of appreciable length.

Leaf blade and venation – form and terminology in cordiform and sagittate leaves

The terminology used to describe the leaves of *Philodendron* presents certain difficulties, particularly when applied to the more complex leaf shapes. Usage has not always been consistent, even in the work of a single author (e.g. Krause 1913). I have attempted to use a terminology that is consistent and clear. The terms are illustrated in Figs. 4A–B, 5, 6, and 7.

All species except *P. goeldii* and *P. leal-costae* have leaf blades which are cordiform-sagittate to sagittate in outline. In these it is convenient for description to distinguish the anterior and posterior portions of the leaf blade; I call these the *anterior division* and *posterior divisions* (Fig. 5A) for the following reasons. Previous authors have usually termed these portions of the leaf blade, respectively, terminal or anterior lobe and basal or posterior lobes. While this is clear enough for entire leaves it creates problems when describing pinnatifid and bipinnatifid ones because the lower order subdivisions are also often referred to as lobes; other terms that have been used for these lower subdivisions are 'segments', 'laciniae', 'partitiones' (= division according to Stearn 1973) and 'lobuli' (see Krause 1913). I use the term 'lobe' for primary and secondary subdivisions of the anterior and posterior divisions (Figs. 5A, 6A–C).

In sagittate leaves (Figs. 4B, 5A) the *anterior division* comprises the portion of the leaf blade above the point of attachment of the petiole. It includes the *midrib* and *primary lateral veins* which branch from it. Primary lateral veins which run for their entirety above a line drawn through the petiole insertion, and perpendicular to the midrib, are considered to belong to the anterior division (Fig. 5A).

When the leaf blade is pinnately lobed (i.e. sinuately lobed, pinnatifid or bipinnatifid; see below for definitions), the lobe that corresponds to each primary lateral vein is termed a *primary lateral lobe* (Figs. 4A, 5A, 6); the *apical lobe* corresponds to the terminal region of the midrib, i.e. the portion beyond the most apically situated primary lateral lobe (Fig. 5A). In bipinnatifid leaves the primary lateral lobes are themselves pinnately lobed and then the lower order lobes are called *secondary lateral lobes* (Figs. 4A, 6C).

The *posterior divisions* are the two basal portions of the leaf blade, situated on either side of and below the petiole attachment (Fig. 5A). Each has a principal vein, the *basal rib*, formed by the coalescence of the major veins. Basal ribs in subgen. *Meconostigma* are always straight and well-developed and are proximally denuded of blade tissue for a varying distance on the basis-copic side (Fig. 5A, 'brd'). The major veins of the posterior divisions are termed *primary acroscopic veins* and *primary basis-copic veins*, according to the side of the basal rib from which they spring (Fig. 5A, 'pasv', 'pbsv'). Primary basis-copic veins are sometimes absent and are always more slender than primary acroscopic veins while the latter are in no way different from the primary lateral veins of the anterior division.

When the leaf blade is pinnately lobed, the corresponding lobes of the posterior divisions are termed *primary acroscopic lobes* and *primary basis-copic lobes*; secondary acroscopic and basis-copic lobes occur in *P. bipinnatifidum*. As with the major veins, primary basis-copic lobes are always more weakly developed

than primary acroscopics and the latter are similar to the primary lateral lobes of the anterior division.

The degree to which the blade margin is lobed is described by the following terms: – *repand* leaves have slightly sinuous, uneven margins (Fig. 16B); *sinuately*

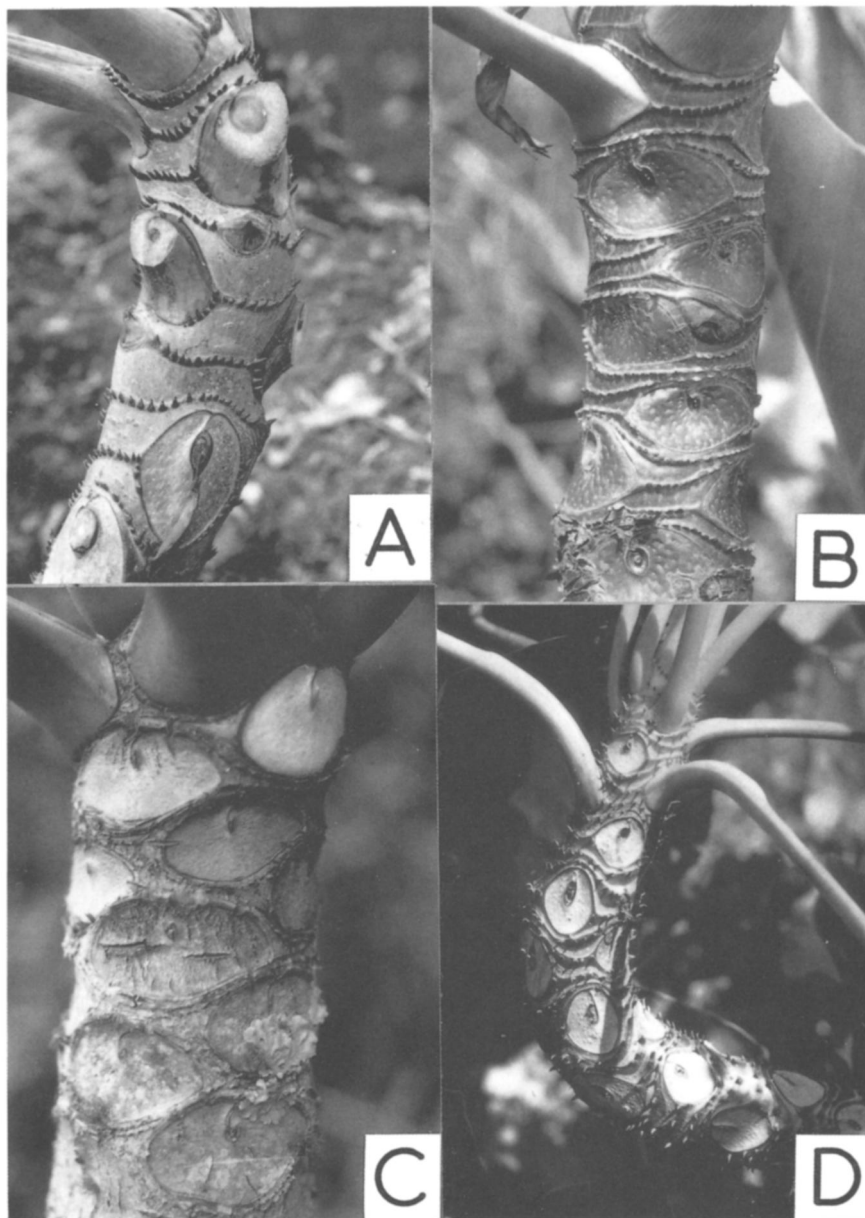


FIG. 3. Stem morphology in *Philodendron* subgen. *Meconostigma*. **A** *P. uliginosum*: northern form from Grão Mogol, Minas Gerais, with more conspicuous and persistent intravaginal squamules (Hatschbach 47113); **B** *P. uliginosum*: form from the Serra do Cipó, further south in Minas Gerais; **C** *P. speciosum*: plant growing on exposed granitic outcrop east of Rio de Janeiro city (S. Mayo et al. 602); **D** *P. corcovadense*: form with very short internodes and conspicuous squamules, plant from coastal Paraná (Hatschbach et al. 46087).

lobed leaves have regular primary lateral lobes but the sinuses between them extend less than halfway to the midrib (Figs. 6B, 17A); *pinnatifid* leaves have deep, regular primary lateral lobes with the sinuses penetrating halfway or more to the midrib, but never completely so (Figs. 6A, 12A, 15B); *bipinnatifid* leaves are pinnatifid leaves in which the primary lateral lobes are sinuately lobed or pinnatifid (Figs. 4A, 12B; see also Figs. 13B–H). *Undulate* margins are those in which undulations occur in a plane perpendicular to that of the leaf blade (Stearn 1973).

Simple linear-lanceolate to ovate, elliptic and obovate blades do not occur in subgen. *Meconostigma*, though they are very common in the other two



FIG. 4. *Philodendron* subgen. *Meconostigma*. **A** *P. bipinnatifidum*: newly unfolded leaf of a plant from the Serra do Cipó, Minas Gerais (S. Mayo et al. 702 [K!]); **B** *P. speciosum*: leaves of a huge plant cultivated by Roberto Burle Marx, near Rio de Janeiro (photo Anne Mayo); **C** *P. uliginosum*: habit of plant in damp streamside in the Serra do Cipó, Minas Gerais (S. Mayo et al. 700); **D** *P. bipinnatifidum*: infructescence of a plant cultivated by R. Reitz, Santa Catarina – the berries are white (A. Mayo 177 [K!]).

subgenera (subgen. *Philodendron* and subgen. *Pteromischum*). Sagittate and cordiform-sagittate leaf blades are commonest in subgen. *Meconostigma* (Figs. 12C, 14A–B, 15C, 16A–C, 17B–C). Sinuately lobed leaves occur in *P. undulatum* (Fig. 17A), while *P. adamantinum* (Fig. 12A) and *P. saxicolum* (Fig. 15B) have pinnatifid leaves and *P. bipinnatifidum* (Figs. 4A, 12B) has bipinnatifid leaves.

Leaf blade and venation – form and terminology in pedately compound leaves

Philodendron goeldii (Fig. 14C) and *P. leal-costae* (Figs. 7, 10D, 15A) have pedately compound leaves, which gives them a transverse-cordiform (reniform) outline shape. In view of their very different appearance, some equivalent (homologous) structures of pedately compound leaves are described by different terms from those used in the previous section.

Here, the leaf blade is divided to the rachis and thus the ‘lobes’ are termed *leaflets* (Fig. 5B). The anterior division comprises the *central leaflet*, while the *lateral leaflets* of each side together constitute each posterior division (Fig. 5B, ‘adiv’, ‘pdiv’). No primary basiscopic lobes are developed, the basal rib, or *rachis*, being entirely denuded basiscopically (Fig. 5B, ‘brd’).

The homologies between pinnately and pedately veined leaves implied by these equivalent terms are based on observations of the leaf ontogeny of juvenile plants of *P. leal-costae* (Fig. 7). As with all species of *Philodendron*, the seedling’s first leaves are cordiform (Fig. 7A), but the blade of succeeding leaves becomes sagittate (Fig. 7B) and then subtripartite (Fig. 7C). Finally, with the change from monopodial to sympodial shoot growth, the pedately compound blade appears (Fig. 7D). My interpretation of this series is that the posterior divisions in Fig. 7C are each equivalent to one of the lateral pairs of leaflets in Fig. 7D; i.e. the subdivision of the leaf is caused ontogenetically by successive ‘splitting’ of the posterior divisions.

4. VEGETATIVE ANATOMY

Stem vasculature

According to French & Tomlinson (1984), the genus is anatomically one of the most diverse in the family. However, they found two constant features in the stem vasculature; i) a permanent cortical vascular system and ii) a peripheral ring of axial bundles to which the adventitious roots are attached. They recognized five anatomical patterns shown by the axial bundles (vascular bundles of the central cylinder) in the genus as a whole. Two of these have so far been found in subgen. *Meconostigma* – ‘Pattern 4’, recorded in *P. bipinnatifidum* (*P. selloum*), and ‘Pattern 5’, found in *P. corcovadense* and *P. speciosum*.

Stomata

In the genus as a whole, the stomata of the leaf blade epidermis usually have 4 to 8 subsidiary cells. No developmental studies have been made, but stomatal structure in species of subgen. *Meconostigma* has been reported by Dilcher & Daghljan (1977) and Grau (1983). Grau studied *P. bipinnatifidum*, *P. undulatum* and *P. pseudoundulatum*. *P. undulatum* was found to be amphistomatic and the others were either entirely hypostomatic or virtually so. In some species, including *P. pseudoundulatum*, rugose areas were noted on the cell walls surrounding the stomata. Dilcher & Daghljan (1977) reported that *P. brasiliense*, *P. speciosum*, *P. tweedianum* and *P. undulatum* were amphistomatic, and *P. corcovadense* and *P. speciosum* were not.

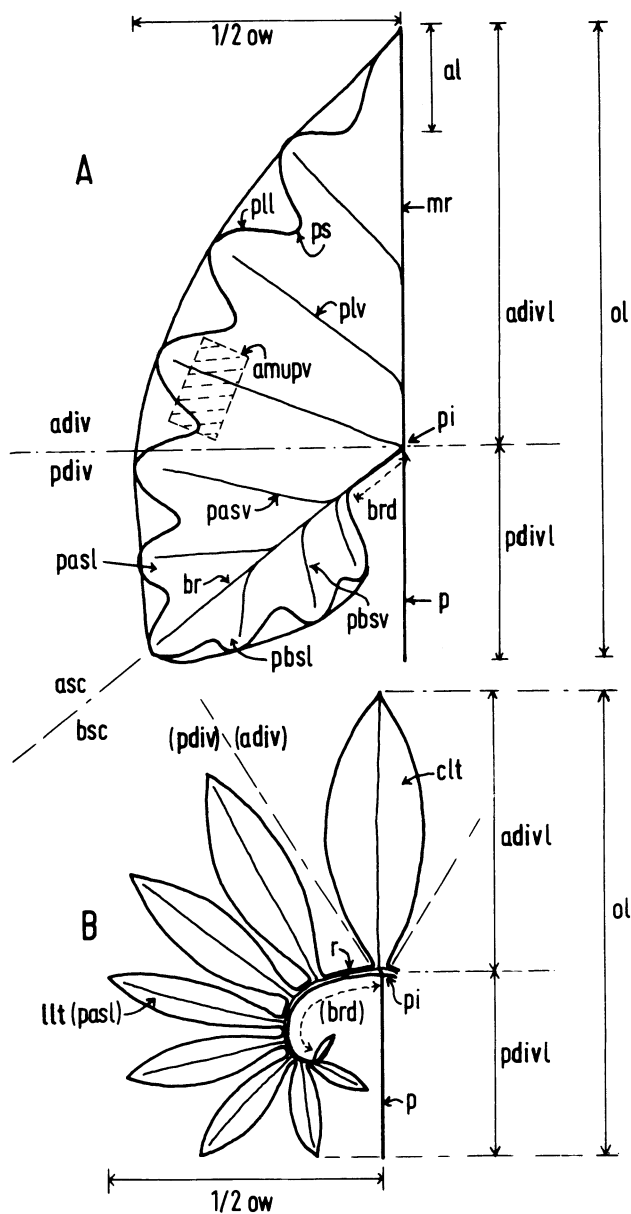


FIG. 5. Definition of terms – leaf morphology in *Philodendron* subgen. *Meconostigma*. **A** sagittate or pinnatifid leaf; **B** pedately compound leaf; adiv: anterior division; adivl: length of anterior division; al: apical lobe; amupv: area of leaf blade in which measurements were made of the distance between the finest parallel veins; asc: acrosopic side of posterior division; br: basal rib; brd: denuded basicopic region of basal rib; bsc: basicopic side of posterior division; clt: central leaflet; llt: lateral leaflet; mr: midrib; ol: overall length; $\frac{1}{2}$ ow: half overall width; p: petiole; pasl: primary acrosopic lobe; pasv: primary acrosopic vein; pbsl: primary basicopic lobe; pbsv: primary basicopic vein; pdiv: posterior division; pdivl: length of posterior division; pi: petiole insertion; pll: primary lateral lobe; plv: primary lateral vein; ps: main sinus; r: rachis.

Epidermis

Grau (1983) found that in three species of subgen. *Meconostigma* the lower epidermis lacked elongated cells over the veins. His suggestion that this character might be diagnostic for the subgenus merits further investigation.

Roots

Roots normally arise from the stem (French, in press) and there is a clear distinction between anchor roots, by which hemiepiphytic species attach themselves to their support, and feeder roots which grow down to the ground and secure a connection with the soil. These two kinds of root each have a characteristic anatomy which has been studied in detail by Porsch (1911) in *P. bipinnatifidum* (as *P. selloum*). Engler (1912) stated that chlorenchyma always occurs in the peripheral zone of the cortex in *Philodendron*.

The central cylinder is surrounded by an endodermis with casparian strips in the radial cell walls. In most species of the genus the central cylinder is circular in transverse section, but in species of *P.* subgen. *Meconostigma* (e.g. *P. speciosum*, *P. bipinnatifidum*) it is 3–5 lobed, a character shared with the

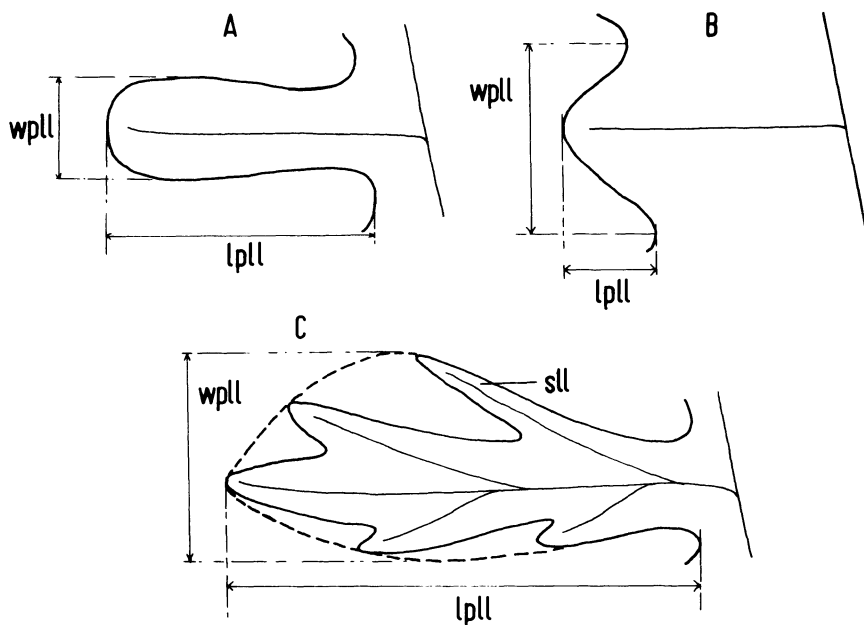


FIG. 6. Definition of terms – leaf morphology in *Philodendron* subgen. *Meconostigma*. Figures show three types of primary lateral lobe of the anterior division of the leaf blade: – **A** pinnatifid leaf (*P. saxicolum*); **B** sinuately lobed leaf (*P. undulatum*); **C** bipinnatifid leaf (*P. bipinnatifidum*); lp: length of primary lateral lobe; sl: secondary lateral lobe; wpll: width of primary lateral lobe.

genus *Rhektophyllum* (Engler 1912; this genus is now a synonym of *Cercestis*, see Bogner 1985). Whether there is any taxonomic significance in this similarity is uncertain but there are other similarities in stamen morphology and anatomy between subgen. *Meconostigma* and *Rhektophyllum* (Mayo 1986).

Another feature of root anatomy which may prove to be characteristic of subgen. *Meconostigma* is the lack of cell wall thickening in the inner endodermis and surrounding cortical layers. Engler (1912) reports this for *P. speciosum* and *P. bipinnatifidum* (including *P. selloum*) and notes that cell wall thickening in these tissues is normal in other species of the genus.

Porsch (1911) found that feeder roots of *P. bipinnatifidum* have a relatively narrower cortex than anchor roots, as well as smaller, thicker-walled cells, more numerous tannin cells, smaller resin canals and more numerous cortical vascular bundles. The central cylinder of feeder roots is more strongly developed with broader lobes and a sclerified axial region. Anchor roots have a parenchymatous pith, smaller sieve elements and fewer isolated phloem strands.

Roots in subgen. *Meconostigma* have certain other interesting features. They are often strongly tuberculate in the larger species (e.g. *P. solimoesense*, *P. goeldii*) with corky, lenticellate bark, and are capable of exceptionally high growth rates. French (in press) cites work by Hinchee which established much faster growth in roots of *P. bipinnatifidum* (7–21·5 mm/day) than in other species (usually less than 10 mm/day). Root growth would be worth further investigation in view of the apparent ability of the roots of *P. leal-costae* to seek out water-containing bromeliad leaf sheaths and other microsites of high humidity in its semiarid environment (Mayo & Barroso 1979, Fonseca Vaz et al. 1984).

In *Philodendron* generally, root resin canals occur in the cortex, and have a thick sclerenchyma sheath in most species investigated. However, Porsch (1911) demonstrated that in *P. bipinnatifidum* the root resin canals have no sclerenchyma sheath but instead a narrow sheath of collenchyma (see also Engler 1912, Solereder & Meyer 1928), suggesting another characteristic of subgen. *Meconostigma*.

5. INFLORESCENCE

Inflorescence characters

The common features of all *Philodendron* inflorescences are as follows: – the peduncle is relatively short, the spathe is erect and persistent until the fruits are ripe, when it abscisses at the base; the basal part is convolute, forming a tube, and the apical part opens widely at anthesis and then closes around the spadix afterwards. The spadix is monoecious with naked unisexual flowers, with the female flowers at the base and the fertile male flowers above; in most species they are separated by a zone of sterile male (staminodial) flowers and rarely there is a terminal zone of sterile male flowers as well.

None of these features is unique to *Philodendron*, being found in other genera of subfamilies *Philodendroideae* and *Lasioideae* (sensu Bogner 1979). Secretion of resin in the inflorescence during anthesis does, however, appear to be unique to *Philodendron*. There is variation in the location of the resin canals, their structure and their relative activity in different parts of the inflorescence.

Within the whole genus there is considerable variation in the number of inflorescences per floral sympodium, spathe and spadix shape, internal spathe coloration, site of resin secretion and position of staminodial zones (Mayo 1986).

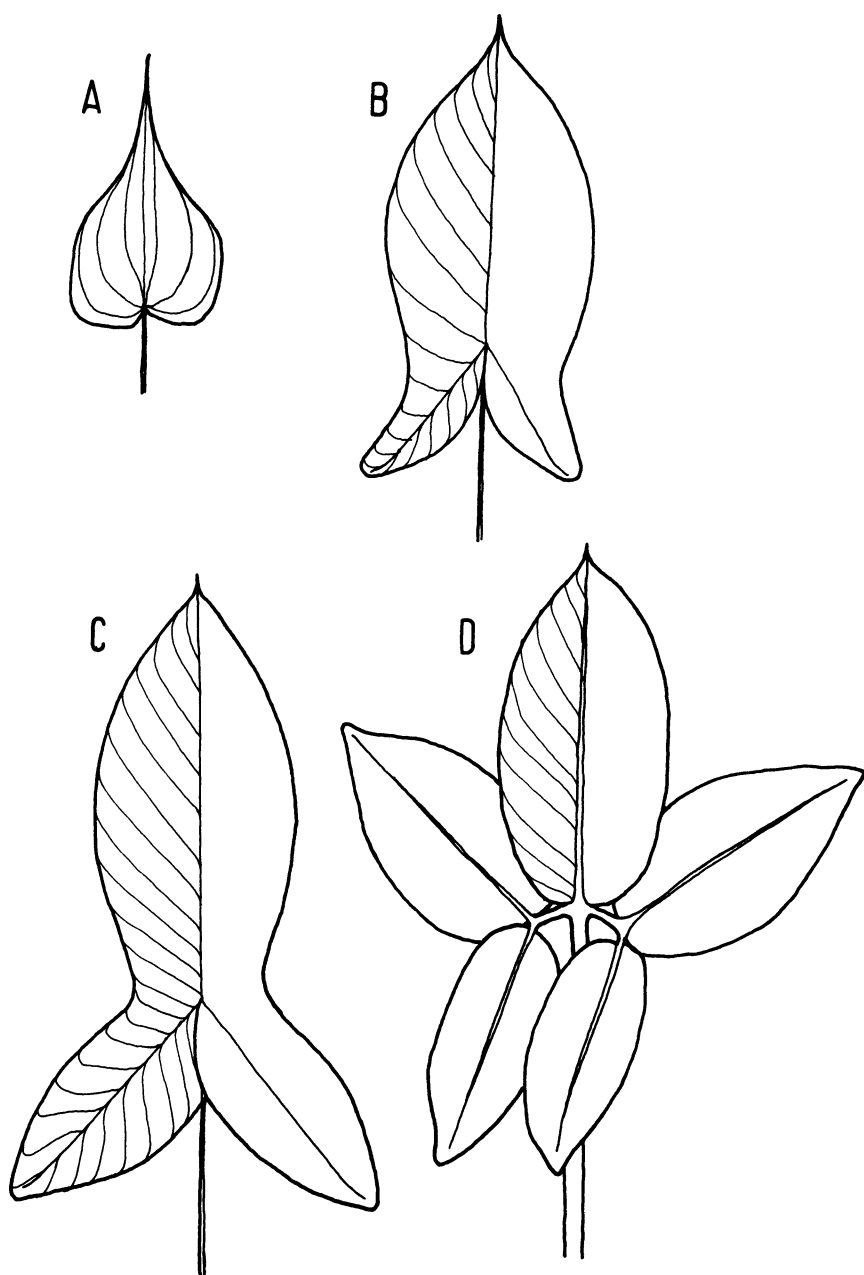


FIG. 7. Heteroblastic leaf sequence in *Philodendron leal-costae* (*P.* subgen. *Meconostigma*) showing the development of a pedately compound leaf from a cordiform one. **A** monopodial leaf of young seedling; **B** monopodial leaf of older seedling; **C** last monopodial leaf, at node corresponding to first node of first sympodial unit; **D** foliage leaf of second sympodial unit; all from *Harley et al.* 19428 (K).

Among other characters (Table 1) subgenus *Meconostigma* (Figs. 8, 9, 10) is characterized by normally solitary inflorescences in each floral sympodium and very thick, weakly constricted or unconstricted spathes with a uniformly white inner surface. Inflorescence resin is secreted from the spathe, and in one species (*P. goeldii*) probably also from canals in the stamen connective (Mayo 1986), but never from canals in the spadix axis. In the spadix the most striking character is the long staminodial zone which equals or exceeds the fertile male zone (Fig. 9) – this is the most useful diagnostic character of the subgenus. This long staminodial zone may be connected with the very large temperature elevations observed during flowering (see below). Colourless extrafloral nectaries occur on the outer surface of the spathe in several species, e.g. *P. goeldii*, *P. leal-costae*, *P. solimoesense*, *P. williamsii*. Figure 9 gives details of the various inflorescence measurements used for taxonomic description of the species.

Anatomy

Details of the anatomy of the spathe, spadix and flowers are dealt with elsewhere (Mayo 1986, 1989b). Floral anatomical characters are taxonomically useful at subgeneric and sectional level.

Gynoecial terminology

The anatomy and morphology of the gynoecium is very variable and has been used extensively in the revision presented below. An account of

TABLE 1. Diagnostic or otherwise important characters of *Philodendron* subgen. *Meconostigma*

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- | | |
|-----|--|
| 1. | Sympodial articles diphyllous, internode between prophyll and preceding foliage leaf never developed, internode between prophyll and succeeding foliage leaf sometimes developed but usually very short. |
| 2. | Leaf blade always cordiform, sagittate or hastate, never unlobed at the base. |
| 3. | Spathe very thick with an abaxial parenchyma zone thicker than 2 mm. |
| 4. | Adaxial spathe resin canals J-shaped in longitudinal section, extending to the epidermal surface and secreting resin at anthesis. |
| 5. | Abaxial spathe resin canals distributed throughout the abaxial parenchyma zone rather than restricted to more or less one layer as in the other subgenera. |
| 6. | Resin not secreted from the spadix axis, rarely secreted from stamens (<i>P. goeldii</i> only). |
| 7. | Spadix with long sterile male zone between fertile male and female zones. |
| 8. | Stamens normally long, slender, more than 3 times longer than wide (except <i>P. leal-costae</i>). |
| 9. | Stamen vascular trace unbranched (French 1986). |
| 10. | Stamen epidermis, except at stamen apex, made up entirely of cells with abundant tannin (cell contents brown in dried and fixed material). |
| 11. | Anther thecae with short, subapical to lateral stomial grooves. |
| 12. | Anther thecae subopposite. |
| 13. | Endothelial thickenings of anthers occasionally present (<i>P. goeldii</i> , <i>P. leal-costae</i> ; French 1985). |
| 14. | Style lobes always present. |
| 15. | Central style dome often present. |
| 16. | Separate styler canals occasionally absent. |
| 17. | Raphides in style usually concentrated in a concentric zone around the styler canals or at the base of the compitum. |
| 18. | Axial gynoecial vascular system present which is independent of the ovule supply (4 species investigated). |
| 19. | Vascular plexus normally present in style (4 species investigated). |
| 20. | Basal vascular complex of gynoecium multistranded (4 species investigated). |
| | At least four vegetative anatomical characters also merit further study as possibly diagnostic: |
| 21. | Absence of elongated epidermal cells over the veins on lower surface of leaf. |
| 22. | Lobed central vascular cylinder in the roots. |
| 23. | Lack of cell wall thickening in the inner root endodermis and neighbouring cortical cells. |
| 24. | Collenchyma rather than sclerenchyma sheaths around root resin canals. |
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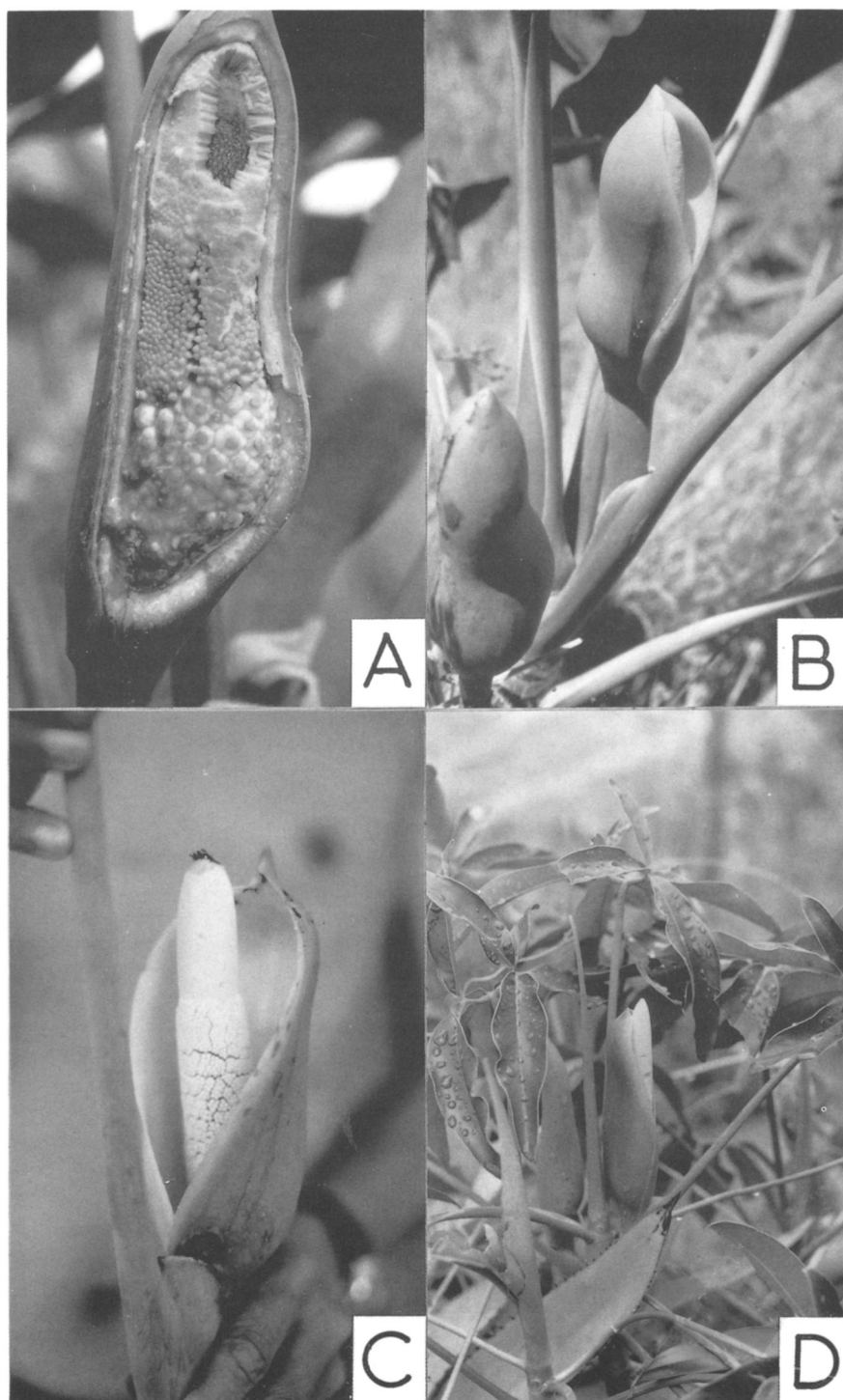


FIG. 8. Inflorescences of *Philodendron* subgen. *Meconostigma*. **A** *P. uliginosum*: postfloral inflorescence showing developing fruits at base and decomposing sterile male and fertile male parts above, Serra do Cipó, Minas Gerais (S. Mayo et al. 700); **B** *P. uliginosum*: inflorescence at anthesis, Serra do Cipó, Minas Gerais, 1981; **C** *P. saxicolum*: inflorescence at anthesis, the lower half of the spadix showing the conspicuous sterile male zone, near Andaraí, Bahia (Harley et al. 18593); **D** *P. leal-costae*: inflorescence at anthesis; note adventitious roots and bromeliad leaf in lower lefthand corner, Milagres, Bahia (Harley et al. 19428).

gynoecial structure has been published elsewhere (Mayo 1989b), but the special terms used in the descriptions require clarification here as well (cf. Figs. 12, 14–17). The *style lobes* are the carpel apices which are conspicuous in subgen. *Meconostigma* and which together constitute the *style crown*; since they are mostly covered by stigmatic tissue they resemble stigma lobes. The *style body* is the tissue between the ovary locules and the style lobes, through which the stylar canals run; this region usually contains an abundance of raphide idioblasts (shown as stippling in Figs. 12, 14–17). The *compitum* is a cavity within the style crown, surrounded by stigmatic epidermis (shown as oblique hatching in Figs. 12, 14–17) into the base of which the stylar canals emerge. The *stylar canals* (shown as thick lines in Figs. 12, 14–17) are the separate canals which connect the compitum to each locule. In many species the central region of the style apex is elongated into a more-or-less cylindrical axial portion, the *central dome*. The central dome may be excavated itself into a pit or even a long canal (*P. solimoesense*, Fig. 15C), and may have lobed margins (*P. goeldii*).

6. FLORAL BIOLOGY

Philodendron is one of the few genera of the Araceae in which pollination biology has been studied in detail. The flowers are protogynous and the stigmas are normally receptive during the 24 hours prior to pollen shedding. Various combinations of morphological and anatomical inflorescence characters occur in the genus which are taxonomically significant and it seems likely that they correspond to different syndromes of floral biology (Mayo 1986). However, comparative studies to investigate this question have not yet been carried out. Most work has been carried out on *P. bipinnatifidum* (syn. *P. selloum*) of subgen. *Meconostigma* and is reviewed here. Data on other species of the genus are rare and are confined to a few species of subgen. *Philodendron* (Hubbard (1985) – *P. giganteum*; Leick (1916) – *P. pinnatifidum*, *P. macrophyllum*, '*P. albomarginatum*', *P. melanochrysum*).

Work on *P. bipinnatifidum* (syn. *P. lundii*) began with Warming's field study (Warming 1867, 1883) of a population in Minas Gerais, Brazil. This study did not include precise details of the pollinators but reported observations concerning thermogenesis (production of heat in the inflorescence during flowering). Schrottky (1910), based on a study in Paraguay, later established the identity of a pollinator – the beetle *Erioscelis emarginata* (Mannh.) (*Dynastinae/Scarabaeidae*). Chodat & Vischer (1920), also working in Paraguay, discovered parasitism of *Philodendron* inflorescences by hymenopteran larvae (see below). The most complete field study of *P. bipinnatifidum* pollination so far published is that of Gottsberger & Amaral (1984). This gives an account of inflorescence and pollinator behaviour, including the thermogenetic cycle, in two populations recognized as the species *P. selloum* and *P. bipinnatifidum* and distinguished by morphology, pollinators and flowering behaviour. Semir, Gibbs and co-workers have also carried out unpublished field studies of *P. bipinnatifidum* in São Paulo state, Brazil (Dr. P. Gibbs, pers. comm.).

Modern studies on cultivated plants have elucidated details of the thermogenetic cycle during flowering. Foster (1949), Sheridan (1960), Brattstrom (1972), Nagy et al. (1972) and Seymour et al. (1983, 1984) have all reported temperature fluctuations of *P. bipinnatifidum* inflorescences. The studies by Nagy, Seymour and co-workers established that the inflorescence regulates its metabolism during the thermogenetic peak so as to maintain a temperature

of between 38 and 46°C. independent of ambient temperature. Thus the absolute temperature rather than the temperature relative to the surrounding air seems to be the important criterion. Seymour et al. (1983) reported that the heat-producing respiration of the spadix could occur either by the cytochrome pathway or the cyanide-insensitive pathway. They suggested that the cyanide-insensitive pathway may be little-used in thermogenesis of this species, in contrast to the situation in *Arum* and *Sauromatum* (Meeuse 1975). Seymour et al. (1984) established that the major energy source for thermogenesis in *P. bipinnatifidum* is not starch, but probably lipid, confirming previous suggestions by Pohl (1932a), who reported oil rather than starch in the cells of the staminodes and stamens.

Studies of the anatomy and phenology of inflorescence secretory activity in the genus have been carried out by Müller (1893), Pohl (1932a, b) and myself (Mayo 1986). Pohl's papers include descriptions of the chemistry of inflorescence resin, the anatomy of the 'movement tissue' which opens and closes the spathe, and a review of previous studies of the floral biology of the species. My work included a comparative study of the sites of resin secretion in the inflorescence and the relationship between secretory function and floral anatomy.

The flowering cycle

Problems remain in understanding the details of phenology and pollination in *P. bipinnatifidum*, the main object of studies so far published, since the various accounts do not provide a uniform picture of events. Figure 11 compares the results of the main studies so far reported. Gottsberger & Amaral (1984) established that distinct patterns of flowering occur in two morphologically distinct populations (*P. selloum*, *P. bipinnatifidum*). In my view these taxa both fall into *P. bipinnatifidum* (see section 12), but this does not necessarily affect their recognition by Gottsberger & Amaral as valid groups, only the names and taxonomic rank assigned to them; they are referred to below as the 'selloum' and 'bipinnatifidum' groups or patterns.

Gottsberger & Amaral's temperature measurements were made mainly in the staminodial zone of the spadix which is, as all authors agree, the source of the most intense heat and odour emissions.

The 'selloum' group has a 3-day flowering cycle with a single temperature peak (Fig. 11A). The cycle begins on day 1 with the loosening of the spathe. During day 2, heating and the emission of the sweet to spicy odour begin, peaking at around 1900 hr, when the pollinating beetles arrive, in this case exclusively *Erioscelis emarginata*. During the ensuing night, spadix temperature drops to 30–35°C and at about 1500 hr. on the following day (day 3), the spathe begins to close. As it does so, resin emerges on the inner surface and pollen is extruded in filaments from about 1530 onwards. The beetles, which have remained in the spathe tube since the evening of day 2, crawl up the spadix as the spathe begins to close on the afternoon of day 3. Resin secretion is greatest at the constriction of the spathe, forcing the beetles to squeeze through a narrow gap so that their bodies become coated with resin. As they crawl higher and cross to the staminate zone the filaments of extruded pollen stick easily to their bodies. The closure of the spathe continues gradually until, at about 1900 hr., the beetles, now grey with pollen, emerge at the very tip of the spathe. Their emergence at this hour coincides with the time of greatest heat and odour emission of day 2 inflorescences, ensuring a high probability of successful cross-pollination.

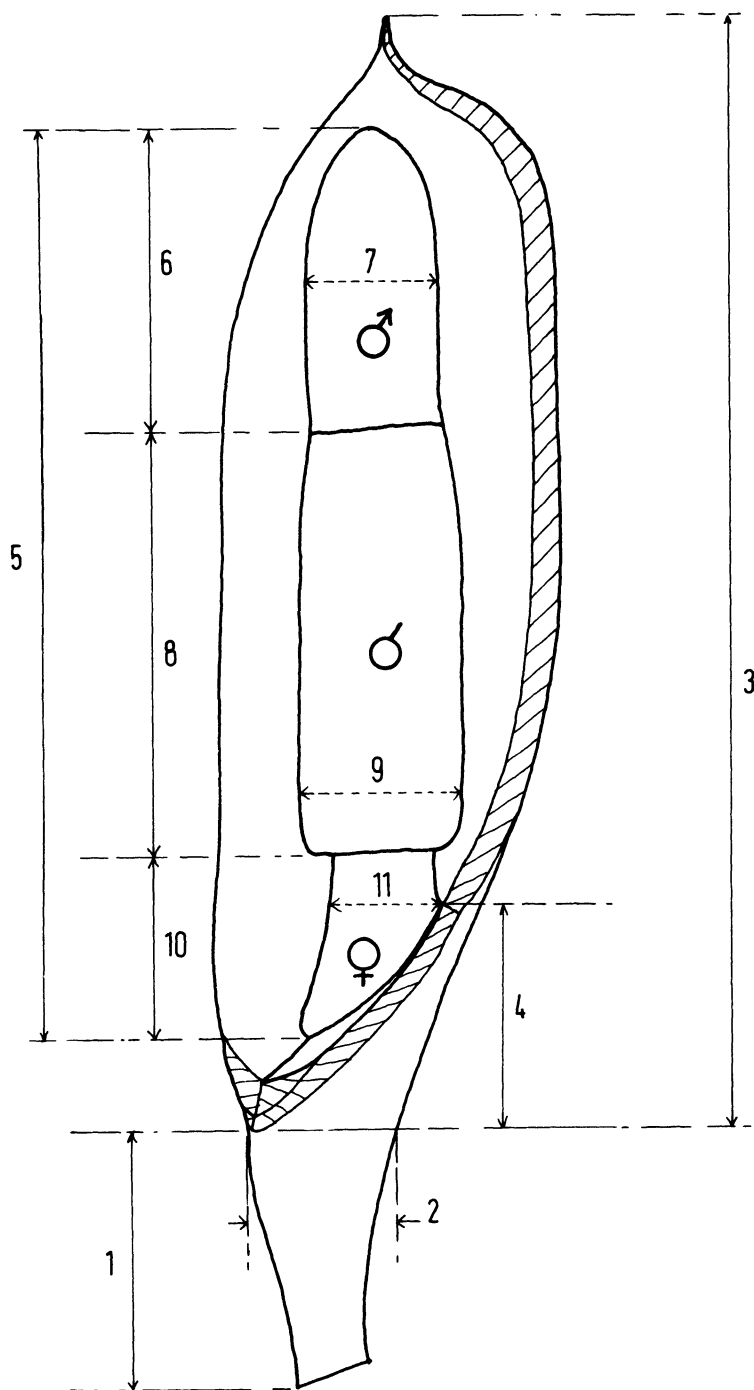


FIG. 9. Definition of terms – Inflorescence morphology in *Philodendron* subgen. *Meconostigma*; 1: peduncle length; 2: peduncle – width at apex; 3: spathe length; 4: spathe decurrency length; 5: spadix length; 6: fertile male zone length; 7: fertile male zone diameter; 8: sterile male zone length; 9: sterile male zone diameter; 10: female zone length; 11: female zone diameter.

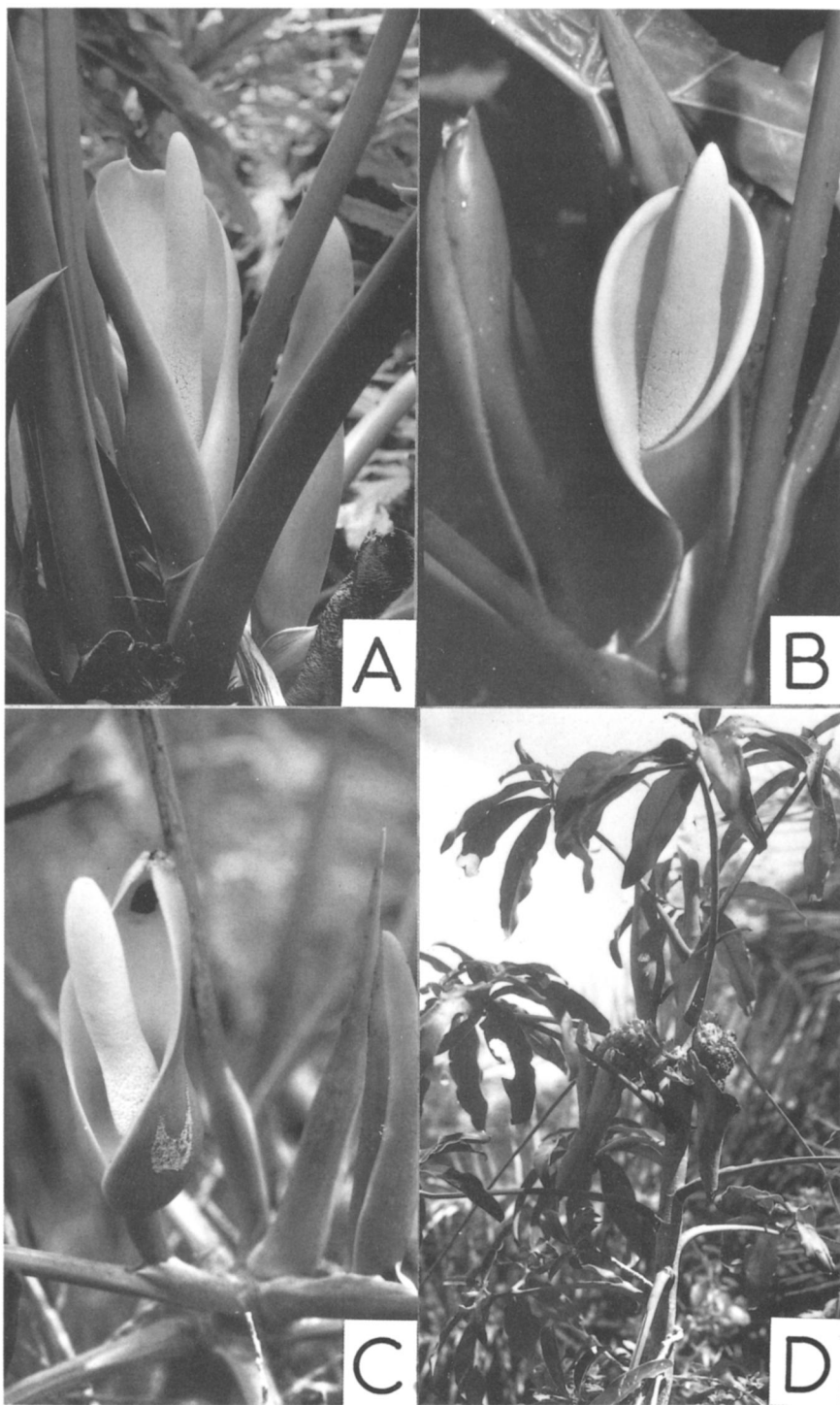


FIG. 10. Inflorescences of *Philodendron* subgen. *Meconostigma*. **A–B** *P. bipinnatifidum*: plants cultivated at the University of Campinas, São Paulo – the outer surface of the spathe is green in **A** and maroon in **B** (photos P. E. Gibbs); **C** *P. adamantinum*: inflorescence at anthesis – the black patch at the spathe apex is insect damage, Trinta Reis, Minas Gerais (S. Mayo *et al.* 707); **D** *P. leal-costae*: plant displaying ripe fruit, Milagres, Bahia (Harley *et al.* 19428).

In the 'bipinnatifidum' group flowering takes place in a 4-day cycle with 3 temperature peaks (Fig. 11B); the peaks are lower and a different, less intense odour is produced. In this pattern, pollen is extruded shortly before resin secretion and both are associated with a temperature peak between 1800 and 1900 hr. on day 3. The spathe remains slightly open throughout the following day as the spadix temperature falls off. On day 4 at about 1900 hr. a third temperature peak occurs (34.3°) and the spathe closes. The pollinating beetles were attracted in fewer numbers and belonged to two species, *Cyclocephala cribrata* Burmeister and *C. variolosa* Burmeister (Dynastinae/Scarabaeidae). They also appeared to visit the inflorescence at each temperature peak, hence on three separate occasions.

Gottsberger & Amaral (1984) conclude from their results that the more highly coordinated phenology, more intense odour and higher temperature peaks and exclusive pollinator species of the 'selloum' group constitute an adaptive syndrome, resulting from the sparser and more dispersed populations of both plant and pollinator species in the drier forests of the Brazilian plateau region where they occur. Pollinator specificity in the 'selloum' group is supported by the observations of Gibbs et al. (1977). They found that flowering individuals of a population of *P. aff. selloum* in the plateau region of São Paulo state consistently attracted a different Dynastine beetle species from that pollinating adjacent trees of *Talauma ovata* (Magnoliaceae), even though the latter has a very similar phenology to the *Philodendron* and was being pollinated at the same time of day. The 'bipinnatifidum' group occurs mainly in the rainforests of the more humid eastern coastal plain and maritime mountain ranges where the populations are more abundant and are thought to have access to a wider range of potential pollinator species. It is surmised therefore that the plant does not need such a highly organized strategy to ensure successful pollination.

Warming's (1867, 1883) observations (Fig. 11E) were carried out on a population at Lagoa Santa, Minas Gerais state, Brazil, and the phenology differs in certain respects from the findings of Gottsberger & Amaral (1984). In general Warming's data more closely resembles the 'selloum' pattern, although the flowering cycle is 2 days long, with the spathe loosening and opening on the morning of day 1 and the main odour and temperature peak (39.5°C max.) occurring at 1800–1900hr. in the evening of the same day (Fig. 11E). After this the temperature falls rapidly and the spathe partially closes during the ensuing night. In late morning of day 2 there is a second, lower temperature peak which rapidly subsides by the afternoon, when resin appears on the spathe inner surface followed later by pollen emission. The spathe finally closes during the evening of day 2.

Both beetles and bees were attracted by the odour and heat emission on day 1; the bees arrived in the afternoon and returned the following morning with the occurrence of the second temperature peak. Warming nevertheless regarded the true pollinators as the beetles which were most abundant at the time of the main temperature and odour peak on day 1 at 1800–1900 hr.

Warming's observations differ in three main respects from the 'selloum' cycle of Gottsberger & Amaral (1984); i) the spathe begins to open a day later relative to the main temperature peak; ii) the spathe begins to close immediately after the heat peak of day 1; iii) the temperature curve of the day following the main temperature peak has a second peak in the morning and a rapid fall soon after; the temperature of the spadix is thus relatively low at

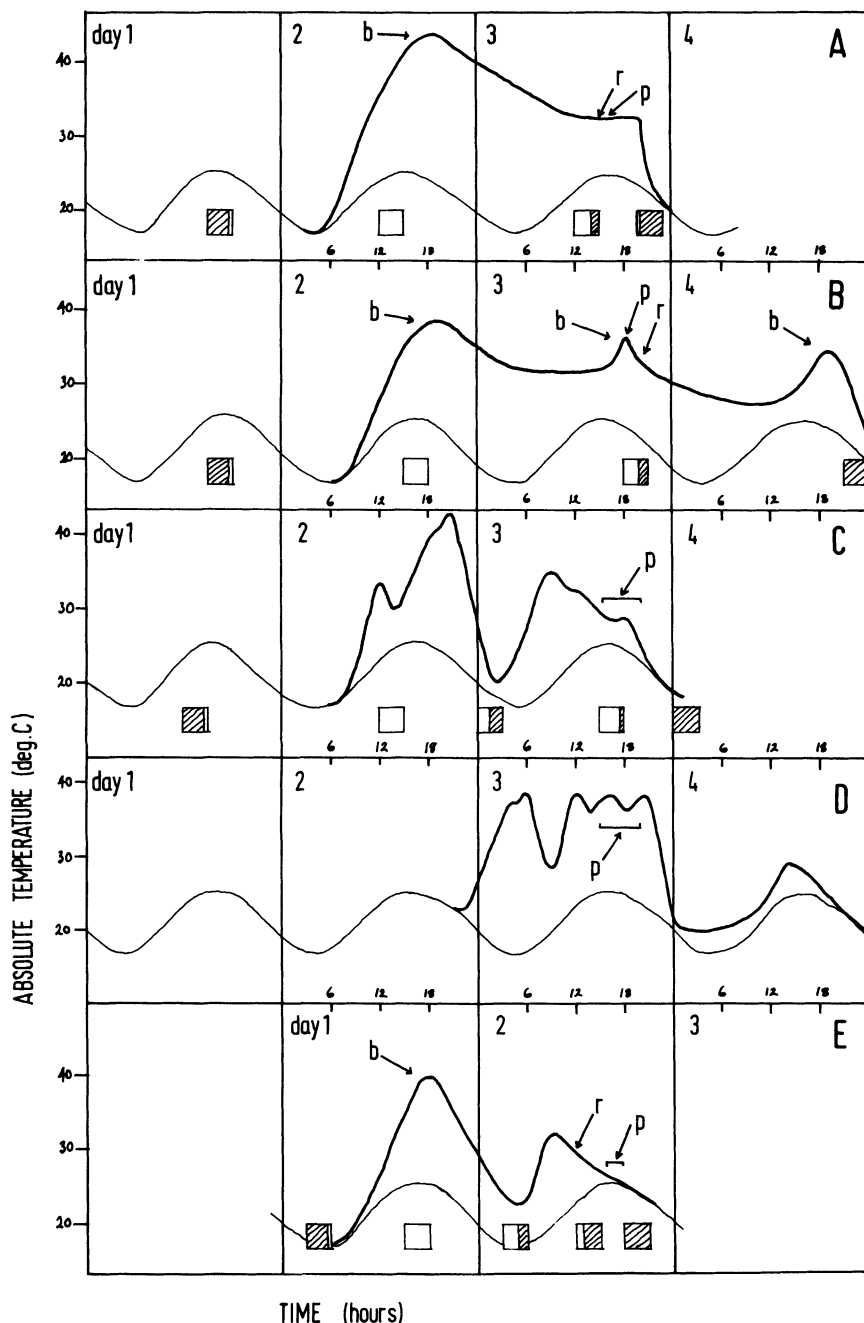


FIG. 11. 3- and 4-day cycles of inflorescence thermogenesis in *Philodendron bipinnatifidum* - a semidiagrammatic comparison of data from literature sources. **A** Gottsberger & Amaral (1984) - pattern of "P. selloum" population; **B** Gottsberger & Amaral (1984) - pattern of "P. bipinnatifidum" population; **C** Seymour et al. (1983) - pattern 1; **D** Seymour et al. (1983) - pattern 2; **E** Warming (1867, 1883); thick lines represent spadix temperature; thin lines represent approximate ambient temperature; squares with diagonal shading (representing closure) and blank areas (representing degree of opening) represent the opening and closing movements of the spathe during anthesis; the small figures on abscissa of each graph represent the time of day; b: beetles observed arriving at inflorescence; r: resin secretion begins to appear on spathe adaxial surface; p: pollen filaments begin to emerge from fertile male zone of spathe; see text for further details.

the time of pollen emission.

Seymour et al. (1983), working with cultivated plants in California, also reported the existence of two distinct patterns of phenology, but these do not correspond in detail with Gottsberger & Amaral's findings. Furthermore, Seymour and colleagues found both patterns in inflorescences from the same plant on different days. They measured temperature in the staminodial zone only, using fine thermocouples connected to automatic recording devices which measured temperature every 30 seconds. Their pattern 1 (Fig. 11C) closely resembles Warming's pattern, although they start the cycle a day earlier. The main difference from Warming's pattern is that the spathe reopens in the afternoon of day 3 when the pollen begins to emerge.

Pattern 2 is a 4-day cycle (Fig. 11D) and shows some resemblance to the 'bipinnatifidum' pattern of Gottsberger & Amaral (1984) with the difference that there is no temperature peak on day 2. Instead there is little activity until after 2200 hr. on day 2 when a heating phase begins culminating in a temperature peak at 0300–0400 hr. on day 3, followed by a short dip and then another temperature increase. After this the temperature remains more or less constant at between 36 and 42°C until about 2000 hr. on the evening of day 3 when pollen is extruded. As in Gottsberger & Amaral's 'bipinnatifidum' pattern, another lower temperature peak occurs in day 4, but this did not happen in all pattern 2 spadices according to the published data. The initial 0300–0400 hr. day 3 peak could possibly be interpreted as a delayed version of the 1900 hr. day 2 peak of Gottsberger & Amaral.

Foster (1949) observed flowering in a cultivated plant of *P. bipinnatifidum* in Florida, but he detected only a single temperature peak at 2000 hr. on day 2, corresponding to the time of pollen extrusion. In this plant the spathe resin was exuded at midday on day 2.

It seems clear from these rather variable results that more work is needed, particularly studies of species in their natural habitat. It would be desirable to study other species of subgen. *Meconostigma* which are different enough for there to be no possibility of taxonomic confusion. Both Seymour et al. (1983) and Gottsberger & Amaral (1984) show that two flowering patterns can occur. Pattern 2 of Seymour et al. and the 'bipinnatifidum' pattern of Gottsberger & Amaral seem to extend the male phase of the flowering cycle, but more detailed studies are needed to establish this. Thus it is not known whether the pollen retains its viability under natural conditions for 24 hours after emission.

Galling by hymenoptera

Galling of *Philodendron* gynoecia by hymenoptera was first reported by Chodat & Vischer (1920), based on studies by C. Ferrière of their collections from Paraguay. In three species of subgen. *Meconostigma*, *P. dubium* (= *P. tweedianum*), *P. undulatum* and *P. petraeum*, two wasp species were observed parasitizing the ovules, *Trichoporus* sp. and *Prodecatoma* sp. Sometimes both species of wasp were found in the same inflorescence.

I have observed similar parasitism by unidentified hymenopterans in Brazilian species of subgen. *Meconostigma* in Minas Gerais (*P. uliginosum*), Santa Catarina (*P. bipinnatifidum*), Paraná (*P. corcovadense*) and Rio de Janeiro (*P. bipinnatifidum*, *P. undulatum*). In *P. bipinnatifidum*, I have observed female wasps inserting their ovipositors down between the gynoecia of a mature inflorescence at female anthesis, and they presumably lay their eggs within the locules. Survey of herbarium material at Kew (K) shows that insect galling

of gynoecia occurs in the other subgenera. Wasps develop within each ovule, which induces abnormally large size and irregular form in the ovule itself. Where it occurs, galling is usually extensive within a single inflorescence.

Chodat & Vischer (1920) postulated that there may be competition for ovules between the parasitic wasps and pollinating beetles. Alternatively, they suggest, the wasps may turn to other sites for their broods during the season when the pollinators are active. Successful fruit set of *P. bipinnatifidum* occurs between November and January (Schrottky 1910, Gottsberger & Amaral 1984), when the adult pollinating beetles are actively flying and mating. During the rest of the year inflorescences may be produced, but these nearly always become galled (Chodat & Vischer 1920).

Possibly the occurrence of wasp parasitism could be linked to the evolution of very high locule numbers in *Philodendron* ovaries (Mayo 1989b). High locule numbers may be an adaptive response to gall wasp parasitism, by 'overloading' the wasp with egg sites. Especially high locule numbers occur in the Amazonian species (*P. goeldii*, *P. solimoesense*, *P. venezuelense*) of *P.* subgen. *Meconostigma*.

Role of inflorescence resin

Previous authors have generally accepted that inflorescence resin in *Philodendron* functions as an adhesive between pollen grains and the body of the pollinator, but this has not been thoroughly investigated. Critical studies are needed in view of recent literature on floral resins. Armbruster (1984) has described other functions for floral resins in angiosperms and has shed doubt on the efficacy of floral resin as a medium for pollen transport in view of its possibly toxic properties and because of the apparent difficulty of transferring pollen embedded in sticky resin from a pollinating insect to a stigma.

In *Philodendron* there can be no doubt that resin and pollen function together in pollen uptake by the pollinator. Apart from the observations of *P. bipinnatifidum* pollination by authors cited earlier, in those species of subgen. *Philodendron* which secrete resin from spadix canals (Mayo 1986), the pollen is mixed completely with resin from the moment of theca dehiscence. Martius (1831) observed this phenomenon over 150 years ago in *P. canniifolium* (= *P. martianum*) and *P. grandifolium*. However, it remains to be demonstrated that: i) pollen enters stigma-receptive inflorescences attached to beetles by resin, and ii) that pollen stuck to beetles by resin is transferred to the stigma and is viable on arrival there. It would be interesting to know whether stigma secretions play a role in pollen transfer.

Floral resins acting as a reward to bee pollinators have been studied in detail by Armbruster (e.g. Armbruster 1984). In *Philodendron* inflorescences, to which bees are known to be attracted, it seems that resin collection is opportunistic and secondary to the primary function of resin secretion. Bees have not been observed to play any part in pollination of *Philodendron* species, nor is the resin displayed for long periods of time, as in plants described by Armbruster (1984). Both Warming (1883) and Pohl (1932a) record the visits of bees to *Philodendron bipinnatifidum* inflorescences and the latter author even suggested that their purpose was to collect resin from the spathe.

7. POLLEN

Grayum (1984) studied the pollen of the following species of subgen. *Meconostigma*:- *P. goeldii*, *P. leal-costae*, *P. solimoesense*, *P. bipinnatifidum*, *P.*

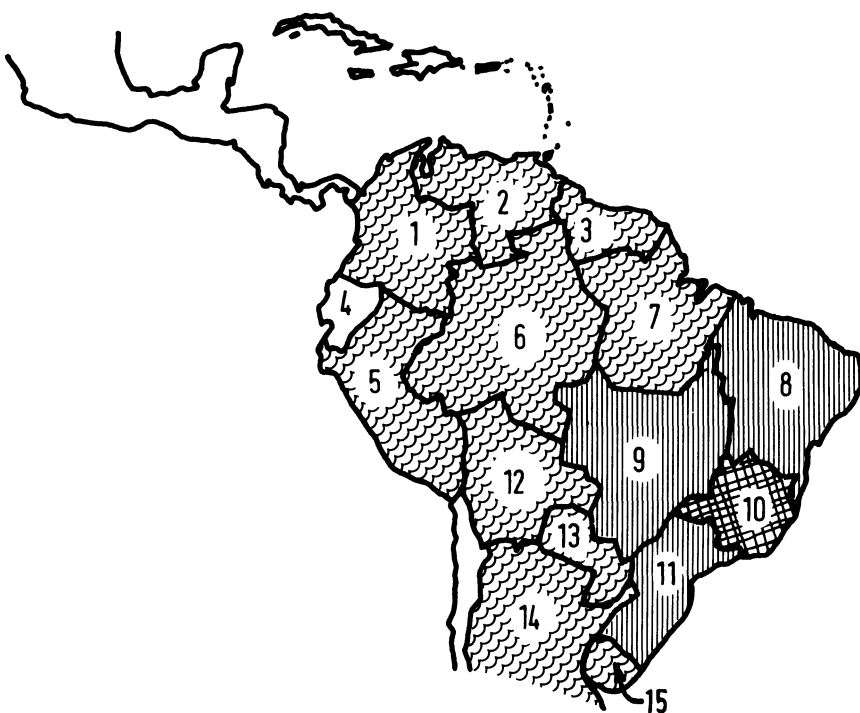
tweedianum. He concluded that the pollen of *P. goeldii* and *P. leal-costae* showed some resemblance in a tendency towards a verrucate exine (pronounced in the latter species), and furthermore that their pollen differed from the rest of the genus. A more detailed pollen survey would be desirable.

8. CYTOLOGY

Petersen (1989), in a recent review of aroid cytology, has drawn attention to the distinctive chromosome number ($2n = 36$) of the three species of subgen. *Meconostigma* so far examined (*P. bipinnatifidum*, *P. speciosum*, *P. undulatum*); the records cited for *P. lundii* and *P. selloum* are treated here as belonging to *P. bipinnatifidum*.

9. GEOGRAPHY

Engler (1899) drew attention to the peculiar 'southern' distribution of *P.* subgen. *Meconostigma* (see also Mayo 1984). The present revision and a recent literature and herbarium survey of species ranges in the three subgenera (Mayo 1986, 1989a) confirm that this pattern is characteristic of subgen. *Meconostigma* and different from those of the other two subgenera. In subgen.



MAP 1. Species density distribution in *Philodendron* subgenus *Meconostigma*. Diagonal wavy lines: 1-3 species; vertical lines: 4-6 species; cross hatching: 9 species. The numbered areas are as follows: - 1: Colombia; 2: Venezuela; 3: Guyana, Surinam, French Guiana; 4: Ecuador; 5: Peru; 6: Brazil - western Amazonia (Amazonas, Rondônia, Roraima, Acre); 7: Brazil - eastern Amazonia (Pará, Amapá); 8: Brazil - northeast (Maranhão, Ceará, Rio Grande do Norte, Paraíba, Pernambuco, Sergipe, Alagoas, Bahia, Piauí); 9: Brazil - central west (Federal District, Mato Grosso, Mato Grosso do Sul, Goiás, Tocantins); 10: Brazil - southeast (Minas Gerais, Espírito Santo, Rio de Janeiro); 11: Brazil - south (São Paulo, Paraná, Santa Catarina, Rio Grande do Sul); 12: Bolivia; 13: Paraguay; 14: Argentina; 15: Uruguay.

Pteromischum and *Philodendron*, Peru, Venezuela, Colombia, Panama and Costa Rica, Ecuador and the western Amazonian region of Brazil are all relatively rich in species. Secondary centres of diversity occur in southeastern Brazil and Mexico but the Caribbean region and subtropical South America are poor in species (Bolivia and the Mato Grosso states of Brazil appear species-poor according to the literature but are seriously under-collected). Except for the very southernmost part, the overall range of subgen. *Meconostigma* falls within the South American ranges of the other two subgenera, but the pattern of diversity is different. *P.* subgen. *Meconostigma* is most diverse in south-eastern Brazil, relatively well-represented in subtropical South America, sparsely represented in Amazonia and absent from the Caribbean, Mexican and Central American regions (Map 1). Further details are given in Maps 2-4 and under the taxonomic accounts of each species.

10. ECOLOGY

Unlike the species of subgenera *Pteromischum* and *Philodendron*, which mostly occur in shaded sites, those of subgen. *Meconostigma* prefer open environments with higher light intensity.

P. saxicolum and *P. adamantinum* are rupicolous plants of montane habitats. *P. leal-costae* occurs in 'restinga' scrub, a type of coastal vegetation on sandy soils, but has been more often collected on isolated granitic outcrops surrounded by semi-arid caatinga. The apparent dependence of this species on the presence of water in leaf sheaths of neighbouring rupicolous bromeliads is discussed below under its description. *P. dardanianum*, *P. uliginosum*, *P. brasiliense*, *P. undulatum* and *P. tweedianum* are aquatic or subaquatic species occurring in freshwater swamps either in lowland sites (*P. tweedianum*, *P. undulatum*) or in montane or submontane river systems. *P. williamsii*, *P. corcovadense*, *P. bipinnatifidum* and possibly *P. speciosum* are forest hemi-epiphytes which grow equally well in rupicolous habitats or even in open coastal sites on sand in the case of the former three. *P. bipinnatifidum* has also been collected in freshwater swamps in habitats similar to those of *P. undulatum*. *P. solimoesense*, *P. goeldii* and *P. venezuelense* are forest hemi-epiphytes but may occur as terrestrial plants in more open vegetation on sandy soils.

The preference for open habitats and the ability to tolerate a certain degree of drought accounts for the success of species of subgen. *Meconostigma* as horticultural landscape plants and must also have had a significant bearing on their evolutionary history and resulting geographical patterns. Modern ideas of vegetation history in tropical America (e.g. as discussed in Prance 1982 and Harley 1988) emphasize the contrasting and perhaps complementary patterns of distribution that could have arisen from successive cycles of forest and savanna expansion. In this context, the success of subgen. *Meconostigma* might be expected to have been greatest during intermediate rather than extreme phases of such cycles; i.e. conditions which fostered open or discontinuous forest canopies but with short dry seasons and relatively high temperatures. Survival strategies in basically unfavourable conditions seem to be represented by the rupicolous *P. leal-costae*, *P. adamantinum*, and *P. saxicolum* in more arid habitats and, perhaps, the hemi-epiphytic habit of several other species in regions of well-developed humid forest such as Amazonia.

11. FOSSIL HISTORY

Dilcher & Daghljan (1977) discovered an important aroid leaf fossil from the Eocene of Tennessee, USA, which they assigned to *Philodendron* subgen. *Meconostigma*, and named *P. limnestis* Dilcher & Daghljan. They compared the cuticular anatomy and venation of the large fossil leaves with several species of the subgenus including *P. brasiliense*, *P. corcovadense*, *P. speciosum*, *P. tweedianum* and *P. undulatum*, emphasizing venation as the more reliable guide to identification.

This discovery is one of the most interesting aroid fossils yet reported and from a geographical standpoint unexpected in view of the strongly "southern" character of the extant range of the subgenus. However, the identification remains open to question, in my opinion, as judged from the published illustrations. The marginal venation of species of subgen. *Meconostigma* does not match that of the fossil especially well. As in the rest of the genus, there is a single submarginal vein in subgen. *Meconostigma*, and veins approaching from the leaf blade bend towards the leaf apex and run subparallel with the margin for only a short distance before fusing with the submarginal vein. According to the published illustrations, the fossil shows at least two parallel submarginal veins, and veins approaching the margin fuse with the innermost submarginal vein without a distinct change of direction. The shape of the posterior divisions also differs since the fossil appears to lack the characteristic basiscopic denudation of the basal ribs found in subgen. *Meconostigma*.

The venation of *P. limnestis* more closely resembles that of the monotypic genus *Typhonodorum*, endemic to Madagascar and a close relative of the North American *Peltandra* (Grayum 1984). Dilcher & Daghljan compared their fossil with thirteen *Araceae* genera, although only *Philodendron* is named. *Peltandra* has leaves very much smaller than those of the fossil. *Typhonodorum* may not have been considered, given its remote geographical location. *Typhonodorum* is a robust to gigantic rooted aquatic plant with sagittate leaf blades reaching over a metre in length. The plants grow in dense stands, as *P. limnestis* may have done. However, *P. limnestis* is clearly distinct from *Typhonodorum* in having about six major basiscopic veins in the posterior segments.

The close relationship between *Peltandra* and *Typhonodorum* suggests that they are relicts of a formerly more widespread species group, of which *P. limnestis* could have formed part. It would clearly be interesting if further comparisons of the fossil with *Typhonodorum* and *Peltandra* were undertaken.

12. TAXONOMIC REVISION

A scheme of the species relationships based on phenetic and cladistic analyses will be published later. For convenience, the arrangement of species given here is alphabetical.

Philodendron Schott subgenus **Meconostigma** (Schott) Engler in Bot. Jahrb. 26: 554 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 3, 128 (1913).

P. c. *Meconostigma* Schott in Schott & Endl., Melet. Bot. 19 (1832); Endlicher, Gen. Pl. 1(3): 237 (1837); Kunth, Enum. pl. 3: 51 (1841), rankless taxon. Type: *P. speciosum* Schott ex Endl.

- P. d. Sphinctrostigma* Schott in Schott & Endl., Melet. Bot. 19 (1832); Endlicher, Gen. Pl. 1(3): 237 (1837); Kunth, Enum. pl. 3: 51 (1841), rankless taxon. Type: *P. bipinnatifidum* Schott ex Endl.
- P. grex Meconostigma* (Schott) Schott, Syn. Aroid. 91 (1856) & Prodr. Syst. Aroid. 262 (1860).
- P. grex Sphinctrostigma* (Schott) Schott, Syn. Aroid. 112 (1856) & Prodr. Syst. Aroid. 297 (1860).
- P. sect. Meconostigma* (Schott) Pfeiffer, Nomencl. Bot. 2(1): 674 (1874); Engler in Martius, Fl. Bras. 3(2): 146 (1878) & in A. & C. De Candolle, Monog. Phanerog. 2: 423 (1879).
- P. sect. Sphinctrostigma* (Schott) Pfeiffer, Nomencl. Bot. 2(1): 674 (1874); Engler in Martius, Fl. Bras. 3(2): 147 (1878) & in A. & C. De Candolle, Monog. Phanerog. 2: 427 (1879).
- Boursea* subgen. *Meconostigma* (Schott) Post & Kuntze, Lexicon gen. phanerog. 63 (1903).

Hemi-epiphytic, rupicolous, terrestrial or emergent aquatic plants. Stem arborescent, often decumbent, sometimes climbing, in hemi-epiphytic plants often pendent with ascending apex; adult stem a sympodium with each unit bearing one bicarinate prophyll, one foliage leaf with a short inconspicuous sheath and an aborted or developed terminal inflorescence; internodes normally very abbreviated and shorter than prophyll scars which may resemble internodes; internode between prophyll and foliage leaf sometimes elongated, hypopodial internode (that preceding prophyll) always suppressed; intravaginal squamules present on internodes especially around leaf base scars, often numerous, usually triangular, acuminate and patent, becoming hard and spinose, persistent in many species. Leaves in a terminal crown, older ones usually regularly deciduous, the leafless lower stem bearing conspicuous spirals of leaf base scars; leaf blade cordiform-sagittate, sagittate, orbicular or transverse-cordiform in outline, base always divided into two posterior divisions separated by a sinus, margins entire, repand, sinuately lobed, pinnatifid, bipinnatifid or leaf blade pedately compound, extreme margin frequently conspicuously paler than blade and cartilaginous. Inflorescence normally solitary, floral sympodium rarely bearing two inflorescences. Peduncle usually shorter than spathe. Spathe weakly or not constricted, tissue very thick, resin canals scattered throughout tissue below abaxial epidermis, those below adaxial epidermis J-shaped in longitudinal section and secreting yellow-amber resin onto inner surface during anthesis, inner surface usually creamy white, rarely entirely carmine-magenta or purple, never red-purple at base only. Spadix rather massive, subequal to spathe, sterile male zone between fertile male and female zone very well-developed, usually longer than fertile male zone, rarely equal or slightly shorter, resin not secreted by spadix axis (in *P. goeldii* resin may be secreted from stamen connectives). Stamens normally long and slender, rarely less than $3 \times$ longer than broad (*P. leal-costae*) and usually much longer, epidermis uniformly tanniniferous except at apex, thecae subopposite, dehiscing by short lateral or subapical stomial grooves or pores, microsporangia rarely with endothecial thickenings (*P. goeldii*, *P. leal-costae*), pollen psilate to coarsely verrucate; staminodes cylindric to clavate, epidermis uniformly tanniniferous except in apical zone; gynoecium with 3–47-locular ovary, ovules usually 2–3 per locule, rarely 1–13, style consisting of apical crown of lobes equal in number to locules, central style

dome often present, separate styler canals usually present, sometimes very short, rarely lacking, raphide idioblasts usually abundant and concentrated around styler canals, stigmatic tissue overlying style lobes, contiguous with that of neighbouring gynoecia. Berries large, many-seeded. Seeds either sarco-testate or with arillate funicle or occasionally both, endosperm abundant.

KEY TO SPECIES OF *Philodendron* SUBGENUS *Meconostigma*

1. Leaf blade transverse-cordiform (reniform) in outline, pedately compound:
 2. Ovary locules 3–4; leaflets 8–11, central leaflet 10–17 cm long; occurring on rocks in semiarid areas or terrestrial in coastal 'restinga' scrub on sand; northeast Brazil.....7. **P. leal-costae** (Fig. 15A, p. 654)
 2. Ovary locules 10–26; leaflets 10–20, central leaflet 18–50 cm long, hemi-epiphytic or terrestrial; commonest along river margins; Amazon basin, French Guiana.....6. **P. goeldii** (Fig. 14C, p. 646)
1. Leaf blade cordiform-sagittate, sagittate or hastate in outline, margins entire, repand, sinuately lobed, pinnatifid or bipinnatifid:
 3. Leaf margin sinuately lobed, pinnatifid or bipinnatifid:
 4. Leaf margin bipinnatifid, rarely pinnatifid but then with primary lateral veins of anterior division (5–)6–9(–10) per side; leaf blade over 50 cm long, primary lateral lobes (12–)17–35(–55) cm long.....2. **P. bipinnatifidum** (Fig. 12B, p. 633)
 4. Leaf margin undulate or pinnatifid; if pinnatifid then with primary lateral veins of anterior division 3–4(–5) per side:
 5. Plant usually aquatic; leaf margin sinuately lobed (sinuses penetrating less than halfway to midrib), primary lateral lobes of anterior division 1·5–6·5(–14) cm long, usually oblique and turned towards leaf apex, primary lateral veins of anterior division 4–7(–8) per side; female zone of spadix (1·5–)4–5 cm long.....13. **P. undulatum** (Fig. 17A, p. 669)
 5. Plant rupicolous; leaf margin pinnatifid (sinuses penetrating at least halfway to midrib), primary lateral lobes of anterior division 5–17·5 cm long, not oblique, primary lateral veins of anterior division 3–4(–5) per side, female zone of spadix 1·4–3·4 cm long:
 6. Leaf blade (32–)35–50 cm long, primary lateral lobes of anterior division 3·5–6·3(–7·5) cm wide, distance between sinuses and midrib progressively greater towards base of anterior division; fertile male zone of spadix 1·5–2·2 cm diam.....8. **P. saxicolum** (Fig. 15B, p. 654)
 6. Leaf blade 17–33 cm long, primary lateral lobes of anterior division 1·4–3·7(–7·4) cm wide, distance between sinuses and midrib usually becoming progressively less towards base of anterior division; fertile male zone of spadix 0·85–1·3 cm diam.....1. **P. adamantinum** (Fig. 12A, p. 633)
 3. Leaf margin entire or repand, or if sinuately lobed then peduncle 16 cm long or more:
 7. Overall length of adult leaf blade more than 60 cm (sometimes 50–60 cm in *P. solimoesense*, an Amazonian species); petiole apex often minutely rugulose-verruculose:
 8. Species from Eastern Brazil; stamens 6 mm long or more; staminodes more than 1·6 mm wide at apex, less than 2·5 × longer than wide; ovary locules 9–13 per ovary:

9. Leaf blade less than twice as long as wide; spathe outside lacking extrafloral nectaries, inside carmine-magenta at anthesis; central style dome lacking. **10. *P. speciosum*** (Fig. 16A, p. 662)
9. Leaf blade more than twice as long as wide; spathe outside with punctate, pale brown extrafloral nectaries, inside cream-white at anthesis; central style dome present. **15. *P. williamsii*** (Fig. 17C, p. 669)
8. Species from Amazonia; stamens less than 6 mm long; staminodes less than 1.6 mm wide at apex, more than 2.5 × longer than wide; ovary locules 17–34(–47) per ovary:
 10. Cataphylls persistent; primary lateral veins of anterior division of leaf blade (5–)6–7; staminodes 4 times as long as apex width (mean value); ovary locules 17–22; style elongated, distinctly narrower than ovary and lacking an axial canal. **14. *P. venezuelense*** (Fig. 17B, p. 669)
 10. Cataphylls deciduous; primary lateral veins of anterior division of leaf blade (3–)4–5(–6); staminodes 3.4 times as long as apex width (mean value); ovary locules 26–34(–47); style short, as broad as ovary with an axial canal or cavity which is very conspicuous in fruit. **9. *P. solimoesense*** (Fig. 15C, p. 654)
7. Overall length of leaf blade less than 60 cm (never occurring in Amazonia), petiole apex smooth:
 11. Peduncle subequal to twice as long as spathe; plants aquatic, aerial portion of stem unbranched; internodes shorter than prophyll scars:
 12. Leaf blade at least twice as long as broad; style longer than ovary. **5. *P. dardanianum*** (Fig. 14B, p. 646)
 12. Leaf blade much less than twice as long as broad; style shorter than ovary:
 13. Intravaginal squamules abundant, broadly triangular, 3–12 mm long, (1.5–)3–7(–9) mm broad at base; style body as wide as ovary, central style dome present. **3. *P. brasiliense*** (Fig. 12C, p. 633)
 13. Intravaginal squamules few, more narrowly triangular, 1.5–5 mm long, 0.5–2.5 mm broad at base; style body slightly narrower than ovary, central style dome usually lacking:
 14. Primary lateral veins of anterior division of leaf blade 3–5 per side; peduncle (16–)20–46(–55) cm long; spadix 12–17.5 cm long; Argentina, Paraguay, Uruguay, (?)S. Brazil. **11. *P. tweedianum*** (Fig. 16B, p. 662)
 14. Primary lateral veins of anterior division of leaf blade (5–)6–7 per side; peduncle 7.5–17(–22) cm long; spadix 9.2–9.9(–11) cm long; central Brazil. **12. *P. uliginosum*** (Fig. 16C, p. 662)
 11. Peduncle only about one third of spathe length; plant hemi-epiphytic or terrestrial; aerial stem branching frequently; internodes usually longer than prophyll scars. **4. *P. corcovadense*** (Fig. 14A, p. 646)

N.B. Krause (1913) included *P. minarum* Engler in subgen. *Meconostigma* but this was an error. An examination of the type collection (*Regnell* III. 1291 [B! C! F! K! LE! M! NY! P! S! U! US!]) showed that its stamen and staminode morphology are typical of subgen. *Philodendron* and that the long sterile zone typical of *P.* subgen. *Meconostigma* is lacking.

1. *Philodendron adamantinum* Schott, Syn. Aroid. 114 (1856) & Prodr. Syst. Aroid. 299 (1860); Engler in Martius, Fl. Brasil. 3(2): 168 (1878) & in A. & C. De Candolle, Monog. Phanerog. 2: 428 (1879) & in Bot. Jahrb. 26: 556 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 134 (1913); Mayo in Aroideana 1(1): fig. 1, p. 21 (1978). Type: Brazil, Minas Gerais state, on rocks in mountains between Sêrro and Tres Barras, on road to Diamantina, May 1818, *Martius*, Observ. no. 1208 (M! holo.).

STEM: decumbent to erect, up to 1.5 m tall, 2.5 cm diam.; *adventitious roots* extending in all directions to 10 m or more; *internodes* usually only 0.1–0.3 mm long, shorter than prophyll scars, sometimes longer, green, \pm glossy; *prophyll scars* 0.7–1 cm long, resembling internodes, green near stem apex, becoming pale greyish brown below and transversely rugose; *intravaginal squamules* minute, 1 mm long or less, not persistent, narrow, acuminate, in rows of 6–12 on either side and below foliage leaf scars; *foliage leaf scars* 1–2 cm wide, elliptic. LEAF: *prophyll* olivaceous green; *petiole* 12–24(–50) cm long, 0.6 cm diam. at apex, sulcate adaxially with sharply angled margins, rounded abaxially, sheath 2.9–6.7 cm long; *leaf blade* pinnatifid, broadly ovate, subcircular or circular in outline with apex rounded to indented and with cordate base, overall length 17–33 cm, overall width 17–30.5 cm, upper surface dark subglossy green, lower surface paler green and glossy; anterior division 11–21 cm long, 17–30 cm wide, apical lobe equalling or shorter than adjacent primary lateral lobes, oblong to triangular, acute to emarginate, mucronate, *primary lateral lobes* 3–4(–5) per side, length in basal part of division 9–17.5 cm, shorter towards division apex, 1.4–3.7(–7.4) cm wide, linear to oblanceolate in outline, often arcuate either acroscopically or basiscopically, apex acute to rounded, sometimes emarginate, margins mostly entire or repand, basal primary lateral lobes often with few, weakly developed (rarely well-developed), obtuse to rounded (rarely oblong-acute) secondary lobes on either side, main sinuses ending 0.2–2.2 cm from midrib, becoming progressively deeper towards base of division, *primary lateral veins* 3–4(–5) per side, arising at angle of 30–70(–80°) to midrib, slightly paler than blade on both surfaces, sometimes pink-tinged on lower surface near petiole insertion; *posterior divisions* 5–11.5 cm long, 0.3–0.43 \times overall blade length, 8.5–14.7 cm wide, basal ribs denuded for 0.2–1.3 cm, primary acroscopic lobes 1–2(–3), sinuses extending to 0.2–1.4 cm from basal rib, rarely with weak secondary lobes, primary basiscopic lobes 1–2(–4), sinuses extending to 0.5–2.8 cm from basal rib. INFLORESCENCE: *peduncle* 2–5 cm long, 0.5–0.8 cm diam.; *spathe* 6.4–14.4 cm long, 1.5–3.4 cm diam. at middle, decurrent for 1–1.7 cm, green on outer surface, inner surface creamy white; *spadix* 5.5–12.5 cm long overall, fertile male zone 2.8–4.6 cm long, 0.85–1.3 cm diam, often somewhat thicker and slightly longer than sterile male zone, sterile male zone 2.4–4.4 cm long, 0.6–1.4 cm diam., female zone 1.4–3.4 cm long, 1.1–1.6 cm diam. FLOWERS: *stamens* 2.5–4 mm long, 0.3–1 mm diam. at apex, oblong or slightly narrowing towards base, subprismatic; *staminodes* 2.3–3.5 mm long, 0.8–1.3 mm diam. at apex, tapering towards base, subprismatic, 5 per flower; *gynoecium* 1.7–2 mm long, cylindric, ovary c. 2 mm diam., cylindric, *locules* 4–8 per ovary, ovules 3–7 per locule, inserted in lower half of ovary axis, lowermost ovules with short funicles, upper ovules with progressively longer funicles, style body lacking, compitum very deep, penetrating to halfway down ovary

axis, lacking raphide cells around basal region, style crown as wide as ovary and not narrowed basally, style lobes abundantly tanniniferous, central dome lacking, stylar canals lacking, compitum opening directly into locules halfway down ovary axis, stigma covering entire style crown or absent on dorsal area of style lobes, contiguous with adjacent stigmas, tannin hairs lacking. FRUIT: berries (immature) 0.9 cm long, 0.6–0.7 cm diam., oblong; seeds 2.5 mm long, 1–1.3 mm diam., ovoid, raphe and funicle fleshy and arillate, testa variably thickened, sarcotestate at each end of seed, less so in middle, containing oily droplets. Figs. 10C, 12A, Map 2C.

HABITAT. Terrestrial in crevices on exposed sandstone and quartzite outcrops; alt. 790–1300m.

BRAZIL. Minas Gerais: Serra do Espinhaço, c. 12 km NE of Diamantina, road to Medanha, 28 Jan. 1969, *Irwin et al.* 22805 (infl., C! F! K! NY! UB! US!); Diamantina, near Agua Fria, 2 Apr. 1957, *Pereira* 2799 [*Pabst* 3635] (infl., K! RB!); Diamantina, hillside on way to crucifix, 16 Jan. 1963, *Duarte & Barroso* 7905 (infl., HB! RB!); Diamantina, cult. at Sítio Santo Antônio da Bica, Guaratiba, Rio de Janeiro by collector, voucher by S. Mayo, *Burle Marx* PHIL 413 (sterile, K!); mountains between Sêro and Tres Barras on road to Diamantina, May 1818, *Martius*, Observ. no. 1208 (sterile, M! holo.); Rio Jequití, c. 25 km E of Diamantina, 17 Mar. 1970, *Irwin et al.* 27775 (infr., AAU! NY! SEL! UB! US!); c. 24 km SW of Diamantina on road to Gouveia, 16 Jan. 1969, *Irwin et al.* 22120 (infl., C! F! NY! US!); Trinta Reis, road between Sêro and Diamantina, 3 Feb. 1987, *S. Mayo et al.* 707 (K! SPF!); Lapinha, about 18 km N of Sêro on road (MG–2) to Diamantina, 23 Feb. 1968, *Irwin et al.* 20699 (infl., B! F! K! NY! S! UB! UC! US!); between Sêro and Datas, on highway MG–2, 19 Jan. 1972, *Hatschbach et al.* 28908 (infl., K! MBM, US!); between Palmital and Tijucal, 4 Apr. 1957, *Pereira* 2851 [*Pabst* 3687] (infl., HB! RB!); município de Conceição do Mato Dentro, Rio Santo Antônio, road to Sêro, 3 Feb. 1987, *S. Mayo et al.* 704 (K! SPF!).

In the original description, Schott (1856) ascribed the authorship of the species name to Martius, but cited no specimens. In his *Prodromus* of four years later, Schott (1860) gave the authority as ‘Martius. (in Herbario)’ and the following citation (transl.): ‘Brazil. Martius. I have seen dried leaves in the Munich herbarium, the remainder is from Martius’ notes’. Schott had a pencil drawing made by Seboth of these leaves (no. 2638 of the Schott *Icones Aroideae* [W]) which corresponds precisely to the type specimen at the Munich herbarium (M).

The label data of the type specimen states (transl.): ‘Grows on the rocks of mountains near Tejuco, Serro Frio. Province of Minas Gerais. Dr. Martius Brazilian Journey. May. 1208’. Tejuco is an old name for the town of Diamantina (Engler 1878: 168; Spix & Martius 1981, 2: 29), while Serro Frio is the term used in the early nineteenth century for that part of the Serra do Espinhaço mountain range surrounding the town of Diamantina (Spix & Martius 1823–1831, Atlas).

More precise localization of the type collection is given in a manuscript (Martius, ms.) in the Martius archive at the Brussels herbarium (BR). This appears to be a copy of the entries relating to *Araceae* from a 6-volume unpublished manuscript at Munich (M) entitled ‘Plantae in itinere brasiliensi annis 1817–1820 a Car. Frid. Phil. Martio descriptae’, and commonly referred to in botanical literature as the ‘Mart. Observ.’ The latter manu-

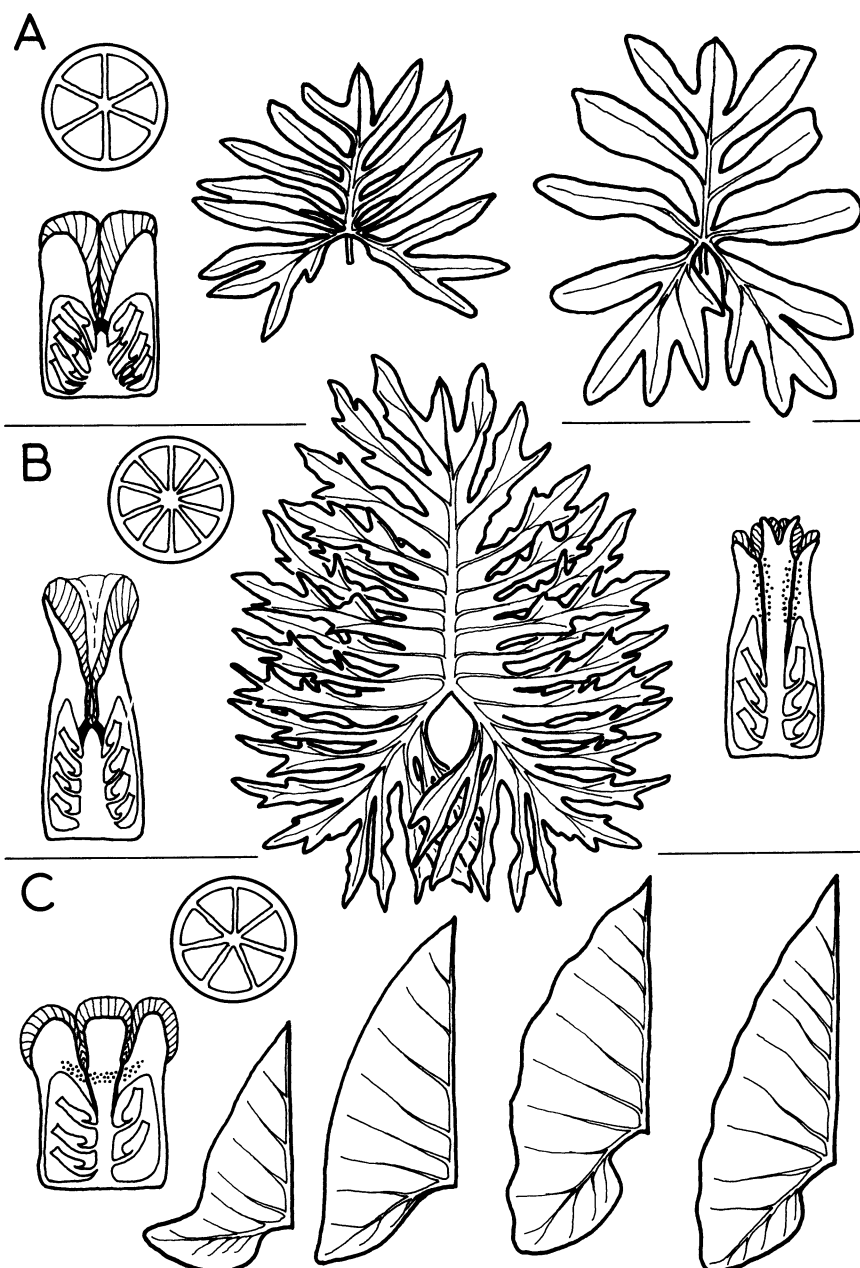


FIG. 12 A–C. *Philodendron* subgen. *Meconostigma*. Leaf blade and gynoeceum (semi-diagrammatic, not to scale); TS of ovary shows approximate mean number of locules; oblique hatching represents stigmatic tissue, thick lines show the course of stylar canals, stippling shows zone of abundant raphide idioblasts. **A** *P. adamantinum*. Left to right: – TS ovary; LS gynoeceum (Harley *et al.* CFCR 6252); leaf blades (Pereira & Pabst 2851; from photo of plant cult. by R. Burle Marx); **B** *P. bipinnatifidum*. Left to right: – LS gynoeceum (Mayo *et al.* 574); TS ovary; leaf blade (from photo of plant cult. by R. Reitz); LS gynoeceum (Goiás, “*P. mello-barretoanum*” form, Burle Marx s.n., Kew spirit no. 44909) – only extreme forms of gynoeceal variation are shown in this figure (see Mayo 1989b for further details); **C** *P. brasiliense*. Left to right: – LS gynoeceum (Usteri 349L); TS ovary; leaf blades (Glaziou 15576; Henschen in Regnell III.1292; Mosén 4399; Davidse & Ramamoorthy 10581).

script consists of Martius's notes on the species of plants he collected during his Brazilian expedition (1817–1820).

In the Brussels manuscript, under no.1208, Martius gives the name 'Philodendron adamantium' and the following locality: 'In saxis Serrae inter Villa de principe et Ramho. Mens. Majo'. 'Ramho' is taken to be a copyist's error for 'Rancho'. In May 1818 Martius was travelling in Minas Gerais northwards along the Serra do Espinhaço. After leaving Vila do Príncipe (today Sêro) on his way to Tejuco (today Diamantina) he and Spix halted at Rancho das Três Barras (today called Três Barras) whilst awaiting permission to enter the so-called Diamond District and thus to proceed to Tejuco, which lay in the centre of this strictly controlled area (Spix & Martius 1981, 2: 26).

The spelling of the specific epithet was changed by Schott (1856) from the manuscript 'adamantium' of Martius to 'adamantinum'. As a result the 'Martius ex Schott' authority previously used is not appropriate.

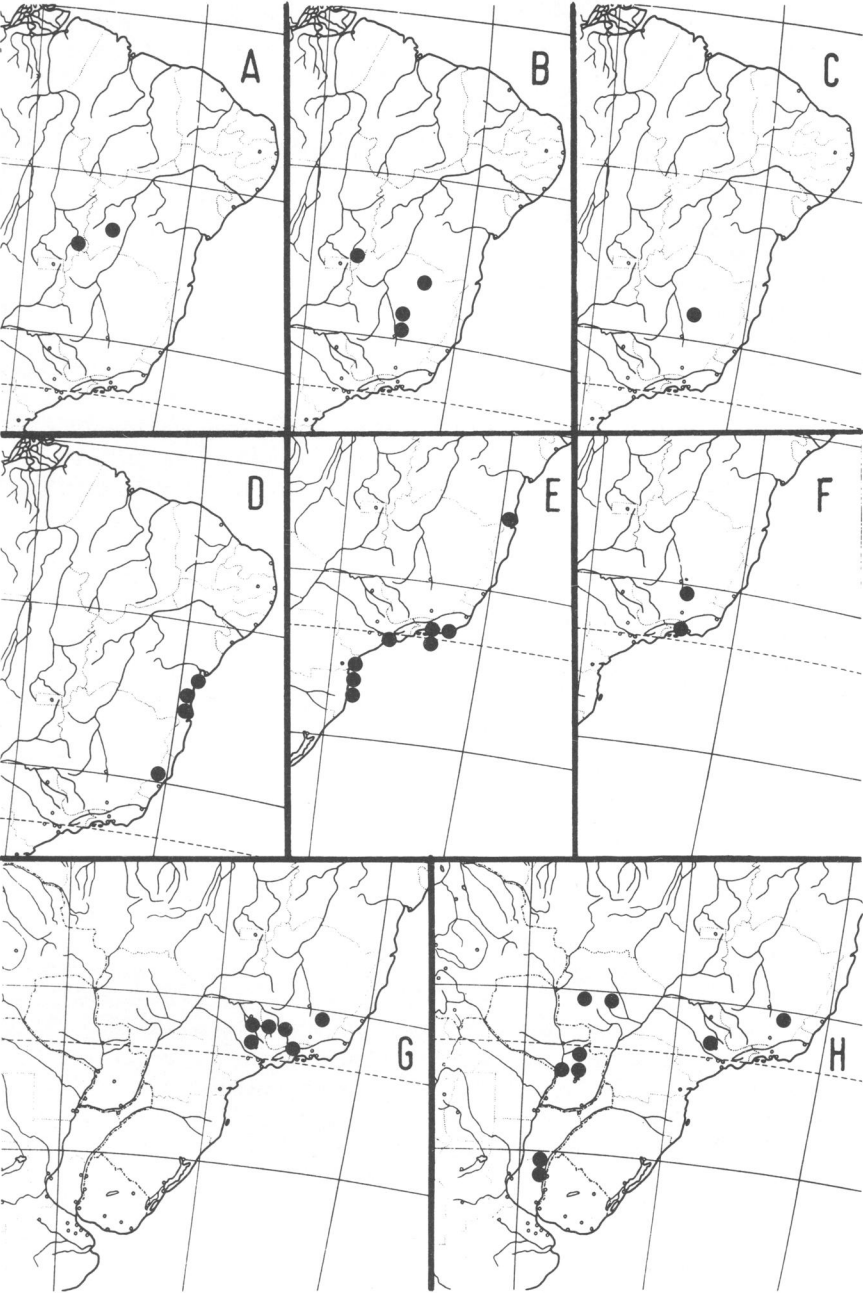
The collection *Lindman in Regnell* A. 1823 1/2 (S) from Paraguay, cited by Engler (1899) and Krause (1913) as *P. adamantinum*, consists of juvenile plants of *P. bipinnatifidum*, as suggested previously by Chodat & Vischer (1920: 340).

2. *Philodendron bipinnatifidum* Schott ex Endlicher, Gen. Pl. 1(3): 237 (1837) [Schott in Wiener Zeitschr. Kunst, Literatur, Theater Mode 1829(3)94: 780 (1829), nom. nud.]; Kunth, Enum. pl. 3: 51 (1841); Schott, Syn. Aroid. 113 (1856) & Prodr. Syst. Aroid. 297 (1860); Engler in Martius, Fl. Bras. 3(2): 168, t.35, 36 (1878) & in A. & C. De Candolle, Monog. Phanerog. 2: 429 (1879); T. & G. Peckolt, Hist. pl. medicin. uteis Brazil 3: 231 (1890); Engler in Bot. Jahrb. 26: 557 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 135 (1913); Decker, Aspect. Biolog. Fl. Bras. 435–441 (1936); Reitz in Sellowia 8: 46 (1958); Barroso in Arquiv. Jard. Bot. Rio de Janeiro 17: 14 (1962); Barbosa in Rodriguesia 26: 319 (1971); Crisci in Rev. Mus. La Plata (Bot.) 11(64): 231 (1971); Crisci & Gancedo in Rev. Mus. La Plata (Bot.) 11(65): 285 (1971); Grau in Lilloa 36(1): 30, fig. 7u (1983); Gottsberger & Amaral in Ber. Deutsch. bot. Gesell. 97: 391 (1984); Croat & Mount in Spichiger, Fl. Paraguay 19 (1988). Type: Plant cultivated at Schoenbrunn Palace Gardens, Vienna, by Schott, originally collected by him in Brazil, probably near Rio de Janeiro; no specimens are known to exist, represented by colour illustrations: – Schott Icones Aroideae nos. 2609, 2610, 2640, 2663–2665 (W; microfiche! in Schott 1984).

[*Arum pinnatifidum* Vellozo, Fl. Flumin. 9: t.110 (1831) & in Arquiv. Mus. Nac. Rio de Janeiro 5: 387 (1881), non Jacq.]

[*Sphinctrostigma bipinnatifidum* Schott ('S. bipinnatifidum') in Schott & Endlicher, Melet. Bot. 19 (1832)]

Philodendron selloum C. Koch in Index sem. hort. reg. bot. berol. 1853, Appendix: 14 [p.4 in reprint] (1854) [in Bot Zeit. 10: 276 (1852), nom. nud.] & in Ann. sci. nat. 4 sér., 1: 341 (1854); Schott, Syn. Aroid. 109 (1856) & Prodr. Syst. Aroid. 298 (1860); Engler in Martius, Fl. Bras. 3(2): 169, t.37 (1878) & in A. & C. De Candolle, Monog. Phanerog. 2: 430 (1879); J.D. Hooker in Bot. Mag. 110: t. 6773 (1884); T. & G. Peckolt, Hist. pl. medicin. uteis Brazil 3: 235 (1890); Engler in Bot. Jahrb. 26: 557 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 134 (1913); Chodat & Vischer in Chodat, Vég. Paraguay 3: 347, figs. 259, 260, 261 (1920);



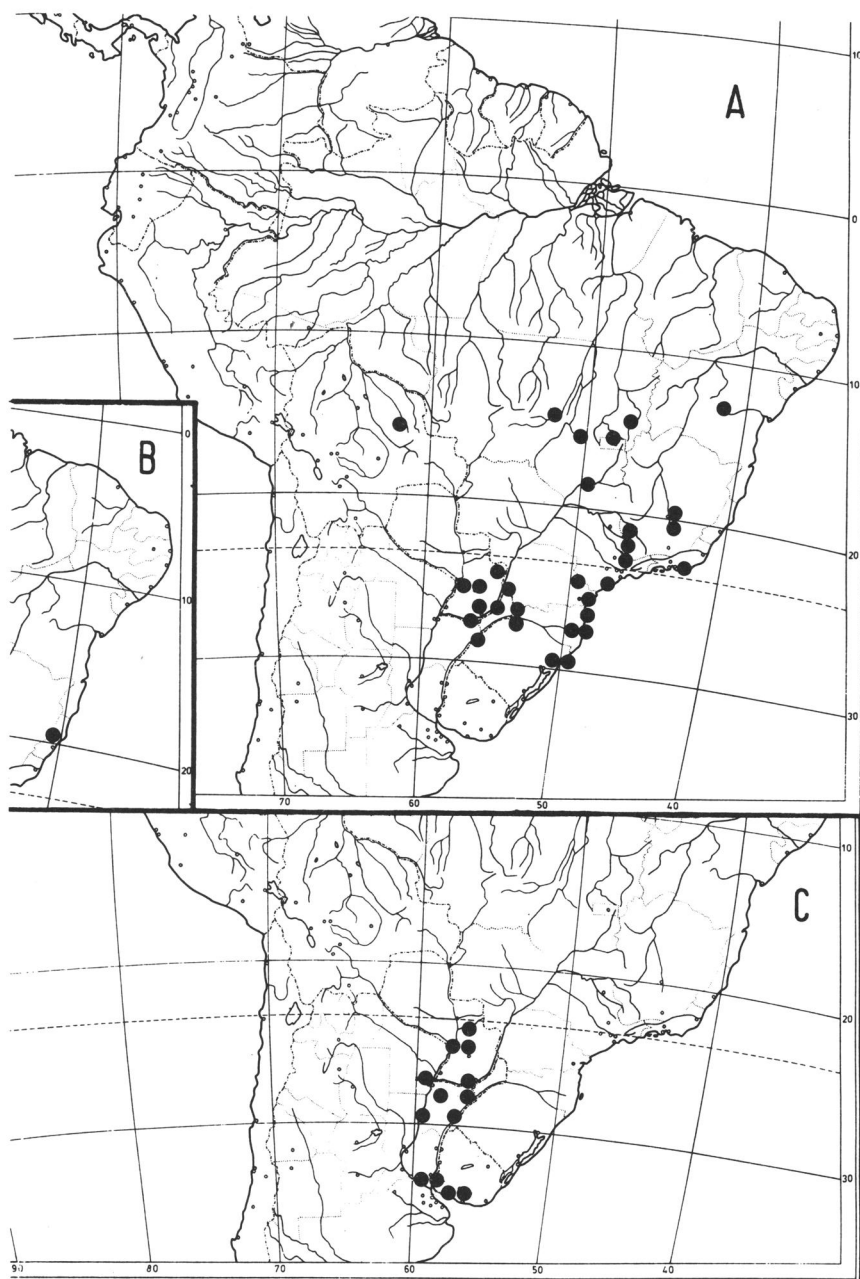
MAP 2. Species ranges in *Philodendron* subgen. *Meconostigma*. **A** *P. dardanianum*; **B** *P. uliginosum*; **C** *P. adamantinum*; **D** *P. williamsii*; **E** *P. corcovadense*; **F** *P. speciosum*; **G** *P. brasiliense*; **H** *P. undulatum*; each spot represents presence of the species within a one-degree square of latitude and longitude.

- Rambo in An. Bot. Herb. Barbosa Rodrigues (Sellowia) 2: 120 (1950); Reitz in Sellowia 8: 43, t.11 (1958); Barroso in Arquiv. Jard. Bot. Rio de Janeiro 17: 13 (1962); Barbosa in Rodriguesia 26: 325 (1971); Gottsberger & Amaral in Ber. Deutsch. bot. Gesell. 97: 391 (1984). Type: Plant cultivated at Berlin Botanic Garden, received from H. Sello who had brought it from England and cultivated it at the Sans Souci Royal garden near Potsdam, *C. Koch* s.n. (B destroyed, K tracing!)
- Philodendron lundii* Warming in Videnskab. Meddelels. Kjöbenhavn 1867 (8–11): 128, t.IV (1867); Engler in Bot. Jahrb. 26: 557 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 135 (1913). Type: Brazil, Minas Gerais, Lagoa Santa, *Warming* s.n. (C! holo.).
- Philodendron bipinnatifidum* Schott ex Endl. var. *lundii* (Warming) Engl. in Martius, Fl. Bras. 3(2): 169 (1878).
- Philodendron sellowii* C. Koch var. *lundii* (Warming) Engl. in Videnskab. Meddelels. Kjöbenhavn 1879–80: 360 (1880).
- ?*Philodendron pygmaeum* Chodat & Vischer in Chodat, Vég. Paraguay 3: 379, fig. 264 (1920). Type: Paraguay, Paraguari, 'Cerro Akahay', 1914, *Chodat & Vischer* R.358 (G not seen, details from Croat & Mount 1988).
- Philodendron mello-barretoanum* G.M. Barroso in Arquiv. Jard. Bot. Rio de Janeiro 15: 94, t.VIII, IX (1957), [Cutak in Missouri Bot. Gard. Bull. 43(7): 110 (1955), nom. nud.]; Barroso in Arquiv. Jard. Bot. Rio de Janeiro 17: 14 (1962); Barbosa in Rodriguesia 26: 323 (1971). Type: Brazil, Goiás, cult. Jardim Botânico do Rio de Janeiro as no. 6579, *R. Burle Marx* s.n. (RB holo!; – RB accession no. 97081).
- Vernacular names: 'Banana do brejo', 'Banana d'Imbe', 'Banana de Imbe', 'Banana de macaco', 'Banana de morcêgo', 'Banana timbó', 'Fruto de macaco', 'Fruto de Imbê', 'Imbê', 'Imbê de comer' (Brazil); 'Banano de monte', 'Guembe', 'Membe' (Argentina, Paraguay).

STEM: erect, decumbent and sprawling or semi-erect, branching sparingly in basal parts, up to 3.5 m tall, 5–13 cm diam.; *adventitious roots* dimorphic in epiphytic plants, anchor roots of smaller diam. attaching plant to host tree, feeder roots of larger diam. connecting stem to soil; *internodes* 1 mm long or less; *prophyll scars* short, up to about 1 cm long; *intravaginal squamules* sometimes absent, up to 20 mm long, 0.5–2.5 mm wide at base, usually triangular and \pm flattened, sometimes rather massive and conic, patent, sparse to densely abundant and persistent; *foliage leaf scars* 4–6 cm long, 3–7 cm wide, circular to transverse-elliptic, paler than rest of stem surface. LEAF: *prophyll* deciduous, up to at least 45 cm long; *petiole* 70–120(–150) cm long, (0.7–)1–1.7 cm diam. at apex, broadly sulcate adaxially with sharply angled margins or flattened or occasionally slightly convex, rounded abaxially, sheath c. 12 cm long on leaves subtending inflorescences; *leaf blade* usually bipinnatifid, either weakly or very strongly so, occasionally pinnatifid, very variable in lobe and sinus shape, broadly cordiform-sagittate in outline, overall length 75–120 cm, overall width 60–120 cm, upper surface glossy dark green, lower surface paler, \pm glossy; *anterior division* 45–83 cm long, (25–)50–100 cm wide at base, apical lobe acute-acuminate to rounded-apiculate, often oblique, longer or shorter than adjacent primary lateral lobes, *primary lateral lobes* (5–)6–9 (–10) per side, basal primary lateral lobes (12–)17–35(–55) cm long, 4–22 cm wide at widest point, outline linear to spatulate, apex \pm triangular with tip acute-acuminate to rounded, margins normally lobed, sometimes very

strongly so, rarely repand or \pm entire, acroscopic secondary lobes (1–)2–5, usually longer and more numerous than basiscopic ones, basiscopic secondary lobes 0–5, the longest (0.8–)3–17 cm long, midveins usually present, main sinuses of basal primary lateral lobes ending 1.5–10 cm from midrib, 0.4–5 cm wide near sinus apex, *primary lateral veins* as many as primary lateral lobes, arising at an angle of 30–90 deg., concolorous with blade on upper surface, whitish-green and often pink- or peach-tinged on lower surface; *posterior divisions* 27–40 cm long, 0.29–0.41 \times overall blade length, 30–37(–60) cm wide, basal ribs denuded for 2–6 cm, primary acroscopic lobes 2–6, the longest 18–35 cm long, usually fewer than primary basiscopic lobes, secondary lobes usually present, primary basiscopic lobes (3–)4–7(–8), longest 9–23 (–37) cm long, secondary lobes rarely developed. INFLORESCENCE: normally solitary, rarely in pairs; *peduncle* 5–10 cm long, (1.5–)2–5 cm diam. at apex, green; *spathe* (12–)16–33 cm long, (2–)3–5.5(–6.5) cm diam. at middle, decurrent for 3–6.5(–8.5) cm, somewhat constricted centrally at anthesis, outer surface of basal half green, maroon-purple or chocolate brown, apical half paler, greener or more yellowish, sometimes with revolute margins when expanded at anthesis, inner surface of spathe entirely creamy white, rarely purple- to rose-tinged in inflorescences which are strongly pigmented on outer surface; *spadix* 15–25(–28.5) cm long overall, fertile male zone (3–)6–8.5 (–9) cm long, (1.5–)2–2.7(–3.2) cm diam., ellipsoid to cylindric, apex acute to rounded, white, sterile male zone longer and thicker than fertile male zone, (5.5–)6.5–11(–14.5) cm long, (1.5–)2–3(–3.2) cm diam. near apex, increasing gradually to (2–)2.5–3.7(–4) cm diam. near base, white, female zone (2.8–)3–5(–5.7) cm long, (1.7–)2–3.3(–4) cm diam., tapering upwards, adnate dorsally to spathe for 1/2 to 3/4 of length. FLOWERS: *stamens* 5–5.5(–6.5) mm long, 0.8–1.2 mm wide at apex, *staminodes* 2–6 mm long, 1–2 mm wide at apex, mostly prismatic in transverse section, cylindric to clavate, truncate at apex, in basal part of sterile zone usually tortuose and longer than the rest; *gynoecium* 3.8–7.5 mm long, ovary 2–3.7 mm diam., cylindric to somewhat barrel-shaped, occasionally with raphide cells in axial region, *locules* (6–)7–13(–15) per ovary, ovules (1–)2–4(–6) per locule, evenly spread on locule axis from base to above middle or even to near apex, style body usually present, as wide as or distinctly narrower than ovary and style crown, sometimes lacking, raphide cells abundant, sparse or absent in axial region around stylar canals, compitum varying from extremely shallow to penetrating deeply into ovary axis, style crown strongly lobed, style lobes tanniniferous or not, central dome varying from absent to very well developed and itself lobed, the lobes naked and projecting beyond stigma hairs, stigma 2–3.8 mm wide, entirely covering style crown lobes or absent from their dorsal sides, contiguous with adjacent stigmas, tannin hairs varying from absent to abundant. FRUIT: *berries* 1.4 cm long, 0.7–0.8 cm wide, \pm cylindric, white or yellow when ripe, with edible, sweet-tasting pulp; *seeds* 3.5–4 mm long, 1.7–1.8 mm diam., subcylindric, slightly broader at micropylar end, either sarcotestate with non-arillate funicle or lacking a sarcotesta and with an arillate funicle and raphe, funicle sometimes bearing a blob of sticky mucilaginous material in ripe seed. Figs. 4A, D, 10A–B, 12B, 13, Map 3A.

HABITAT. Hemi-epiphytic or terrestrial in rainforest, gallery forests, and various seasonal forest types including cerrado; terrestrial or rooted-aquatic in open swampy areas, occasionally rupicolous in open shrubby coastal and



MAP 3. Species ranges in *Philodendron* subgen. *Meconostigma*. A *P. bipinnatifidum*; B *P. sp. A*; C *P. tweedianum*; each spot represents presence of the species within a one-degree square of latitude and longitude.

submontane vegetation, alt. 0–1000m.

ARGENTINA. Prov. Corrientes: *Bonpland* 991 (sterile, P!); Dep. Ituzaingó, Estancia Rincón Chico, 23–24 Oct. 1974, *Tressens et al.* 327 (infl., CTES!); Dep. Santo Tomé, Estancia Garruchos, potrero Curuzu, 7 Feb. 1972, *Krapovickas et al.* 21277 (infr. CTES!). Prov. Misiones: Puerto Helvecia, Sept. 1967, *Schulz* 17865 (sterile, CTES!); Dep. San Martín, Puerto Leoni, Nov. 1967, *Crisci* 81 (infl., K! US!).

BOLIVIA. Dep. Santa Cruz: prov. Ñuflo de Chavez, Ascensión de Guarayos, 26 Apr. 1977, *Krapovickas & Schinini* 31727 (infr., CTES!).

BRAZIL. Goiás: Serra Geral do Paraná, 3 km S of São João da Aliança, 23 Mar. 1973, *Anderson et al.* 7805 (infr., F! NY! US!); Serra dos Pirineus, 75 km N of Corumbá de Goiás on road to Niquelândia, valley of Rio Maranhão, 21 Jan. 1968, *Irwin et al.* 18956 (NY! UB! US!); Goiás Velha, by Rio Mantelgomes, 27 June 1828, *Burchell* 7290 (sterile, K!). Minas Gerais: município de Ituiutaba, Carmo, 30 Aug. 1949, *Macedo* 1914 (infr., UC!); Lagoa Santa, *Warming* s.n. (sterile, C!); Caldas, 26 Dec. 1864, *Regnell* ser. III 1293 (infl., F! K! P! S! US!); Paraná: Jaguariahyba, 29 Nov. 1915, *Dusén* 17386 (infl., F! G! NY! S! US!). Rio Grande do Sul: Município Herval Sêco, road between Palmeira and Redentora after Vila Dois Irmãos, 30 Jan. 1973, *Valls & Irgang* ICN 21637 (infl., CTES! ICN); Faxinal, Torres, 1977, *Baptista* ICN 42294 (sterile, CTES! ICN); Glorinha, Gravataí, 14 Dec. 1949, *Rambo* 44782 (sterile, L! P!). Rio de Janeiro: Serra de Caracol, near Santa Cecília, 25 Dec. 1875, *Mosén* 4398 (infl., K! P! S!); Cabo Frio, Arraial do Cabo, Pontal beach, 13 Aug. 1953, *Segadas-Vianna et al.* Restinga-I 824 (infl., NY! US!). Santa Catarina: município Dionísio Cerqueira, Tracotinga, 20 km W of Rio Capetinga on road to Dionísio Cerqueira, 30 Dec. 1956, *Smith & Reitz* 9633 (infr., US!); município de São Miguel d'Oeste, 40 km SE of Campo Erê, 26 Dec. 1956, *Smith et al.* 9277 (infr., B! US!); município de Balneário de Camboriú, Estaleiro Grande, 1 Feb. 1983, *S. Mayo et al.* 574 (infl., K!); município São José, Angelina, 15 Nov. 1956, *Smith et al.* 7632 (infl., US!); Ilha de Santa Catarina, 1832, *Gaudichaud* 147 (infl., G! K! L! P!); São Paulo: Rio Capivary, 1 Aug. 1827, *Burchell* 4933 (K!); near Benedictine monastery at Santos, 16 Sept. 1826, *Burchell* 3041 (infl., K!); Serra do Mar, SW of Peruibe, Estação Ecológica de Jureia, 9 Feb. 1983, *S. Mayo et al.* 589 (sterile, K!).

PARAGUAY. Dep. Caaguazú, Ayo, Ihú, 12 Dec. 1982, *Schinini* 22984 (infr., CTES! K!); Asunción, Mercado Petirossi, 7 Sept. 1976, *Schinini & Bordas* 13605 (sterile, CTES!); Cordillera de Altos, Dec. 1885–1895, *Hassler* 1729 (infl. fragment, G!); Villarrica, Oct. 1932, *Jorgensen* 4599a (infl., C! F! MO! NY! S! US!).

CULTIVATED. Austria: cult. [as *P. selloum*] Vienna, Schoenbrunn Palace, s.d., *Schott* s.n. (sterile, K!); probably from Schoenbrunn Palace, Vienna, s.d., probably *Schott* s.n. (infl., L!). Brazil: Rio de Janeiro, Barra de Guaratiba, cult. R. Burle Marx at Sítio Santo Antônio da Bica, originally from Goiás, Goiás Velha, voucher by S. Mayo, 14 Feb. 1983, *Burle Marx* BM III (infr., K!); same locality, originally from Goiás, Goiás Velha, voucher by S. Mayo, 14 Feb. 1983, *Burle Marx* BM IV (infl. infr., K!); same locality, originally from Mato Grosso, Xavantina, voucher by S. Mayo, 15 Feb. 1983, *Burle Marx* BM V (sterile, K!); same locality, originally from Minas Gerais, voucher by S. Mayo, 16 Feb. 1983, *Burle Marx* PHIL 3 (sterile, K!); same locality, voucher by S. Mayo, 16 Feb. 1983, *Burle Marx* PHIL 8 (infl., K!); same locality, originally from Goiás, voucher by S. Mayo, 16 Feb. 1983, *Burle*

Marx PHIL 250 (infl., K!); same locality, originally probably from Goiás (*P. mello-barretoanum*), voucher by S. Mayo, 16 Feb. 1983, *Burle Marx* s.n. (infl., K!); cult. Jardim Botânico do Rio de Janeiro, originally from Goiás (*P. mello-barretoanum*), *Burle Marx* s.n. (infl., RB 97081!); São Paulo, Campinas, cult. Instituto Agrônômico, 30 Nov. 1982, *Gibbs* 82/1 (UEC!); unlocalized, *Glaziou* 16498 (sterile, C! K!); cult. São Cristovão, Quinta da Bôa Vista, 1887, *Glaziou* 16499 (sterile, BR! C! G! K! LE!); same locality, 1887, *Glaziou* 17322 (sterile, BR! C! F! G! K! US!); Germany: cult. Berlin, tracing by N. E. Brown of specimen by *Koch* s.n. (infl., K! illustration); cult. Berlin Botanic Garden, originally from Brazil, Minas Gerais, *Engler Araceae* no. 171 (sterile, GH! K! L! LE! M! US!); cult. Univ. Breslau, originally from Brazil, *Engler Araceae* no. 291 (infl., B! K! LE!); United Kingdom: cult. Mr Tillet, Sprowston Lodge, Norwich, voucher of plant illustrated in Bot. Mag. t. 6773, vouchers made Mar. 1873, June 1883, 18 Mar. 1884, by N. E. Brown s.n. (infl., K!); cult. Kew, originally from Glaziou, Rio de Janeiro, voucher 18 Aug. 1887, label no. 33 188/1880, N. E. Brown s.n. (sterile, K!).

Philodendron bipinnatifidum as circumscribed here is a very variable taxon in morphology and colour of leaf and inflorescence. The main unifying character is the bipinnatifid leaf blade, consisting of generally six to nine primary lateral lobes per side in the anterior division, with the main sinuses extending at least three quarters of the distance towards the midrib; however, not all forms are bipinnatifid (Fig. 13A). Like other authors who have studied this species complex in the relatively recent past (Reitz 1958, Crisci 1971) I have taken a broad view of the species. This seems the only practical way of dealing with taxonomic difficulties for which current knowledge does not provide satisfactory solutions. Figures 12B, 13 give an indication of the wide range of leaf lobe shapes and gynoeceal morphology encountered in this study. Relatively few collections are complete enough to permit adequate correlation of vegetative and floral characters and many are of cultivated rather than field-collected plants. Large parts of the range have not yet been sampled adequately (Map 3A). Within the material studied, no clear geographical trends in morphological variation were noted, but this is probably the result of inadequate sampling. It seems probable that geographically discrete forms exist but these will only become recognizable after further study.

The original description of *P. bipinnatifidum* was made by Schott from a collection he brought back to Vienna from Brazil and which presumably came from near Rio de Janeiro city (Mayo 1990); no specimens have survived. Schott's illustrations and manuscript description (Schott 1984) show that his plant had a spathe tube coloured purple-brown externally, a gynoeceum with a well-developed central style dome and the female zone adnate to the spathe for about half its length. Schott considered his plant to be identical to Vellozo's '*Arum pinnatifidum*', also from near Rio de Janeiro.

Philodendron selloum was described by C. Koch from material cultivated at the Berlin Botanic Garden which had been sent by H. Sello, head gardener at Sans Souci, the Imperial Prussian estate at Potsdam, and a colleague and correspondent of Koch. In an article in the Botanische Zeitung which appeared before the first valid description, Koch (1852) noted that his *P. selloum* matched Vellozo's '*Arum pinnatifidum*' and also a Gaudichaud collection in the Berlin herbarium (B) (possibly a duplicate of *Gaudichaud* 147 from Santa Catarina). Koch considered Schott's *P. bipinnatifidum* to be

a different species, stating that both Bouché and Sello, who had visited Schoenbrunn and seen Schott's plant there, agreed with this opinion. Koch concludes somewhat testily that he had some time earlier requested material

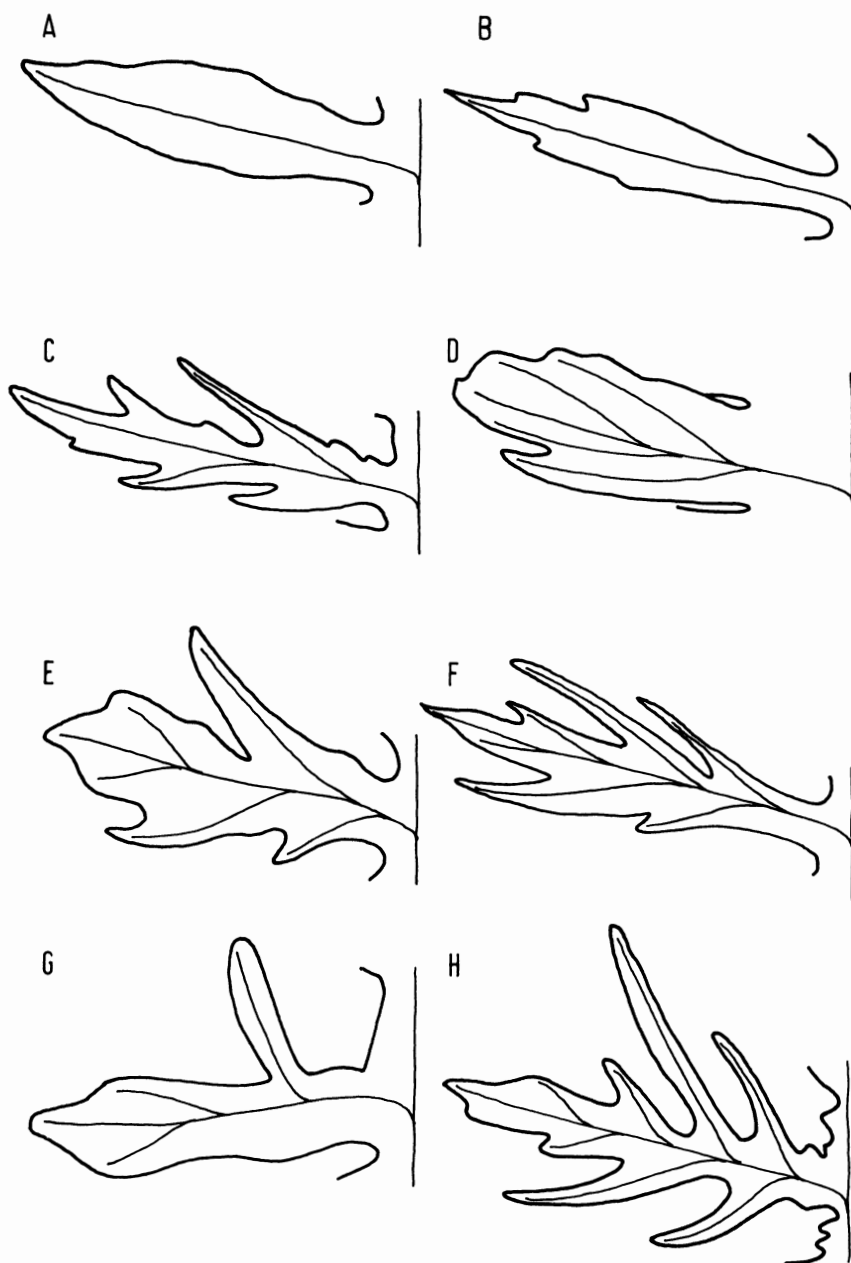


FIG. 13. *Philodendron bipinnatifidum* – Variation in shape of primary lateral lobes near base of anterior division of leaf blade (semi-diagrammatic; not to scale). **A** Irwin *et al.* 18956; **B** S. Mayo *et al.* 589; **C** Glaziou 16499; **D** Burle Marx PHIL 8; **E** Burle Marx PHIL 250; **F** Burle Marx BM V; **G** Anderson *et al.* 7805; **H** Burle Marx PHIL 3.

of *P. bipinnatifidum* from Schoenbrunn, but without result; '... in the meanwhile' Koch continues (transl.): 'I name the plant in Sans Souci *Philodendron selloum* after its owner...' and promised a description once he had seen fertile material. In his later publication (Koch 1854), however, he does not mention inflorescences, and so must have decided to go ahead with publication in any case. He distinguished *P. selloum* by its very short stem, *P. bipinnatifidum* having a thick root-bearing stem.

It seems possible that the confusion that has always existed between *P. bipinnatifidum* and *P. selloum* may thus have its origin in professional rivalry between Koch and Schott. Although, technically speaking, the name had been validly published in 1837, Schott did not publish a complete description of *P. bipinnatifidum* until 1856 (Schott 1856). Koch seems to have decided to go ahead with the publication of a name based on a very dubious distinction, perhaps because of an unwillingness to turn the matter over to Schott and a desire to attach his own name to a very fine ornamental species. There were doubtless real grounds for impatience with Schott, who did not publish a complete species-level treatise of the family (Schott 1860) until only five years before his death during a period when a flood of fascinating new ornamental aroids was entering European horticulture.

The application of these two names has proved difficult for later authors. Schott left useful evidence of *P. bipinnatifidum* in the form of his *Icones Aroideae* (see Schott 1984), but no Schott illustration of this species was published until the microfiche of 1984. He also left plates of *P. selloum*, which may be of the original Sello plant (Schott *Icones Aroideae* nos. 2641, 2642, 2643, 2645, 2738, 2739). These show a plant with a spathe tube coloured green externally, a pistil with a deep style funnel and no central dome, and the female zone of the spadix adnate for over half its length to the spathe. Other than this the only evidence for Koch's type plant is a tracing made by N. E. Brown (K) of a leaf and inflorescence in Koch's herbarium, which was destroyed at Berlin during the Second World War. Engler (1878: 170), who studied Schott's illustrations, distinguished *P. selloum* by its green spathe tube longer than the spathe blade, and the entirely adnate female zone.

More recently Gottsberger & Amaral (1984) have taken up these names and distinguished between the two taxa, giving the characters in some detail, but without making a critical evaluation of the protologues. According to them *P. selloum* has smaller inflorescences (19–22(–35) cm long) which are solitary in each leaf sheath, the spathe is green externally and light yellowish within, and the species occurs on the inland Brazilian plateaux in seasonal climates. *P. bipinnatifidum* on the other hand has larger inflorescences up to 30–40 cm long which are borne in pairs in each leaf sheath, the spathe is purple-red externally and light pink within, and the species occurs in the weakly seasonal coastal and submontane forests of the Atlantic littoral region of Brazil. These authors further support the distinction with descriptions of different patterns of flowering in each taxon. It has not been possible in the present study to confirm that these two groups of characters are consistently correlated within the broader geographical range of the species complex. The observations of Gottsberger & Amaral are nevertheless important in circumscribing two natural forms of the 'wide' species recognized here, and may provide a basis for formally recognized taxa once the broad picture is clearer.

Warming (1867) described as *P. lundii* a form from Minas Gerais with particularly strongly lobed leaves – even the primary basiscopic lobes of the

posterior divisions are strongly pinnatifid. Engler reduced this taxon to a variety first of *P. bipinnatifidum* and then of *P. selloum*, and it was eventually resurrected as a species by Krause (1913).

P. pygmaeum Chodat & Vischer is treated here as probably a depauperate plant of *P. bipinnatifidum*; I have not examined the type specimen.

P. mello-barretoanum G. M. Barroso was collected originally by Roberto Burle Marx in Goiás and differs from other forms mainly in the possession of few but large, conical, broad-based intravaginal squamules. The populations of Goiás, Mato Grosso and Mato Grosso do Sul are particularly poorly known and it would not be surprising if further variation was discovered in those regions.

I have observed (though did not collect) a form of *P. bipinnatifidum* in two locations in central Bahia, a river valley near Livramento do Brumado and on rocks in caatinga between Jussiape and Barra de Estiva. These plants had pinnatifid rather than bipinnatifid leaves. Pio Corrêa (1931) has reported the species from as far north as Alagôas, and this, together with the observations from Bahia, suggests a widespread, if sparse, distribution in north-east Brazil.

P. bipinnatifidum is an important plant in indigenous cultures in Paraguay, northern Argentina and probably Brazil. In a fine paper, Crisci & Gancedo (1971) discuss the use of the roots for binding and the berries as a sweet food and medicinal source. Peckolt & Peckolt (1890) describe its medicinal properties under the names *P. bipinnatifidum* and *P. selloum*.

3. *Philodendron brasiliense* Engler in Martius, Fl. Bras. 3(2); 168 (1878) & in A. & C. De Candolle, Monog. Phanerog. 2: 427 (1879) & in Bot. Jahrb. 26: 554, 555 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 131, fig. 44K–R (1913). Types: Brazil, Minas Gerais state, Caldas, Rio Verde, Feb.–Mar. 1868, *Henschen in Herb. Regnell* III. no. 1292 (S! syn., P! US! isosyn.); Caldas, 4 Dec. 1854, *Lindberg* 578a (inflo. BR! syn.); Caldas, Jan. 1855, *Lindberg* 638 (infl. BR! syn.); Caldas, 1845, *Widgren* s.n. (S! syn.).

P. cymbispathum Engler in Bot. Jahrb. 26: 555 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 131, fig. 44A–J (1913). Type: Brazil, Minas Gerais state, 'locus humidis atque ad ripas fluviorum', *Glaziou* 16497 (B! holo., C! K! LE! P! iso.).

Vernacular names: 'Banana do brejo', 'Banana do chacá'.

STEM: rhizomatous, creeping and \pm submerged basally, erect and aerial apically, 50–60 cm tall, (3–)4–6 cm thick; internodes 1–2 mm long; prophyll scars (2–)4–6 mm long; intravaginal squamules persistent, conspicuous, numerous, 3–12 mm long, (1.5–)3–7(–9) mm broad at base, triangular-flattened, acute-acuminate, in rows along true internodes; foliage leaf scars \pm orbicular on older stem portion. LEAF: petiole 24–50 cm long, usually a little longer than blade, 0.6–1.0 cm diam. at apex; leaf blade sagittate to hastate, margins entire to repand, rarely sinuately lobed, overall length 28–50 cm, overall width 23–42 cm; anterior division 23–38 cm long, 22–41 cm wide, apex acute or subacute, sometimes obtuse, primary lateral veins 5–7(–9) per side, arising at an angle of (30–)40–70(–75) degrees to midrib; posterior divisions (5–)8–11(–13) cm long, 0.2–0.3 \times overall blade length, 12–21(–26) cm wide, basal ribs denuded for (0.8–)1.5–4.5 cm, tip subacute to rounded, primary acroscopic veins 2–3(–4), primary basiscopic veins (2–)3–4(–5). INFLORESCENCE: peduncle 10–20 cm long, 0.5–1.5 cm diam. at apex; spathe

9–13(–15) cm long, approx. (2–)3–4(–5) cm diam. at middle, decurrent for (0·5–)1·5–3 cm, green on outer surface, white on inner surface; *spadix* 7·5–13 cm long overall, fertile male zone 2–4 cm long, 1–1·6(–1·9) cm diam., cylindric, sterile male zone (2·5–)3·3–5·4 cm long, 1–1·6(–2·0) cm diam., cylindric, female zone 1·3–2·5(–4·5) cm long, (0·6–)1–1·8 cm diam. near base, tapering towards apex. FLOWERS: *stamens* 3·5–4 mm long, 0·7–1 mm diam. at apex; *staminodes* 3–4(–4·5) mm long, (0·8–)1–2 mm diam. at apex, subclavate, tapering towards base, apex truncate; *gynoecium* (2·5–)3·3–3·5 mm long, ovary \pm as broad as stigma, cylindric, *locules* (4–)6–8 (–9), ovules (1–)2–3(–5) per locule, axile, inserted from base to just above middle of locule, style body as wide as ovary, raphide cells concentrated around stylar canals, compitum not penetrating ovary, style lobes tanniniferous, central dome present, equalling or shorter than style lobes, stylar canals entering locules subapically, stigma 1·5–2·5 mm broad, tannin hairs present in stigma. FRUIT: not seen. Fig. 12C, Map 2G.

HABITAT. In open grass- and sedge-marshes; alt. 500–1000m. approx.

BRAZIL. Unlocalized, 1885–86, *Glaziou* 16497 (infl., B! C! K! LE! P!). Minas Gerais: Carandaí, 13 Nov. 1953, *Duarte* 3473 (infl., MO!); Caldas, Feb. – Mar. 1868, *Henschen in Herb. Regnell* III. 1292 (infl., P! S! US!); c. 12 km SW of São Gonçalo do Sapucaí, 19 km NE of intersection of highways 381 and 459, 25 Feb. 1976, *Davidse & Ramamoorthy* 10581 (infl., MO!). São Paulo: unlocalized, *Usteri* 349L (K!); S. Simão, km 10, 21 Nov. 1889, *Löfgren* (?) 278 (infl., C!); Serra de Caracol, 5 Jan. 1876, *Mosén* 4399 (infl., P! S!); near Pindamonhangaba, 12 Oct. 1961, *Pereira* 5905 & *Pabst* (RB!); Serra de Bocaina, 1883–84, *Glaziou* 15576 (infl., C! K! LE! P!).

Most of the material collected from the Planalto region of Goiás and Minas Gerais which has been identified in the past as *P. brasiliense* is treated here as a new species, *P. uliginosum* (q.v. for discussion of differences). True *P. brasiliense* is known mainly from nineteenth century collections and occurs in southwestern Minas Gerais and northern São Paulo states. It is most conveniently recognized by the larger and more numerous intravaginal squamules. New collections of this species are needed.

4. *Philodendron corcovadense* Kunth, Enum. pl. 3: 49 (1841); Schott, Syn. Aroid. 94 (1856) & Prodr. Syst. Aroid. 264 (1860); Engler in Martius, Fl. Bras. 3(2): 166 (1878) & in A. & C. De Candolle, Monog. Phanerog. 2: 424 (1879) & in Bot. Jahrb. 26: 555 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 129 (1913). Types: Illustration of 'Arum arborescens' by J. M. C. Vellozo in Flora Fluminensis 9: t.115 (1831) (syn.); Brazil, Rio de Janeiro, Corcovado mountain, *Luschnath* s.n. (KIEL? syn., not seen).

P. melanorrhizum Reitz in Sellowia 9: 50, t.10 (1958). Type: Brazil, Santa Catarina, Itajaí, Luís Alves, Braço Joaquim, 14 Dec. 1954, *Klein* 917 (HBR! holo., NY! UC! US! iso.).

Vernacular name: 'Cipó preto' (Santa Catarina).

STEM: \pm erect, often forming extensive scrambling branching system up to 4m long, or epiphytic plants hanging down with the shoot tips turning upwards, (1·2–)1·5–3 cm thick; *adventitious roots* up to 1·5 cm diam. when mature, becoming woody, black and tuberculate, differentiated into feeding and clasping roots, the latter forming extensive support system in epiphytic

plants; *internodes* 0·1–1·6 cm long, green when young, becoming chestnut or coppery brown and eventually grey with age; *prophyll scars* 0·1–0·2(–0·6) cm long, usually shorter than internodes; *intravaginal squamules* short, 1–3·5(–4) mm long, 1–1·5(–2) mm wide, \pm elliptic in section, not strongly flattened, jutting out and \pm recurved, sharply-pointed, usually arranged in rows near apex of each internode just below prophyll scar but also occurring in middle of internode; *foliage leaf scars* suborbicular to elliptic, sometimes oblique, usually longer than broad, 1·1–2·8 cm long, 0·9–1·5(–2) cm wide. LEAF: *prophyll* 17–30 cm long; *petiole* 22–46 cm long, 0·3–0·5(–0·8) cm diam. at apex, broadly sulcate adaxially with angled margins, sometimes with central ridge, sheath 5–11 cm long; *leaf blade* sagittate, margins repand, overall length 23–40(–50) cm long, overall width 15–24(–35) cm wide, upper surface dark \pm glossy green with paler main veins, lower surface paler with whitish-green sometimes pink-tinged primary lateral veins; *anterior division* 15·5–26(–33) cm long, 13·5–24(–27·5) cm wide, apex usually acute-acuminate, sometimes subacute-cuspidate, *primary lateral veins* 3–5 per side, arising at an angle of (30–)40–85° near base, cross veinlets of finest parallel veins usually very distinct in both dried and fresh material; *posterior divisions* retrorse, introrse or sometimes slightly extrorse, 7·5–14 cm long, 0·3 \times overall blade length, 7·5–13 cm wide, basal ribs denuded proximally on basiscopic side for (0·8–)1·5–4 cm, tip acute to subacute and rounded at extremity, primary acroscopic veins (1–)2–3(–5), primary basiscopic veins 0–3, weaker, basiscopic lamina areas well-developed, usually not overlapping. INFLORESCENCE: *peduncle* shorter than spathe, 3–7(–11) cm long, 0·5–0·8 cm diam. at apex; *spathe* 12–18 cm long, 2–3·5 cm diam. at middle, green on outer surface, uniformly white within, decurrent for 4–8 cm; *spadix* 10–17 cm long, fertile male zone 1·5–3 cm long, 0·8–1·7 cm diam., sterile male zone 3·5–7·5 cm long, 1–2·2 cm diam., \pm cylindric, female zone 1·6–2 cm long or more (dorsally), ca. 1·3–2 cm diam., conspicuously adnate to spathe for up to 5 cm. FLOWERS: *stamens* 4 per flower, 3–5 mm long, 0·6–1 mm wide at apex, tapering to base; *staminodes* 5–6 per flower, 3–5·5 mm long, 0·9–1·3(–1·5) mm diam. at apex, prismatic, truncate at apex, tapering to base; *gynoecium* 3–4 mm long, ovary \pm cylindric, 2–3 mm diam., raphide cells common in upper walls of locules, *locules* 4–6(–12) per ovary, ovules (1–)2–3(–4) per locule, inserted on basal half of axis, style body short, \pm as wide as ovary, with dense axial raphide concentration around stylar canals, compitum not penetrating ovary, central dome lacking or present but weakly developed, stylar canals entering locules subapically or almost halfway down, stigma at anthesis not seen. FRUIT: no ripe fertile berries seen, galled berries yellow-orange at maturity. Figs. 3D, 14A, Map 2E.

HABITAT. Terrestrial in coastal restinga scrub on sandy soils and hemiepiphytic in coastal rainforest and tall restinga forest, alt. 0–450m.

BRAZIL. Bahia: coastal zone, 13 km along road from Una to Ilhéus, 15·13 N, 39·04 W, 23 Jan. 1977, *Harley et al.* 18187 (sterile, CEPEC! K!). Paraná: município de Antonina, Bairro Alto, near Baía de Paranaguá, 4 Feb. 1983, *Hatschbach et al.* 46087 (sterile, K! MBM!); Jacarehy, 2 Sept. 1914, *Jönsson* 918a (sterile, K!). Rio de Janeiro: Copacabana, 24 Nov. 1884, *Glaziou* 15570 (infl., C! G! K! LE! P!); município de Araruama, Zacara, near Brejo do Espinho, 19 Aug. 1982, *Araújo et al.* 5109 (F! GUA, K!); Maricá, near Bambuí, 5 Nov. 1976, *Bogner* 1150 (infl. K! infr. M!); Cabo Frio, Arraial do

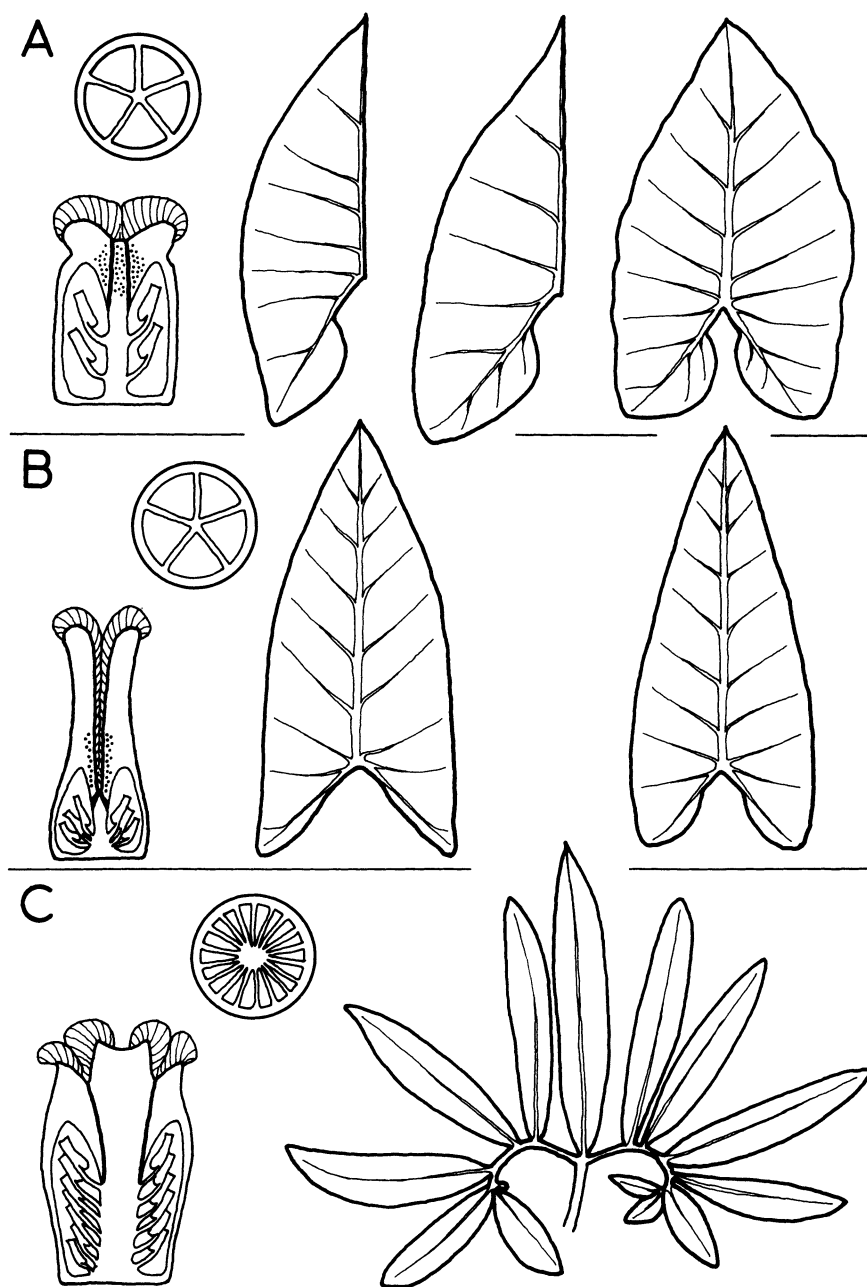


FIG. 14. A–C. *Philodendron* subgen. *Meconostigma*. Leaf blade and gynoceium (semi-diagrammatic, not to scale); TS of ovary shows approximate mean number of locules; oblique hatching represents stigmatic tissue, thick lines show the course of styler canals, stippling shows a zone of abundant raphide idioblasts. A *P. corcovadense*. Left to right: – LS gynoceium (Bogner 1150); TS ovary; leaf blades (Harley et al. 18187; Araujo et al. 5109; from photo of plant cult. by R. Reitz); B *P. dardanianum*. Left to right: – LS gynoceium (Irwin et al. 14570); TS ovary; leaf blades (Irwin et al. 14570; Harley et al. 21963); C *P. goeldii*. Left to right: – LS gynoceium (Lecouflet s.n.); TS ovary; leaf blade (from photo of Burle Marx PHIL 399).

Cabo, Pontal beach, 13 Aug. 1953, *Segadas-Vianna et al.* 833 (NY! R, US!). Santa Catarina: Itajaí, Cunhas, 29 Nov. 1954, *Klein* 845 (infl., infr., HBR! NY!); Itajaí, Luís Alves, 10 Jan. 1956, *Reitz & Klein* 2357 (infl. infr., B! UC! US!); Garuva, Tres Barras, 19 Dec. 1957, *Reitz & Klein* 5771 (infl., B! HBR!). São Paulo: Santos, Buturoca, river banks, 15 Dec. 1874, *Mosén* 3023 (infl., S!).

Kunth cited two elements in the protologue, Vellozo's illustration in 'Flora Fluminensis' (Vellozo 1831 vol. 9: t.115) and a specimen in the herbarium of Lucae collected by Luschnath. Stafleu & Cowan (1981) note that Lucae's herbarium, previously at KIEL, was destroyed. Urban (1906) states that Bernhard Luschnath was a gardener from St. Petersburg who collected with Ludwig Riedel between 1831 and 1833 near Rio de Janeiro, where he created a garden for growing on plants to be sent back to Europe. Schott (1860) seems not to have seen Luschnath's specimen since he cites only collections by Riedel and Widgren:—'Brasiliae provincia Rio de Janeiro. Riedel – v.s. spontan. in Herb. Hort. Petropol. et Holmiensi (a Widgren. collect.)' (Schott 1860). These two specimens still exist and bear Schott's autograph: Riedel's specimen (at LE!) has label data stating 'XV. Rio Janeiro 1832. Aroideae. Riedel'. Widgren's specimen (at S!) has the label data: '762 Caladium hastatum Brasilien. Widgren'. Engler (1879) and Krause (1913), however, both cite a Luschnath collection, corresponding to that cited by Kunth, from the Corcovado mountain, Rio de Janeiro, and cite it as deposited at the Kiel herbarium (KIEL). I have been unable to locate this collection or a duplicate of it.

Widgren 762 is reproduced in a drawing at the Vienna Natural History Museum (Schott Icones no. 2518 [W], see also Schott 1984) which Engler later copied and distributed as 'A. Engler: Araceae No. 70'. Curiously, Engler described it in the accompanying data as the Luschnath collection from the Corcovado Mountain at Rio de Janeiro and does not mention either Schott or Widgren. In the absence of a specimen attributable to Luschnath I cannot find a solution to this conundrum. The illustrations prepared by Schott and Engler match the Widgren specimen exactly and there is no connection between the specimens cited by Schott and Luschnath's syntype other than the fact that Luschnath worked with Riedel. Luschnath and Widgren worked in Brazil at different, non-overlapping periods (Urban 1906). Despite the confusion there is no reason to doubt that all these elements, including Vellozo's illustration, belong to the same species.

Schott identified the illustration Schott Icones Aroideae 2518 and one of a Gaudichaud collection (S.I.A. 2519) as *P. gaudichaudianum* Schott. This name does not appear to have been validly published. Both drawings are clearly of *P. corcovadense*.

The single sterile specimen seen from Bahia (*Harley et al.* 18187) differs from most other collections in having internodes shorter than the prophyll scars – very short internodes may also occur elsewhere in the species range, however, as shown in Fig. 3D in a plant from Paraná. A plant seen by me (but not collected) at Itacaré, Bahia (14·17 S, 38·59 W) had an extensive branching stem system several metres tall and occurred on a forested, rocky marine foreshore within the spray zone; this is a typical habit and habitat for *P. corcovadense*, which in the state of Rio de Janeiro may be found in dune scrub in strongly maritime conditions.

Little morphological difference is apparent between the Rio and Santa Catarina populations. This may be the result of inadequate sampling but on available evidence there seems no reason to maintain *P. melanorrhizum* Reitz as a separate taxon. The southern populations appear to have more numerous and stouter, spiny intravaginal squamules, but this alone seems insufficient as a species distinction.

In Santa Catarina the plant is called 'cipó preto' (black liane) and was employed as cordage for boat-building, among other uses, due to its resistance to decomposition (Reitz 1958).

5. *Philodendron dardanianum* Mayo sp. nov., *P. brasiliensi* Engler affinis sed stylo quam ovarium longiore, infundibulo styli in ovarium penetranti, stylo sine lobo centrali tholiformi, staminodiis crassioribus, squamulis intravaginalibus caulis carentibus, lamina folii angustiore lanceolato-sagittata differt. Typus: Brazil, *Harley et al.* 21963 (holotypus CEPEC! isotypi K! MO! US!).

STEM: decumbent, to 1m tall, up to about 4.5 cm in diam., *internodes* 0.5–9 mm long; *prophyll scars* 4–8 mm long; *intravaginal squamules* lacking; *foliage leaf scars* obliquely and transversely elliptic, 2 cm long, 3 cm wide. LEAF: *prophyll* c. 23 cm long; *petiole* 36–46 cm long, 0.6–0.7 cm diam. at apex, sheath 9–11 cm long; *leaf blade* elongate-sagittate, coriaceous, yellow-green, margins entire, sometimes repand, overall length 39–46 cm long, overall width 16–21 cm; *anterior division* 30–35 cm long, 16–21 cm wide, apex acute to subacute, *primary lateral veins* 5–7 per side, arising at an angle of 40–75° to midrib, paler than blade on upper surface; *posterior divisions* 8–10 cm long, 0.2 × overall blade length, 9–10 cm wide, basal ribs denuded for 2.5–3.5 cm, tip obtuse to rounded, primary acroscopic veins 1–2, primary basiscopic veins lacking. INFLORESCENCE: *peduncle* (8.5–)15.5–21 cm long, 1–2 cm diam. at apex; *spathe* (11–)12.5–16.5 cm long, (1.3–)1.5–3 cm diam., decurrent for 2–3.5 cm, outer surface green to pale green; *spadix* 10–12.5 cm long, fertile male zone 2.8–3.5 cm long, 1.3–1.4 cm diam., ellipsoid, thicker than upper part of sterile zone, sterile male zone 5–5.5 cm long, 1.2–1.4(–1.8) cm diam., subcylindric, thicker at base, female zone 2.5–3 cm long, 1.1–1.5 cm diam. FLOWERS: *stamens* 4 mm long, 1.1–1.4 mm diam. at apex; *staminodes* 3.3–3.8 mm long, 1.9–2.5 mm diam. at apex, shortly and squatly clavate, tapering strongly to base, prismatic, apex ± truncate; *gynoecium* 6–6.5 mm long, ± flask-shaped, ovary 2–3 mm long, 2.5–3 mm diam., ± ventricose, broader than style, *locules* 4–6, ovules 2–3 per locule, inserted in cluster towards locule base, style longer than ovary, c. 4 mm long, compitum very long, penetrating ovary axis usually as far as the upper third but sometimes to halfway down, ridged along its length, raphide cells concentrated around lower half, style crown distinctly lobed, tannin cells only sparsely present in style lobes, central dome lacking, stylar canals short, entering locules about halfway down, stigma 3.5–4 mm diam., covering style lobes, ± lacking tannin hairs. FRUIT: not seen. Fig. 14B, Map 2A.

HABITAT: In riverine marshes (*Harley et al.* 21963) or among rocks (*Irwin et al.* 14570), river margins in cerrado; alt. 580–800m.

BRAZIL. Bahia: 37 km N from Correntina on road to Inhaúmas, 13.07 S, 44.47 W, 29 Apr. 1980, *Harley et al.* 21963 (infl., CEPEC! K! MO! US!).

Goiás: Rio da Prata, vicinity of Posse, 14°00 S, 46°00 W, 9 Apr. 1966, *Irwin et al.* 14570 (NY! S! US!).

This species is named for Professor Dárdano de Andrade Lima in memory of his great contribution to Brazilian botany, especially of the northeastern region of the country.

So far, this species is known only from the watershed separating the drainage of the Rio São Francisco from that of the Amazon Basin and which forms the border between Bahia and Goiás states. Its affinities lie with *P. uliginosum* (q.v.) and *P. brasiliense* but the leaf blade is relatively longer than broad and the style greatly elongated. Indeed, the gynoeceum resembles that of *P. williamsii* but for the lack of a central dome. Other diagnostic features of *P. dardanianum* are the short, thick staminodes, the absence of intravaginal squamules on mature stems and the long narrow leaves in which the posterior divisions have only a weakly-developed area of lamina on the basiscopic side.

6. *Philodendron goeldii* G. M. Barroso in Arquiv. Jard. Bot. Rio de Janeiro 15: 95, t.10 (1957); Mayo & Barroso in Aroideana 2(3): 91 (1979); Madison in Aroideana 2(3): 77, fig. 14 (1979). Type: Brazil, Manaus, Flores (várzea), 30 Sept. 1903, *Goeldi* (MG 3879!).

['Oambé-címa' Spruce in Hooker's Journ. Bot. 5: 247 (1853)].

Thamatophyllum spruceanum Schott in Bonplandia 7(3): 31 (1859) & Prodr. Syst. Aroid. 581 (1860); Engler in Martius, Fl. Bras. 3(2): 215 (1878) & in A. & C. De Candolle, Monog. Phanerog. 2: 636 (1879); J. D. Hooker in Bentham & J. D. Hooker, Gen. Pl. 3(3): 973 (1883); Engler in Engler & Prantl, Nat. Pflanzenfam. II.3: 135 (1887); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 137 (1913); Bunting in Rev. Fac. Agron. (Maracay) 10: 271 (1980). Type: Brazil [inundated forest in angle between Rio Negro and Solimões, 1851], 'Oambé cima', *Spruce* 120 (Museum no., K! holo.).

Philodendron spruceanum (Schott) G. M. Barroso in Arquiv. Jard. Bot. Rio de Janeiro 17: 14 (1962), comb. invalid., non. G. S. Bunting (1975).

Vernacular names: 'Oambé-címa', 'Tschuma', 'Cipó imbé', 'Corona de neron', 'Philoscheff' (US horticulture), 'Cipó ambé', 'Crown of Nero' (US horticulture).

STEM: erect or hanging, sometimes tortuose, up to 8 m long, 2.5–7 cm diam., woody-fibrous, cut stem and roots exuding viscous resin which turns yellow-orange; *adventitious roots* very long in epiphytic plants, hanging down to ground, up to 1 cm diam., sparingly branched; *internodes* 0.1–8 cm long, dark green, smooth; *prophyll scars* 0.1–1 cm long, paler and usually much shorter than internodes; *intravaginal squamules* usually lacking, few when present, c. 4 mm long, 3 mm wide at base, flattened-triangular, acuminate, not persisting; *foliage leaf scars* transverse-elliptic, or suborbicular to elliptic, situated at apical end of internode, 2.5–3.2 cm long, 2–4 cm wide, pale grey to whitish. LEAF: *prophyll* 20–40 cm long, yellow-green; *petiole* 36–140 cm long, apex densely and minutely rugulose-verruculose, 0.5–1.1 cm diam., basally transverse-elliptic to terete in cross-section, with broadly triangular adaxial ridge, dull green, sheath 4.5–20 cm long; *leaf blade* pedately compound, transverse-elliptic to reniform in outline, overall length up to 62 cm, overall width to 80 cm; *leaflets* 10–20, pendent, sessile or rarely shortly petiolulate, borne on a pair of retrorse rachises, widely separated centrally,

becoming progressively more crowded laterally, upper surface dark glossy green, lower surface paler and dull, venation concolorous with blade, leaflet midrib excurrent into an apiculum only in central leaflet, no primary lateral veins present, cross veinlets of finest parallel veins sometimes distinct in dried material, *central leaflet* as long as or shorter than adjacent lateral leaflets, 18–50 cm long, 5–10 cm wide, oblong-elliptic, acuminate, base acute to rounded, *first lateral leaflets* inserted 3·5–6·5 cm from central leaflet, up to 50 cm long, 11 cm wide, acuminate to acute, otherwise as central leaflet, *outermost lateral leaflets* progressively smaller. INFLORESCENCE: 1 per leaf axil, rarely 2 and then the second inflorescence subtended by a 2-keeled prophyll; *peduncle* shorter than spathe, (2·5–)3·5–7(–10) cm long, 1–2·5 cm diam. at apex; *spathe* 11·5–24(–30) cm long, (2–)3–5(–6) cm diam. at middle, \pm cylindric, decurrent for 2–6 cm, outer surface glossy green with scattered, frequent to numerous, paler punctate extrafloral nectaries, inner surface glossy cream, resin secretion more abundant in lower half; *spadix* 11·5–20 cm long, fertile male zone 2–4(–5) cm long, 1·2–1·9 cm diam., thickest at base, conic, acute-acuminate at apex, sterile male zone 4·5–10 cm long, 1·4–2·8 cm diam., subcylindric, slightly thicker towards base, female zone 2·5–6·5 cm long, (1·3–)2–2·5 cm diam., apical portion cylindric or tapering to apex. FLOWERS: *stamens* 3–4 per flower, (2–)3·5–5 mm long, 0·5–1 mm wide at apex, tapering to base; *staminodes* 3–5·5 mm long, lowermost longer and distinctly stipitate, (0·5–)0·8–1·3 mm wide and truncate at apex, cylindric-prismatic; *gynoecium* 5–6 mm long, ovary subcylindric, 3·5–4 mm diam., tapering to base, septa with scattered raphide cells, *locules* 10–26, ovules 4–13 per locule, with abundant raphide cells at micropylar end, inserted on axile placenta extending to apex or apical third of locule, style body lacking raphide cell concentration around stylar canals, compitum a \pm shallow, circular channel not penetrating far into style body, shallowly ridged on outer face, style crown weakly lobed, style lobes short, spreading widely, central dome overtopping style crown, with irregularly lobed raised margin, often with shallow central pit, stylar canals long, entering locules subapically or in upper third, stigma 3–4·5 mm wide, stigma hairs covering inner face of compitum and margins but not centre of central dome, tannin hairs numerous. FRUIT: *berry* 1·5–2 cm long, 1–1·3 cm diam., \pm cylindric, rounded at apex, greenish-white when ripe; *seed* 3·5–4·5 mm long, 1·2–2·5 mm diam., subcylindric, often tapering slightly at one end, raphe forming prominent, fleshy aril along one side of seed, filled with oily droplets, testa with numerous raphide cells at micropylar end, micropyle umbonulate. Fig. 14C, Map 4B.

HABITAT. Terrestrial with very abbreviated internodes or climbing and hemi-epiphytic with longer internodes; in permanently flooded (igapó) forest, seasonally flooded (várzea) forest, terra firme forest, Amazonian 'caatinga' (somewhat stunted, xeromorphic forests on nutrient-poor soils, especially white sand), or closed secondary forest by roadsides, common on river margins both as terrestrial and epiphytic plants; alt. 30–400m.

BRAZIL. Acre: Cruzeiro do Sul, Estrada Alemanha, 8 May 1971, *Maas et al.* P12810 (infr., F! K! M! NY! S! U! US!). Amazonas: Alto Rio Negro, paraná Arirarrá, 160 km upriver from Barcelos, 13 Oct. 1978, *Madison et al.* PFE 192 (INPA! SEL! as 6192); road from Manaus to Caracaraí, km 22, 11 Nov. 1966, *Prance et al.* 3093 (infl., NY! US!); Manaus, Rio Negro, road to Aleixo, 12 Aug. – 1 Sept. 1936, *Krukoff* 8037 (sterile, A! F! GH! K! MO! NY!);

Pará: município Tucuruí, banks of Rio Tocantins, 1–5 km upriver from Represa Tucuruí, 3°45'S, 49°40'W, 22 March 1980, *Plowman et al.* 9911 (sterile, MO! NY!). Roraima: Rio Xeriuini, 17 Apr. 1974, *Pires et al.* 14026 (infl., US!).

COLOMBIA. Guainia: c. 30 km S of San Carlos do Rio Negro (Venez.) and San Felipe (Colomb.), by Isla Cigarrón, 1°44'N, 67°02'W, 3 Feb. 1980, *Liesner & Clark* 9022 (infl., MO!).

FRENCH GUIANA. Montagne de Kaw, \pm 3 km after junction with road to crique Gabrielle, Feb. 1978, *Blanc* 243 (sterile, CAY!); Route du Brésil, \pm 2 km after bridge over riv. Comté, 18 March 1977, *Poncy* 94 (sterile, MO!); Saül, Tracé ORSTOM La Fumée-La Douana, 5 March 1977, *de Granville* 2808 (sterile, CAY!).

PERU. Loreto: Maynas, Depto. Iquitos, Zungaro Cocha road, near Shushuna ravine, 30 Mar. 1981, *Rimachi* Y. 5566 (infl., MO!); Maynas, Iquitos district, vicinity of Santo Tomás, along Rio Nanay, 3°45'S, 73°22'W, 11 Nov. 1980, *Croat* 51248 (ripe infr., MO!); Maynas, Sanagal, right bank of the Rio Itaya, 1 hour downstream from Iquitos, near Yanayaco, 4°10'S, 73°23'W, 9 Aug. 1980, *Vásquez et al.* 415 (infl., MO!).

VENEZUELA. Territorio Federal Amazonas: Depto. Atapabo, banks of Caño Yagua (RH tributary of Rio Orinoco) between Chipital and Boca Caño Yagua, 3°31'N, 66°44'W, 19 Jan. 1979, *Huber* 3142 (infl., M! MO! NY!); Caño de Cholo, 16 km NE of San Carlos de Rio Negro, 4 km SW of Solano, 1°56'N, 66°58'W, 29 Jan. 1980, *Liesner* 8885 (inflo., MO! NY!); Rio Yatua between Cerro Araucaua and Piedra Catipán, 1°35'N, 66°25'W, 10 Apr. 1970, *Steyermark & Bunting* 102505 (infl., infr., MO! NY! U! US!).

CULTIVATED. Brazil: Cult. R. Burle Marx, Sítio Santo Antônio da Bica, Barra de Guaratiba, Rio de Janeiro state, voucher by S. Mayo, 16 Feb. 1983, *Burle Marx* PHIL 399 (infl., K!).

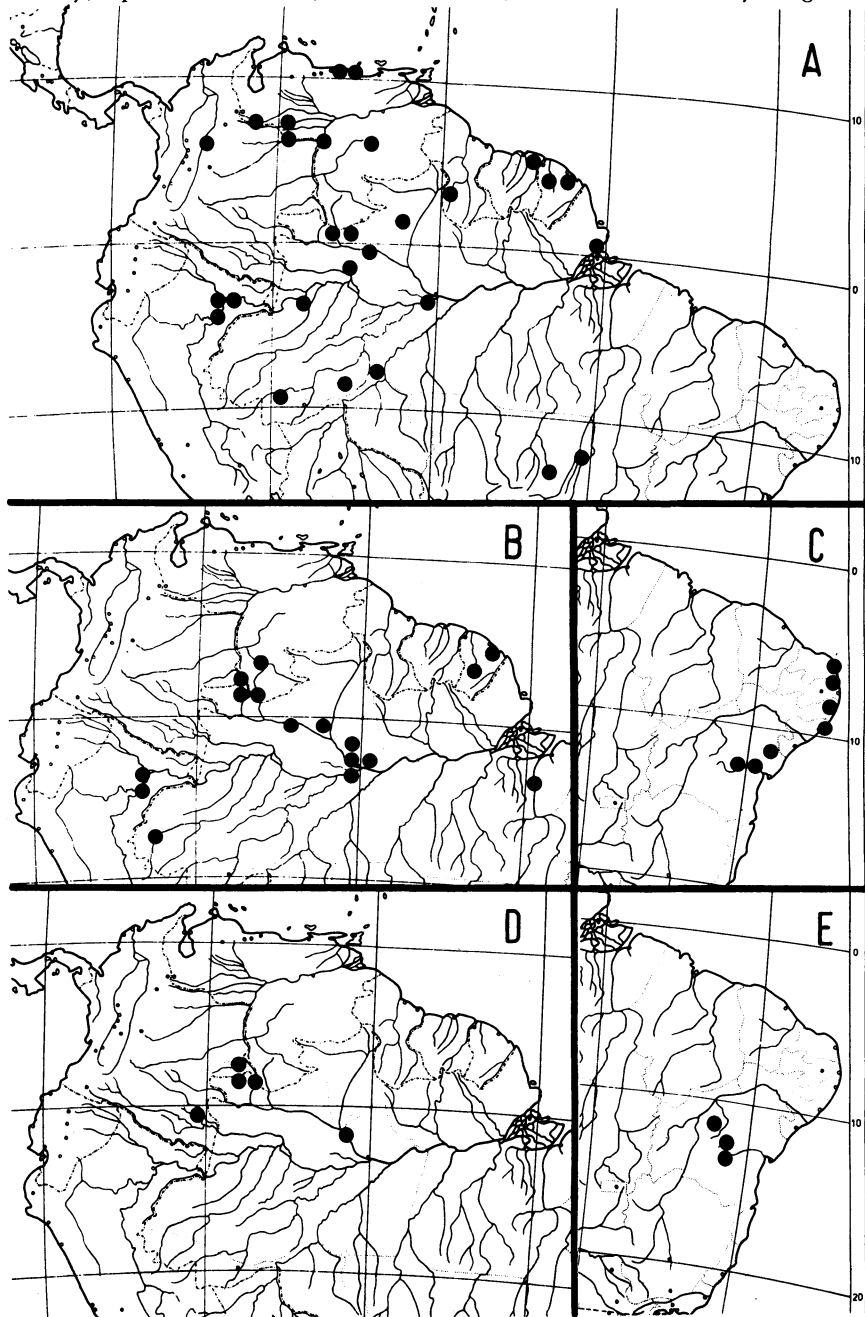
The similarities between *P. goeldii* and *P. leal-costae* are discussed under the latter species. *P. goeldii* seems unique in possessing resin canals within the stamens (Mayo 1986). The gynoeceal morphology is similar to that of *P. solimoesense*, another Amazonian species which, however, is rather different in vegetative morphology. The two latter species share the following gynoeceal characters; very high numbers of locules, massive central dome with a central pit, a circular, shallow, channel-like compitum and relatively high numbers of ovules per locule.

The species was first described by Schott (1859) as *Thaumatophyllum spruceanum*, from a collection by Richard Spruce near Manaus in Brazil. A detailed account of the history of this name and the reasons for its exclusion from *Philodendron* by earlier authors is given by Mayo & Barroso (1979). Barroso (1962) made the new combination *Philodendron spruceanum* (Schott) G. M. Barroso, but invalidly according to Article 33.2 of the Code (Greuter et al. 1988). G. S. Bunting (1975) later published a quite different new species, *P. spruceanum* Bunting, based on the type *Steyermark & Bunting* 102665, thus preoccupying the combination in *Philodendron*.

7. *Philodendron leal-costae* Mayo & G. M. Barroso in *Aroideana* 2(3): 82, figs. 1–5 (1979); Fonseca Vaz, Andreata & Guedes in *Anais* 34 Congr. Nac. Bot. (Porto Alegre – RS – Brazil) 2: 229, figs. 1–2 (1984); Mayo in *Anais* 34 Congr. Nac. Bot. (Porto Alegre – RS – Brazil) 2: 222, fig. 5 (1984). Type: Brazil, Bahia state, Serra do Jatobá, Nossa Senhora dos Milagres,

Morro do Couro, 12°54S, 39°52W, 6 March 1977, *Harley et al.* 19428 (infl. infr., CEPEC! holo., K! M! MO! NY! P! RB! SEL! US! iso.).

STEM: erect to decumbent and scrambling over other plants, branching basally, up to 150 cm tall, 1–2 cm diam.; *adventitious roots* very long and



MAP 4. Species ranges in *Philodendron* subgen. *Meconostigma*. A *P. solimoesense*; B *P. goeldii*; C *P. leal-costae*; D *P. venezuelense*; E *P. saxicolum*; each spot represents presence of the species within a one-degree square of latitude and longitude.

growing rapidly in all directions, extending and ramifying within leaf sheaths of neighbouring bromeliads or in shaded litter, yellowish-brown, 0.4 cm diam; *internodes* 3–7 cm long, smooth and grey except for apical few yellow-green internodes, bearing acuminate, recurved lateral buds, often situated halfway along internode; *prophyll scars* 0.1–0.3 cm long, inconspicuous; *intravaginal squamules* lacking; *foliage leaf scars* 1–1.5 cm long, inconspicuous, suborbicular, not markedly different in colour from internode epidermis. LEAF: *prophyll* 13–22 cm long, green linear-triangular, deciduous; *petiole* 12–22 cm long, 0.4 cm diam. at apex, longer than central leaflet, convex above with narrowly keeled margins, rounded below, sheath 3.5–4 cm long; *leaf blade* pedately compound, subcircular to transverse-elliptic in outline, overall length up to about 32 cm, overall width up to about 32 cm, divided to base; *leaflets* (5–)8–11, sessile, central one distant from nearest laterals, lateral ones progressively more crowded towards extremities of rachises and held spirally and suberect, upper surface dark \pm glossy green, lower surface paler, no primary lateral veins present, cross veinlets of finest parallel veins fine-reticulate on lower surface in dried material, *central leaflet* 10–17 cm long, 2–6 cm wide, oblong-elliptic, acute to obtuse, midrib excurrent into apiculum (only in central leaflet), base subacute to rounded, *first lateral leaflets* inserted 0.7–2 cm from central leaflet, midrib evanescent before reaching non-apiculate apex, *outer lateral leaflets* progressively smaller towards extremities of rachises. INFLORESCENCE: *peduncle* 2.5–4.5 cm long, 1.5 cm diam. at apex; *spathe* 8–15 cm long, 3 cm diam. at middle, larger in fruit, ovoid-cylindric, decurrent for 1.5 cm, outer surface green with white-membranous margins, sparsely covered with brown punctate extrafloral nectaries, inner surface whitish cream; *spadix* 10.5–13 cm long, fertile male zone 3.7–4 cm long, 1.1 cm diam., \pm cylindric, acute at apex, sterile male zone 5.5–5.8 cm long, 1.2–1.4 cm diam., subcylindric, slightly thicker towards base, female zone 1–1.5 cm long, 1 cm diam. FLOWERS: *stamens* 2.75 mm long, 0.7 \times 1.8 mm wide at apex, slightly tapering to base, stomial grooves extending almost to apex, no resin canals in connective; *staminodes* 4–6 per flower, 2–2.5 mm long, 1.7–2.3 mm wide at apex, \pm prismatic in transverse section, flattened at apex, broadly clavate-obovate with narrow stipitate base; *gynoeceum* 3 mm long, compressed-cylindric, ovary subcylindric, 2 mm diam., upper walls with frequent raphides, *locules* 3–4, ovules 1–2 per locule, inserted on axile placenta in basal third of locule, style body lacking, compitum penetrating ovary \pm to level of entry into locules, surrounded by raphide concentration, 3–4 lobed in cross-section, style crown equal in width to ovary, broadly and shallowly 3–4 lobed, style lobes densely tanniniferous, central dome lacking, stylar canals very short to lacking, stigma contiguous with neighbouring stigmas, pale yellow, \pm lacking tannin hairs. FRUIT: *berry* 0.8–1 cm long, 0.7–1.1 cm diam., compressed-subcylindric, scarlet when ripe, few-seeded; *seed* 4–6 mm long, 3–4 mm diam., ovoid to stout-cylindric, peach pink, outer integument forming sarcotesta rich in oily droplets, many raphides forming a layer in inner integument at boundary with endosperm, especially at micropylar end, embryo lageniform, 3 mm long, 1 mm diam. Figs. 1B, 7, 8D, 10D, 15A, Map 4C.

HABITAT. Terrestrial on rock outcrops in semi-arid thorn scrub ('caatinga') or in coastal scrub forest on sand ('restinga'), usually (?always) in association with populations of Bromeliaceae; alt. 0–600m approx.

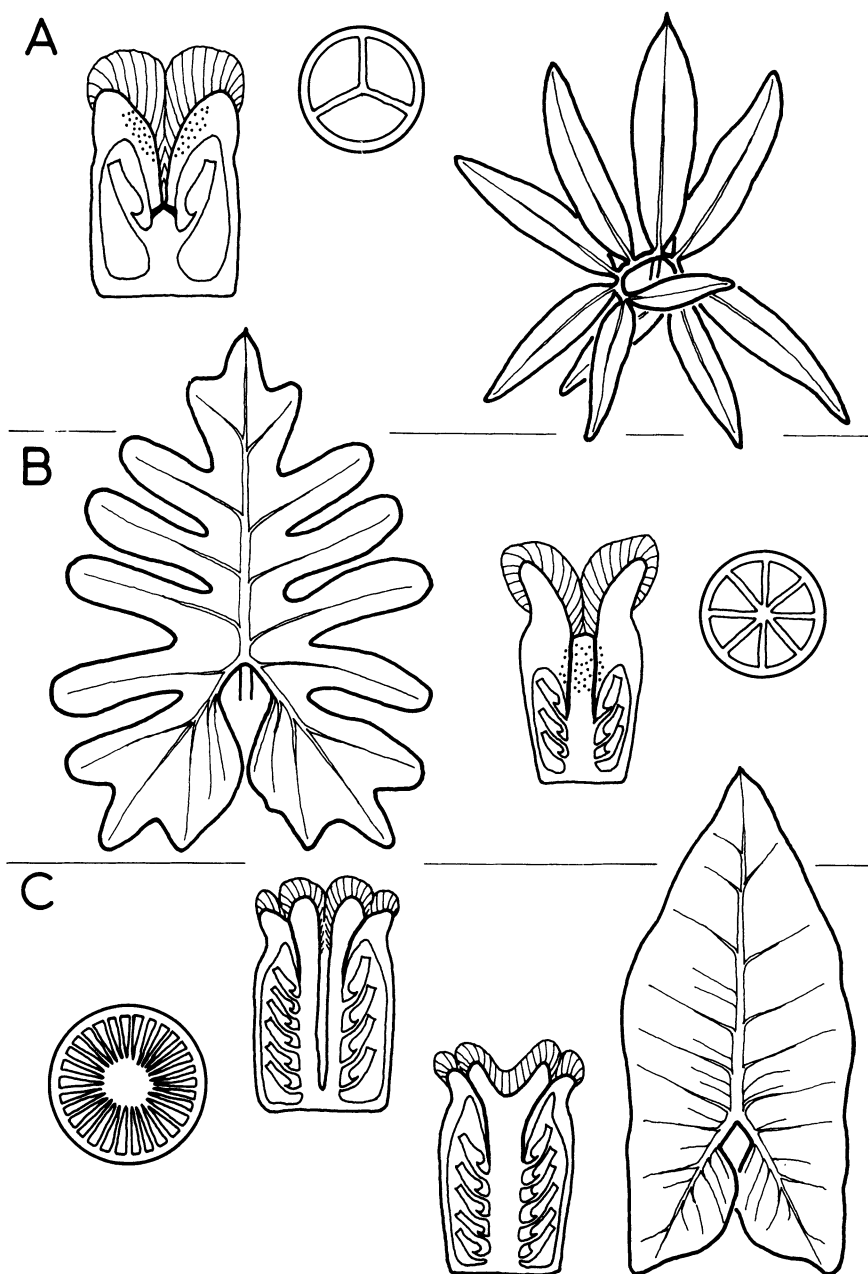


FIG. 15. A–C. *Philodendron* subgen. *Meconostigma*. Leaf blade and gynoeceum (semi-diagrammatic, not to scale); TS of ovary shows approximate mean number of locules; oblique hatching represents stigmatic tissue, thick lines show the course of stylar canals, stippling shows a zone of abundant raphide idioblasts. A *P. leal-costae*. Left to right: – LS gynoeceum (Harley et al. 19428); TS ovary; leaf blade (Harley et al. 19428); B *P. saxicolum*. Left to right: – leaf blade (Pereira 2083); LS gynoeceum (Lewis et al. CFR 7028); TS ovary; C *P. solimoense*. Left to right: – TS ovary; LS gynoeceum (Burle Marx PHIL 430, Croat 18207); leaf blade (from photo of Burle Marx PHIL 430).

BRAZIL. Alagôas: município de Marechal Deodoro, Massagueira, 30 Jan. 1982, *Fonseca Vaz* 347 (RB); Barra de São Miguel, 19 Oct. 1982, *Ramalho Campêlo et al.* 2014 (sterile, K! RB). Bahia: Aporá, BA405 highway, 11°33'S, 38°07'W, 17 Feb. 1978, *Orlandi* 154 (RB, RBR); near Milagres, 1974, *Barroso* s.n. (RB); 211 km SW of Tanquinho, highway BR 116, 31 Mar. 1976, *Davidse et al.* 11669 (ripe infr., B! K! MO! SEL! US!); Serra do Jatobá, Nossa Senhora dos Milagres, Morro do Couro, 12°54'S, 39°52'W, 6 Mar. 1977, *Harley et al.* 19428 (infl. infr., type, CEPEC! K! M! MO! NY! P! RB! SEL! US!); BR 116 highway, 3 km N of Milagres, 16 Jul. 1982, *Hatschbach* 45073 (sterile, K! MBM); município de Iaçú, near Lajedo Alto, 21 Jun. 1983, *Bautista* s.n. (photos only, K!). Paraíba: Areia, sertão, 28 Mar. 1947, *Moraes Vasconcellos* 2971 (infr., US!). Pernambuco: Camocim de São Felix, sítio Palmeira, 10 Feb. 1967, *Andrade Lima* 67–4915 (IPA! RB).

CULTIVATED. Brazil: originally from Milagres, Bahia state, coll. and cult. R. Burle Marx, Sítio Santo Antônio da Bica, Barra de Guaratiba, Rio de Janeiro state, voucher by S. Mayo, 15 Feb. 1983, *Burle Marx* BM IX (sterile, K!).

Philodendron leal-costae is remarkable for its association in the natural habitat with populations of terrestrial *Bromeliaceae*; it extends its root system into the leaf sheaths of the bromeliads. *Fonseca Vaz et al.* (1984) cite records for this species in Northeast Brazil which considerably extend its range from the Bahian locality whence it was first described. They include two records for the state of Rio Grande do Norte (Estremóz and Natal) reported to them by L. Emygdio de Mello Filho – no specimens are cited for these records however. They also give a first identification of an associated bromeliad, *Hohenbergia stellata* Schultz. f. All wild plants so far observed in the natural habitat grow in dry conditions, either in restinga or in caatinga vegetation. However, *Fonseca Vaz et al.* (1984) note that the plants cultivated by R. Burle Marx near Rio de Janeiro do not depend on *Bromeliaceae* for root attachment. The relationship between *P. leal-costae* and *Bromeliaceae* populations may thus depend on the prevailing climatic conditions, being necessary only in semi-arid regions. In cultivation at Kew, *P. leal-costae* roots were observed to grow in air extremely quickly compared to other species, suggesting some degree of physiological adaptation for rapid growth.

The physical association with *Bromeliaceae* is probably maintained, at least partly, by the more successful germination of seeds which fall into bromeliad leaf sheaths. I observed seedlings growing thus at Milagres, Bahia.

P. leal-costae closely resembles *P. goeldii* in some characters, in particular the common possession of pedately compound leaves, relatively well-developed internodes, and endothelial thickenings in the stamens (French 1985, Mayo 1986). There are, however, notable differences. The ecology of *P. leal-costae* is very distinctive; it appears to be capable of withstanding a greater degree of aridity than any other species of *P.* subgen. *Meconostigma*. Important morphological differences are the few ovary locules, small number of ovules per locule and lack of separate stylar canals; the seeds are exceptionally large with a well-developed sarcotesta.

The ovary locules of a flowering spadix from the type collection contained numerous minute spindle-shaped bodies adhering to the mucilaginous layer of the ovules and funicle. These are probably the larvae or eggs of a parasitic hymenopteran, laid in a late-flowering inflorescence (see Section 6). Ripe

infructescences with abundant ungalled seed were collected at the same time in March (also by *Davidse et al.* 11669) and the seed later germinated readily.

8. *P. saxicolum* *Krause* in Engler, *Das Pflanzenreich* 60 (IV. 23Db): 133 (1913); Mayo in *Aroideana* 1(1); 7, fig. 5 (1978). Type: Brazil, Bahia state, Serra do Sincorá, Nov. 1906, *E. Ule* 7568 (holotype B!, isotype L!).

[*'P. sp. near saxicolum'* Mayo in *Aroideana* 1(1); 9, fig. 6 (1978)].

STEM: erect, decumbent or spreading, branching near base, 0.6–3 m tall or more, up to 4.5 cm diam., forming extensive shoot system in larger plants; *adventitious roots* numerous, spreading widely in all directions, light rusty brown and smooth when young, soon becoming corky, rugose and eventually silvery-grey with age, 0.5–1.3 cm diam., *internodes* 0.5–1 mm long; *prophyll scars* 0.5–7 mm long, becoming pale silvery grey almost immediately after prophyll abscission, paler than true internodes; *intravaginal squamules* minute, 0.5–1 mm long, 0.4–0.8 mm broad, triangular or dentate or erose, only visible on newly exposed internodes, not persistent; *foliage leaf scars* 1–2 cm long, 2.5–3 cm wide, transverse-ovate-elliptic, pale grey. LEAF: *prophyll* about 16 cm long, 3.7 cm diam. at base; *petiole* (20–)36–44 (–58) cm long, 0.7 cm diam. at apex, sulcate adaxially with sharply angled margins, sometimes convex or flattened, rounded abaxially, light somewhat glaucous green, sheath (1–)2.2–9 cm long; *leaf blade* pinnatifid, \pm pendent from suberect to spreading petioles, broadly cordiform-sagittate in outline, overall length (32–)35–50 cm, overall width (23–)31–38 cm, upper surface dark green and usually strongly bluish-glaucous, lower surface paler, dull and less strongly glaucous; *anterior division* (20–)21.5–26.5 cm long, 30–38 cm wide, apical lobe subtriangular, usually oblique, acute to obtuse, cuspidate, *primary lateral lobes* 3–4 (–5) per side, basal primary lateral lobes (3.5–)5–13 cm long, 3.5–6.3 (–7.5) cm wide, becoming shorter towards apex of division, usually oblong, sometimes triangular or oblanceolate, rarely short and broadly triangular, with obtuse, rounded, or \pm emarginate tips, rarely subtruncate or deeply notched, lobe margins entire, occasionally repand, main sinuses penetrating progressively less deeply towards base of division, *primary lateral veins* 3–4 (–5) per side, arising at an angle of 20–90 (–100°) to midrib, yellowish green on upper surface, cream yellow on lower surface; *posterior divisions* 11–20 cm long, 0.3–0.48 \times overall blade length, (11–)12.5–18 cm wide, denuded proximally on basiscopic side for (2.5–)2.8–4.5 cm, primary acroscopic lobes 1–2 (–3), primary basiscopic lobes (1–)2–3, normally weak, short. INFLORESCENCE: *peduncle* 6–8.5 cm long, 2.1–2.4 cm diam. at apex, dull glaucous green; *spathe* 9–16 cm long, 3.2–4.8 cm diam. in middle, decurrent for 1–3.3 cm, outer surface dull, pale to mid-green, glaucous, margins whitish, inner surface \pm glossy, yellowish-white; *spadix* 10.5–14.3 cm long overall, fertile male zone 3.5–4.7 cm long, 1.5–2.2 cm diam., cream to white, sterile male zone 4–6 cm long, 1.8–2.6 cm diam., thicker and longer than male zone, cream to white, female zone 1.5–3.2 cm long, 1.4–2.3 cm diam., tapering upwards. FLOWERS: *stamens* 4.5–5.2 mm long, 0.5–0.9 mm diam. at apex; *staminodes* 5.3–7.6 mm long, 0.8–2 mm diam. at apex, prismatic and truncate towards apex of zone, terete and rounded apically towards base of zone; *gynoecium* 3.5–5.7 mm long, ovary 1.6–2.7 mm diam., cylindric, *locules* 6–11, ovules 2–4 per locule, inserted on locule axis one above the other from base to above middle, evenly spread,

style body slightly narrower than ovary or style crown, axial region around stylar canals densely filled with raphide cells, compitum strongly ridged, not penetrating ovary, style crown deeply lobed, style lobes \pm erect, densely tanniniferous, central dome lacking or very weakly developed, stigma 2.2–2.9 (–3.5) mm diam., \pm lacking on dorsal side of style lobes, contiguous with adjacent stigmas, translucent pale yellow at anthesis, tannin hairs lacking. FRUIT: *berry* many-seeded, 1 cm long, 0.5–0.6 cm diam., cylindric; *seed* 2.5–4.5 mm long, 1.4–2.4 mm diam., oblong-ovoid, sometimes galled, testa sarcotestate surrounding inner body and containing oily droplets, raphide cells numerous in inner integument. Figs. 8C, 15B, Map 4E.

HABITAT. Terrestrial on exposed conglomerate sandstone outcrops; alt. 400–1000 m.

BRAZIL. Bahia: Serra do Açuruá, São Inácio, 0.5 km S of town, Pedra da Mulher, c. 11.07S, 42.44W, 25 Feb. 1977, *Harley et al.* 19038A (sterile, CEPEC! K! US!); Serra do Brejão, c. 14 km NW of Lençóis, 12.27S, 41.27W, 22 May 1980, *Harley et al.* 22404 (infl., CEPEC! K! SPF! US!); road between Andaraí and Mucugê, near the Rio Paraguaçu, 21 July 1981, *Pirani et al.* CFCR 1626 [SPF 18498] (infr., K! SPF!); 5 km S of Andaraí on road to Mucugê by bridge over Rio Paraguaçu, 12.50S, 41.19W, 12 Feb. 1977, *Harley et al.* 18593 (infl., AAU! CEPEC! K! M! MO! NY! SEL! SPF! U! US!); by Rio Cumbuca, 3 km N of Mucugê on the Andaraí road, 13.00S, 41.23W, 5 Feb. 1974, *Harley et al.* 16004 (infl., CEPEC! K! NY! U!); vicinity of Mucugê, 15 June 1984, *Hatschbach & Kummrow* 47918 (infr., K! MBM); 3 km S of Mucugê on road to Jussiape, 13.00S, 41.24W, 26 Jul. 1979, *Mori et al.* 12648 (infr., CEPEC K!); 'Serra do Sincorá', probably a few km WSW of Novo Acre, near Riacho Vendinha, Nov. 1906, *Ule* 7568 (infl., B holol. L iso!; F! GH! NY! photos).

There is some doubt as to the precise itinerary followed by Ernst Ule, the collector of the type specimen, in October–November 1906 when he travelled from Maracás to the Serra do Sincorá and back. Harms (1916:163) states that in September 1906 he travelled from Cachoeira and São Felix (near Salvador) to Tamburi and thence to Maracás. In October he travelled about 30 km south-west to Caldeirão and from there to the Serra do Sincorá, returning in November by the same route to Salvador. Ule himself described the caatinga and campo rupestre vegetation of the areas around Maracás and Caldeirão (Ule 1908a, 1908b), but gave no details of his collecting localities in the Serra do Sincorá. The latter name is today usually applied generally to the whole of the southeastern massif of the Chapada Diamantina, stretching from Lençóis in the north down to Ituaçu in the south. However, Ule evidently could not have visited a very extensive part of this region since he wrote (Ule 1908b) 'I had discovered a mountain range in the Serra do Sincorá where the rocks were abundantly overgrown with tree-like *Vellozias*. Unfortunately I did not take any photographs there because of the lack of time.'

A clue to the whereabouts of this locality has been provided by Susyn Andrews in her study of Bahian *Aquifoliaceae* (Andrews 1989). A specimen of *Ilex* collected by Ule bears the label data 'Serra da Vendinha, Sincorá, 1100 m.' Modern maps of the area (SUDENE 1976) record a Riacho [stream] Vendinha about 3–4 km WSW of Novo Acre and a little further west an area of high ground rising to over 1000 m., beyond which lies the settlement of Sincorá Velho. It seems likely that this may be very near the type locality of

P. saxicolum, and is incidentally the southernmost site yet recorded for the species.

A very small and isolated population exists near the town of São Inácio in the more arid region of the Serra do Açuruá (*Harley et al* 19038A), well to the north of the main distribution area of *P. saxicolum*. This plant was discussed by Mayo (1978) under the name '*P. sp. near saxicolum*'. No inflorescences were found when the population was seen and only vegetative vouchers exist. In comparison to the populations further south the leaves are smaller, more acutely tipped and have more deeply cut primary lateral lobes. The glaucous colour of the leaf so characteristic of the species in the Serra do Sincorá is also lacking here. In other respects, however, this northern population agrees with typical *P. saxicolum* in vegetative morphology. The local inhabitants of this former diamond-mining district use the roots, when hollowed out, for storing diamonds. Only a single plant was known in the neighbourhood and possibly the São Inácio plant represents a last remnant of a more extensive range during earlier more mesic conditions (see section 10).

9. *P. solimoesense* A. C. Smith in J. Arn. Arb. 20: 289 (1939); Bunting in Rev. Fac. Agron. (Maracay) 10: 246 (1980). Type: Brazil, Amazonas state, Rio Solimões, municipality of São Paulo de Olivença, basin of Creek Belem, Oct. – Dec. 1936, *Krukoff* 8861 (infr., holotype NY! isotype F!).

[*P. 'williamsii* – *speciosum* complex' Madison in Aroideana 2(3): figs. 2–6 (1979)].

STEM: climbing or hanging with erect tip in epiphytic plants, erect to prostrate in terrestrial plants, 1–6 m long, 4–7(–15) cm diam.; *adventitious roots* hanging down to ground, 1.5 cm diam., tuberculate-aculeate with corky, grey, lenticellate bark; *internodes* 0.1–0.3 cm long; *prophyll scars* 0.1–1(–1.5) cm long, paler and longer than internodes; *intravaginal squamules* usually numerous, occasionally lacking, 2–7 mm long, 1–2 mm wide at base, triangular-acuminate, usually \pm flattened, patent, whitish, crowded together in dense rows on internodes, wearing off on older part of stem; *foliage leaf scars* transverse-elliptic to suborbicular, 2.5–3.5 cm long, 2.5–3 cm wide, whitish-grey. LEAF: *prophyll* c. 25 cm long, green or purple, deciduous; *petiole* 50–100(–114) cm long, apex 0.6–1.3 cm diam., often rugulose, adaxially flattened or with broad central ridge, margins \pm sharply angled, sheath 6–13 cm long; *leaf blade* sagittate, margins repand, overall length 50–94 cm, overall width (23.5–)27–48 cm, upper surface dark green, lower surface paler, dull or glossy on both surfaces; *anterior division* 30–67 cm long, (23.5–)27–40(–48) cm wide, apex obliquely acute-acuminate, more rarely subacute to obtuse and cuspidate, *primary lateral veins* (3–)4–5(–6) per side, arising at angle of (50–)55–90°, slightly paler than blade on upper surface, concolorous on lower surface, cross veinlets between finest parallel veins sometimes distinct in dried material; *posterior divisions* retrorse, sometimes slightly extrorse, 17–27(–30) cm long, 0.25–0.33(–0.42) \times overall blade length, 12–24 cm wide, basal ribs denuded for (1.7–)3.5–5.5(–7.5) cm, tip usually acute, more rarely subacute or obtuse, rounded at extremity, primary acroscopic veins (1–)2–3(–4), very rarely up to 8, primary basisopic veins (0–)1–7, weaker, basisopic lamina area variable, usually moderately developed. INFLORESCENCE: *peduncle* (2–)4.5–12(–13.5) cm long, 1.5–2(–3) cm diam. at apex, tapering to base, green; *spathe* 13–31 cm long, 2.5–4.5(–5.5) cm

diam. at middle, larger in fruit, \pm cylindric, outer surface glossy light green, becoming yellow with ripening of berries, with punctate, non-pigmented extrafloral nectaries especially near apex, inner surface creamy white throughout, decurrent for 2.5–4 cm; *spadix* 10.5–28 cm long, fertile male zone 3.5–7.5(–10) cm long, 1.3–2.2 cm diam., ellipsoid, more rarely subcylindric or clavate, acute, sterile male zone 5–8.5(–10) cm long, (0.9–)1.2–2.6(–2.9) cm diam., subcylindric, tapering slightly to apex, female zone (2.5–)3.5–6.5(–7) cm long, 1.4–2.4 cm diam. FLOWERS: *stamens* 3–5.5 mm long, 0.5–0.9 mm diam. at apex; *staminodes* 3–5.5 mm long, (0.7–)1–1.5 mm diam. at apex, at base of zone longer stouter apically with convex apex, becoming less clavate, more prismatic and apically truncate towards apex of zone; *gynoeceum* (3–)4–6 mm long, ovary cylindric or slightly tapering to base, 4.5–5 mm diam., *locules* 26–34(–47) per ovary, ovules 4–5 per locule, inserted from base to apex, evenly spaced, style body as wide as or slightly wider than ovary, lacking raphide cells, compitum shallow, not penetrating ovary, forming a circular channel, style crown weakly lobed, tissue abundantly tanniniferous, with abundant druses, central dome equalling style crown, broad and massive, with deep (sometimes shallow) axial canal which may descend almost to base of ovary axis, and is conspicuous in fruit and post-anthesis flowers, stilar canals entering locules subapically, stigma (3–)3.5–4(–5.5) mm broad, contiguous with neighbouring stigmas, tannin hairs numerous. FRUIT: ripe infructescence ca. 12 cm long, 4–4.5 cm diam.; *berry* white, orange or red (fide different collectors) with sweet fermenting odour, compressed-subcylindric, 1–1.3 cm long, 1–1.3 cm diam., style crown persistent as circular channel around axial cavity; *seed* ovoid-ellipsoid, 1.7–2 mm long, 0.8–1.2 mm diam., raphe and funicle arillate, enlarged with oily contents but not enclosing seed, testa not sarcotestate. Fig. 15C, Map 4A.

HABITAT. Hemi-epiphyte, often high-climbing, in terra firme or flooded blackwater (igapó) forests or riverine and lacustrine gallery forests, also terrestrial and then erect or prostrate on sandy soils; alt. 0–250 m.

BRAZIL. Acre: Rio Yaco basin, near mouth of Rio Macuahán, 9.20S, 69.00W, 9 Aug. 1933, *Krukoff* 5383 (A! K! MICH! NY! S! U! US!). Amapá: coastal region, Rio Pereira, km 108 on road to Amapá, 13 Jul. 1962, *Murça Pires & Cavalcante* 52176 (sterile, K! NY! S!). Amazonas: Rio Negro between Ilha Uabetuba and Ilha da Silva, 14 Oct. 1971, *Prance et al.* 15249 (infr., INPA! K! NY! U! US!); Rio Japurá, município de Marañ, near Marañ, Lago Marañ, 1.51S, 65.36W, 4–5 Dec. 1982, *Plowman et al.* 12248 (infr., K! MO!); Rio Madeira basin, município de Humaita, between Rio Livramento and Rio Ipixuna, 11 Nov. 1934, *Krukoff* 7160 (infr., A! K!); Mato Grosso: 12.49S, 51.46W, 51 km S of Base Camp of Royal Society/Royal Geog. Soc. expedition 1967–1969, Córrego do Gato, 17 Oct. 1968, *Harley et al.* 10705 (infr., K!); 12.54S, 51.52W, Xavantina–São Felix road, 4 km N of Royal Society/Royal Geog. Soc. expedition 1967–1969 Base camp, 24 Apr. 1968, *Ratter et al.* R 1159 (K!); near Garapú, 13.12S, 52.34W, 30 Sept. 1964, *Irwin & Soderstrom* 6469 (NY! US!).

COLOMBIA. Santander: Magdalena valley, Campo Capote, 30 km E of Carare, 29 Sept. 1977, *Gentry & Renteria* 20052 (infr., MO!).

FRENCH GUIANA. NW of Sinnamary, W from km 105, St. Elie track, 5.30N, 48.00W, 6 July 1982, *Croat* 53844 (sterile, CAY! MO!); Montsinerny, track to Risque, 12 Dec. 1979, *Cremers* 6058 (infr., CAY! K!).

GUYANA. Rupununi River, Oct. 1889, *Jenman* 5767 (sterile, K!).

PERU. Loreto: 12 km SW of Iquitos, 16 Jul. 1972, *Croat* 18207 (infr., F! K! MO!); Maynas, Quisto Cocha, 20 Jun. 1970, *McDaniel* 13584 (infl. infr., MO!); Requena, km 6 on road from Jenaro Herrera to Angamos, 4°55'S, 73°45'W, 12 March 1984, *Spichiger et al.* 1500 (MO!).

SURINAM. Mapure Creek, headwaters, Nov. 1953, *Bergamini* GS/72 (NY!).

VENEZUELA. Territorio Federal Amazonas: 1°35'N, 66°10'W, rio Yatua, foot of Cerro Araucaua, 15 Apr. 1970, *Steyermark & Bunting* 102655 (infl., MO! NY! U!); 3 May 1968, *Steyermark & Bunting* 103273 (MO! NY!). Apure: Distrito Muñoz, Caño Guaritico, Hato Matadero, 5 km W of Bruzual-San Fernando highway, 7°45'N, 69°17'W, 4 Mar. 1978, *Davidse & González* 14835 (infl. infr., F! MO! US!); Distrito Pedro Camejo, 7·5 km WNW of Paso de Cinaruco, S bank of rio Cinaruco, 6°33'N, 67°35'W, 3 May 1977, *Davidse & González* 12601 (MO!); Distrito Pedro Camejo, rio Capanaparo between Caños La Pica and La Guardia, 14 airline km SW of Urañon, 6°54'N, 67°18'W, 6–7 May 1977, *Davidse & González* 12810 (infr., MO!). Bolivar: rio Parguaza, 1–3 km above El Carmen, 50 km above river mouth, 26 Dec. 1955, *Wurdack & Monachino* 40958 (infl., NY! US!); rio Caura, 2–8 km S of Salto Para (Las Pavas), 6°13'N, 64°28'W, 10 May 1982, *Morillo & Liesner* 9122 (MO!). Miranda: hills between Carenero and Chirimena, 4–5 km N of Carenero, 22 Nov. 1969, *Steyermark & Bunting* 102325 (sterile, MO! NY! US!); 10 airline km W of Cúpira, Cerros del Bachillar, above Quebrada Corozal, S of Santa Cruz, 10°9'N, 65–48'W, 20–26 Mar. 1978, *Steyermark & Davidse* 116870 (F! MO! NY!).

This widespread species appears to be the only member of *P.* subgen. *Meconostigma* which occurs north of the Amazon basin, both in coastal Venezuela and in the Rio Magdalena valley of Colombia. The gynoecial and seed morphology are strikingly similar to those of *P. goeldii*, and the locule number is the highest of any species of the *Araceae*.

10. *P. speciosum* Schott ex Endlicher, Gen. Pl. 1(3): 237 (1837); Kunth, Enum. Pl. 3: 51 (1841); Schott, Syn. Aroid. 91 (1856) & Icon. Aroid. t.6–10 (1857) & Prodr. Syst. Aroid. 262 (1860); Engler in Martius, Fl. Bras. 3(2): 167 (1878) & in A. & C. De Candolle, Monog. Phanerog. 2: 426 (1879); T. & G. Peckolt, Hist. pl. medicin. uteis Brazil 3: 230 (1890); Engler in Bot. Jahrb. 26: 555 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 130 (1913). Type: Illustrations in Schott Icones Aroideae collection at Vienna Natural History Museum of a plant probably collected by Schott between 1817 and 1821 around Rio de Janeiro city, Brazil; no specimens are known to exist, represented by colour illustrations:– Reliquiae Schottianae no. 497, Schott Icones Aroideae 2520–2529, 2743–2746 (W!; microfiche in Schott 1984).

[*Meconostigma speciosum* Schott ('*M. speciosum*') in Schott & Endlicher, Melet. Bot. 19 (1832)].

Vernacular names:– 'Aringa-iba', 'Arringa-iba', 'Aninga-iba' (Peckolt & Peckolt 1890).

STEM: erect and decumbent, branching in horizontal portion, erect portion 50–100 cm tall, stout, trunk-like, 6–9 cm thick; *adventitious roots* relatively few on aerial part of stem, running down stem, not widely spreading; *internodes*

extremely short, < 1 mm long, dark brown; *prophyll scars* 1–4 mm long, longer and paler than internodes, greyish; *intravaginal squamules* short, 1–2 mm long, 1–2 mm wide, flattened-triangular to \pm square, inconspicuous, situated on internode on either side and below each foliage leaf scar; *foliage leaf scars* suborbicular to transverse-elliptic, 5–7 cm wide, whitish- to silvery-grey. LEAF: *prophyll* green with maroon-red apical margin, deciduous; *petiole* 68–100 cm long, 0.8–1 cm diam. at apex, broadly sulcate adaxially with sharply-angled margins, at apex with a shallow central adaxial ridge and often with transverse-rugulose epidermis, sheath c. 13.5 cm long; *leaf blade* sagittate, margins repand, overall length 62–96 cm, overall width 43–60 cm, upper surface dark \pm glossy green with \pm concolorous primary lateral veins, lower surface paler, the primary lateral veins paler still and with slight pink to purplish tinge; *anterior division* 45–60 cm long, 40–60 cm wide, apex acute to obtuse with acuminate to cuspidate tip, *primary lateral veins* 5(–6) per side, arising at an angle of 40–75°, cross veinlets between finest parallel veins usually distinct in dried material, especially near margin; *posterior divisions* usually somewhat introrse, (15–)22–36 cm long, (0.2–)0.3–0.4 \times overall blade length, 19–33 cm wide, basal ribs denuded proximally on basiscopic side for (3.5–)5–7 cm, tip acute to obtuse and rounded at extremity, primary acroscopic veins 3–4, primary basiscopic veins (2–)4–7(–9), basiscopic lamina areas well-developed, sometimes overlapping. INFLORESCENCE: *peduncle* shorter than spathe, 5–13(–26?) cm long, (1.1–)1.7–3.4 cm diam. at apex, strongly tapering to base, exerted a little from leaf sheath; *spathe* 21–32 cm long, 4–4.5 cm diam. at middle, \pm cylindric, even in fruit swollen only slightly in basal half, decurrent for 4–5.5 cm, outer surface dull darkish green with red-maroon margin, inner surface carmine-magenta apically becoming \pm green at very base; *spadix* (14–)15.5–30 cm long, sometimes distinctly shorter than spathe, fertile male zone 5–10 cm long, 2–3 cm diam., \pm cylindric, sterile male zone 6–7 cm long, 1.6–2.7 cm diam., somewhat thicker towards the base, female zone c. 4 cm long, 1.5 cm diam. FLOWERS: *stamens* 3–4 per flower, 6.2–6.5 mm long, 0.6–1.2 mm diam. at apex, shorter and thicker at base of male zone; *staminodes* 6–8 per flower, those in upper portion of sterile zone 4–4.5 mm long, 1.7–1.8 mm diam. at apex, those in lower portion 5–5.5 mm long, 2.3–2.4 mm diam. at apex, clavate usually with flattened apex, somewhat prismatic, tapering and twisting to one side towards base; *gynoecium* 5–5.5 mm long, ovary subcylindric-ovoid, c. 3 mm long, 2.7 mm diam., raphide cells common in septa, upper ovary walls and ovary axis, *locules* 9–11 per ovary, ovules 2–3(–4) per locule, inserted on basal half of axis, style body lacking, base of style crown slightly narrower than ovary, densely filled with druse cells immediately above ovary locules, compitum penetrating deeply into ovary to halfway down ovary axis, strongly ridged to base, raphide cells common around basal part, style crown strongly lobed, style lobes spreading with dense concentrations of druse cells and sparse tannin cells in subepidermal tissue of dorsal surface, central dome lacking, stylar canals short and entering locules about halfway down, stigma c. 4 mm diam., lacking tannin hairs, hairs inserted all over style lobes except on dorsal surface. FRUIT: *berry* compressed-cylindric, rhomboid at base, \pm cylindric at apex, 1.2–1.3 cm long, 0.9–1 cm diam. at apex, yellow-orange; *seed* compressed ovoid-ellipsoid, 1–3 per locule, 5–5.5 mm long, 2.7–3.1 mm diam., testa very thick, \pm opaque forming a sarcotesta surrounding \pm cylindric inner body comprising inner integument, endosperm and embryo.

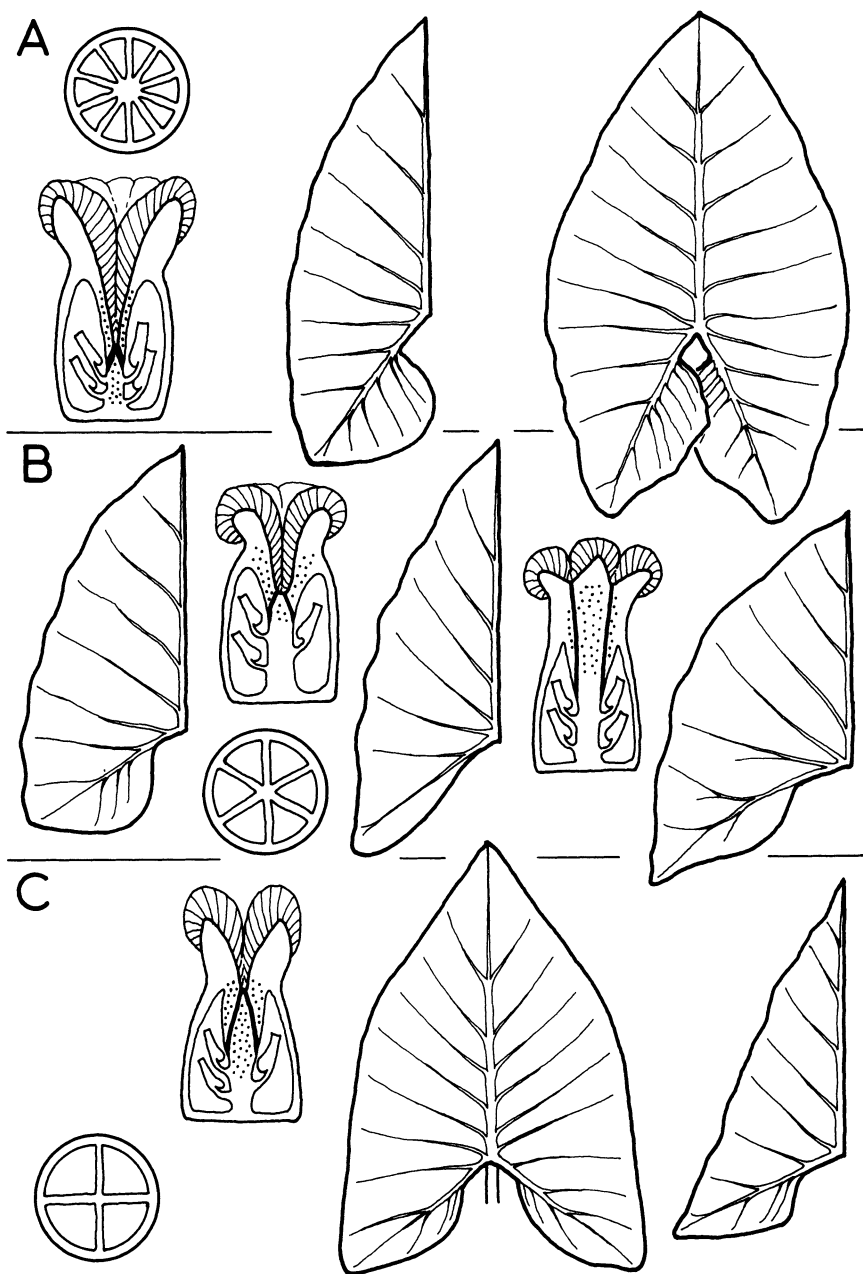


FIG. 16. **A–C.** *Philodendron* subgen. *Meconostigma*. Leaf blade and gynoeceium (semi-diagrammatic, not to scale); TS of ovary shows approximate mean number of locules; oblique hatching represents stigmatic tissue, thick lines show the course of stylar canals, stippling shows a zone of abundant raphide idioblasts. **A.** *P. speciosum*. Left to right: – LS gynoeceium (no data [L]); TS ovary; leaf blades (*S. Mayo et al.* 602, *Burle Marx* BM II); **B** *P. tweedianum*. Left to right: – leaf blade (*Krapovickas & Cristobal* 21721); LS gynoeceium (*Pedersen* 2978); TS ovary; leaf blade (*Pedersen* 2978); LS gynoeceium (*Schinini & Bordas* 21300); leaf blade (*Arbo et al.* 691); **C** *P. uliginosum*. Left to right: – TS ovary; LS gynoeceium (*Hatschbach* 47113); leaf blades (*Irwin et al.* 20622, *Hatschbach* 47113).

Figs. 3C, 4B, 16A, Map 2F.

HABITAT. Terrestrial, rupicolous (*S. Mayo et al.* 602) or hemi-epiphytic (*Duarte* 4129), rainforest or low scrubby forest on granite outcrop by sea; alt. 50–500 m approx.

BRAZIL. Rio de Janeiro: Serra de Petrópolis, 1952, *Duarte* 4129 (infr., MO!); município de Niterói, Itaipuaçu, Pico de Alto Moirão, 18 Feb. 1983, *S. Mayo et al.* 602 (sterile, K! RB!).

CULTIVATED. Europe: No data, autographed by Schott (infl. and leaf on separate sheets, L!). Germany: cult. University of Kiel botanic garden, *Engler Araceae* no. 50 (leaf and drawing of infl., C! G! GH! K! L! LE! M! S! US!). Brazil: collected near Mariana, Minas Gerais, Brazil and cult. R. Burle Marx at Sítio Santo Antonio da Bica, Barra de Guaratiba, Rio de Janeiro state, 14 Feb. 1983, voucher by S. J. Mayo, *Burle Marx* BM II (sterile, K!).

P. speciosum is one of the species collected around Rio de Janeiro by Schott himself and later brought back and cultivated in Vienna, probably at the Schoenbrunn Palace gardens. It is possible that other specimens in European gardens, e.g. that cultivated at Kiel University and distributed as herbarium specimens by Engler (*Engler Araceae* no. 50), were derived from this first introduction.

The illustrations in the Schott Icones Aroideae collection at the Vienna Natural History Museum (W) should be regarded as the type material, rather than the published plates (Schott 1857). It is likely that they represent the original collection made by Schott. They were partially published by Schott in his 'Icones Aroidearum' t.6–10 (Schott 1857), a folio publication of hand-coloured illustrations lacking text; t.6 corresponds to Schott Icones Aroideae no. 2522, t.7 to S.I.A. nos. 2745 and 2746 combined, t.8 to S.I.A. nos. 2743, 2744 and 2527 combined, t.9 to S.I.A. nos. 2524, 2525 (in part) and 2526 combined, t.10 to S.I.A. nos. 2523, 2525 (in part) and 2529 combined. Engler's illustration, distributed as part of 'A. Engler: Araceae n. 50' is a copy of part of S.I.A. no. 2520, though not acknowledged as such.

Engler confused this species with *P. brasiliense* from his earliest account of the genus onwards (Engler 1878, 1879, 1899) and Krause (1913) followed suit. Three of the five specimens cited under *P. speciosum* in the 'Pflanzenreich' (Krause 1913) belong to *P. brasiliense* (*Glaziov* 9024, 15576, *Löfgren* 728 ('1528')) and the remaining two (*Sello* 137, *Pilger* 672) have not been traced.

Duarte's collection from the Serra de Petrópolis (*Duarte* 4129) is notable for its long peduncle and short spadix which set it apart from the type collection and Burle Marx's cultivated specimen. More collections are required; the concept of *P. speciosum* presented here is based mainly on Schott's plates, Burle Marx's collection (BM II), the Leiden specimen bearing Schott's autograph and *S. Mayo et al.* 602.

P. speciosum appears to be endemic to the region near the city of Rio de Janeiro, and is closely related to *P. williamsii*. Characters which link the two species include leaf morphology, habit, gynoeceal morphology, the large inflorescence and the large seeds with a distinctive sarcotesta. It seems possible that *P. speciosum* is a vicariant sister-taxon of *P. williamsii*.

The interesting work of Theodoro and Gustavo Peckolt (Peckolt & Peckolt 1890) gives a short but accurate botanical description, the three vernacular names cited above and the following medicinal uses (transl.):— 'The leaves and stem possess a sharply caustic sap and when crushed are used as a

poultice to heal boils [‘tumores’]. Witchdoctors boil the crushed leaves with urine and use the liquid topically to treat pains in the joints. The seeds are used commonly in a dose of 4–6 grains as a remedy for intestinal worms (anthelmintic). The root, reduced to powder, is used in a dose of 0·3–1 gram’.

11. *Philodendron tweedianum* Schott in Bonplandia 7: 29 (1859) & Prodr. Syst. Aroid. 263 (1860); Engler in Martius, Fl. Bras. 3 (2) :165 (1878) & in A. & C. De Candolle, Monog. Phanerog. 2: 424 (1879) & in Bot. Jahrb. 26: 555 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 29 (1913); Hauman in Physis 8(28): 101 (1925); Herter, Fl. Illustr. Uruguay 1: 186, t.741 (1943); Burkart in Darwiniana 11: 494, 515 (1957); Barroso in Arquiv. Jard. Bot. Rio de Janeiro 17: 5–17 (1962); Crisci in Rev. Mus. La Plata (Bot.) 11 (64): 229 (1971); Marchesi in Lombardo, Fl. Montevidensis 3: 343, t. 141 (1984); Croat & Mount in Spichiger, Fl. Paraguay 23 (1988). Type: Argentina, Entre Rios, delta region of Rio Paraná (specimen data ‘Flum: Parana’), *Tweedie* s.n. (infl., K! holo., LE! iso.).

P. dubium Chodat & Vischer in Chodat, Vég. Paraguay 3: 341, 342, 375, figs. 254, 278, 278bis (1920). Type: Paraguay, Lago Ypacaraí, *Chodat & Vischer* 359 (G, not seen).

Vernacular name: ‘Guembataya’.

STEM: erect, 50 (–100) cm tall, 5–15 cm diam., decumbent, or rhizomatous, subterranean and appearing acaulous at soil surface, usually forming extensive stands; *adventitious roots* present, c. 0·8 cm diam.; *internodes* less than 1 mm long; *prophyll scars* less than 1 mm long; *intravaginal squamules* frequent to numerous, not long-persistent, 3–5 mm long, 1–2·5 mm wide at base, triangular-lanceolate, usually flattened; *foliage leaf scars* transverse-elliptic, c. 1 cm long, 2·3 cm wide. LEAF: *prophyll* 20–40 cm long; *petiole* (32–)40–90 (–104) cm long, usually distinctly longer than blade, 0·6–1 cm diam. at apex, above flattened to broadly sulcate with rounded margins; *leaf blade* normally broadly sagittate, somewhat glaucous, margins normally weakly repand, rarely subentire or sinuately lobed, overall length 30–52(–56) cm, overall width (21·5–)24–42(–44) cm; *anterior division* 20–37 cm long, 21–42 cm wide, normally wider than long, widest at base, apex subacute to rounded and apiculate, *primary lateral veins* 3–5 per side, concentrated towards segment base, arising at angle of (30–)40–90° to midrib; *posterior divisions* 10–20 cm long, 0·3–0·4 × overall blade length, 12–22(–25) cm wide, basal ribs denuded for 1·5–3 cm, tip normally retrorse, more rarely introrse or extrorse, acute-acuminate to broadly rounded, primary acroscopic veins 1–3, primary basisopic veins 0–5, often very weak when present, width of basisopic lamina very variable. INFLORESCENCE: *peduncle* (16–)20–46(–55) cm long, 1–2 cm diam. at apex, *spathe* tapering towards apex, (9–)12–20 cm long, (2–)2·5–4(–4·3) cm diam. at middle, decurrent for (2·5–)3–4·5 cm, pale green on outer surface, cream-white on inner surface; *spadix* 12–17·5 cm long, fertile male zone (3·5–)4–5·5(–6·8) cm long, 1·1–1·8 cm diam., ± cylindric, narrower than sterile male zone, sterile male zone (4–)5·7–10 (–11) cm long, slightly conical, tapering from 1·6–2·4 cm diam. at base to 1·3–1·8 cm diam. at apex, female zone 1·3–2·5(–2·7) cm long, 1–2(–2·3) cm diam. FLOWERS: *stamens* 2·7–4 mm long, (0·6–)0·7–1(–1·3) mm diam. at apex; *staminodes* (1·3–)2–5 mm long, 1–1·8 mm diam. at apex, clavate,

usually tapering evenly towards the base, occasionally more abruptly swollen at apex; *gynoeceium* 3–4.5 mm long, ovary a little narrower than stigma, \pm cylindric, raphide cells common to abundant in subepidermal tissue of ovary walls from apex to base, *locules* 4–8, ovules (1–2) per locule, inserted near base and at middle of ovary, well spaced from one another, style body slightly narrower than style crown and ovary, densely packed with abundant raphide cells around stylar canals, compitum not penetrating ovary, style crown with tanniniferous style lobes, central dome usually lacking, occasionally present and then equalling style lobes in height, stylar canals entering locules sub-apically, stigma (1.5–)1.8–2(–2.7) mm wide, containing many tannin hairs. No fertile fruit seen. Fig. 16B, Map 3C.

HABITAT. In open riverine marshes ('pajonales' of Burkart 1957) on sandy soil, forming dense stands up to 50 m across. Crisci (1971) states that in drier soils the stems become subterranean, as described by Chodat & Vischer (1920) for *P. dubium*, while in wetter conditions the stems are aerial. Marchesi (1984) notes that at Montevideo the flowering season is from January to April; further north flowering seems to occur more or less throughout the year; alt. 0–200 m.

ARGENTINA. Corrientes: Dep. Ituzaingó, 2 Oct. 1978, *Schinini & Vanni* 15699 (infl., C! CTES! MO!); Dep. Mburucuyá, Estancia Santa Teresa, 10 Nov. 1954, *Pedersen* 2978 (infl., BR! C! G! GH! K! MO! NY! P! S! U! US!); Dep. Concepción, Carambola, 24 Nov. 1982, *Pedersen* 13462 (infl. infr., C! CTES!); Entre Ríos: Rio Paraná, *Tweedie* s.n. (infl., K! LE!).

PARAGUAY. Dep. Central, San Bernardino, 16 May 1973, *Schinini* 7902 (infl., CTES! UC!); Dep. Cordillera, road between San Bernardino and Altos, 17 Oct. 1981, *Schinini & Bordas* 21300 (infl. infr., CTES! K!); Dep. Paraguari, Yaguarón, 24 Sept. 1967, *Krapovickas & Cristobal* 13235 (infl. infr., CTES! UC!);

The distribution of this species is interesting and seems to include the most southerly extension of the genus (Marchesi 1984). Crisci (1971) notes that cultivated plants lose their leaves in winter at Buenos Aires. Hauman (1925) considered that the species originated in Paraguay or Mato Grosso (Brazil) and had been carried down by river to the mouths of the Rios Paraná and Uruguay. Its vigorous vegetative reproduction in marshy conditions could have been an important factor in a range extension to temperate latitudes since in all fruiting material seen, the seeds were either galled by insects or lacking altogether.

No collections from Brazil have been seen, although it seems very likely that *P. tweedianum* occurs there, at least along the Rios Uruguay, Paraná and their tributaries. Hauman (1925) considered that Tweedie's type collection came from the delta region of the Rio Paraná in the province of Entre Ríos, Argentina, and had been collected during an expedition to the lower Rio Uruguay and the Paraná delta in 1832. Tweedie's type specimen (K! LE!) has no locality information except 'Flum. Parana. A showy aquatic of the Parana – the whole plant is very pungent'. Schott (1860) cited the collection as from Brazil, but there is no evidence that he had access to any further information than presently exists; his pencil drawing of the specimen (Schott Icones Aroideae no. 2530 at W, see Schott 1984) includes only the data found on the Kew holotype. Although Hauman (1925) asserts that Tweedie never visited Brazil, Urban (1906) gives his 1832 itinerary as being from Buenos

Aires up the Rio Uruguay and back, and thence to Rio de Janeiro via the coasts of Uruguay, and the Brazilian states of Rio Grande do Sul and Santa Catarina. Nevertheless, Hauman's opinion of the type collection's origin is doubtless correct since Tweedie would not have encountered the Rio Paraná except at its delta.

I have been unable to locate Chodat & Vischer's type specimen of *P. dubium* (Chodat & Vischer 359). The other specimen cited by them in the original description, Hassler 1713 (G!) consists only of an inflorescence which more closely resembles that of *P. undulatum*; its identification is uncertain. Chodat & Vischer's own material should therefore be regarded as the basis of their concept of *P. dubium* in view of the detailed field study described and illustrated in Chodat & Vischer (1920). I have followed Hauman (1925) and Crisci (1971) in reducing this species to the synonymy of *P. tweedianum* on the basis of the description and figures, and especially the characteristic rhizomatous habit.

Schulz, in notes accompanying sterile collections from Paraguay (Schulz 17848, CTES!) and Argentina (Schulz 17838), records that indigenous people use the petioles for cordage.

12. *Philodendron uliginosum* Mayo, sp. nov. *P. brasiliensi* Engler affinis, sed squamulis intravaginalibus caulis minoribus, loculis ovarii paucioribus, stylo sine lobo centrali tholiformi differt. Typus: Brazil, Minas Gerais, Santana do Riacho, 25 Oct. 1974, Hatschbach & Koszicki 35350 (infl., holotypus MBM! isotypi K! US!).

STEM: erect, 35–150 cm tall, up to c. 5 cm diam., sometimes branching at base to form clumps; *adventitious roots* not seen above ground; *internodes* 0.5–5 mm long, greyish-brown; *prophyll scars* 0.3–1.4 cm long, glossy greyish brown; *intravaginal squamules* inconspicuous, sometimes persistent, often lacking, small, patent, 1.5–3.5 mm long, 0.5–1.7 mm broad at base, triangular, acuminate, distant, inconspicuous on older part of stem; *foliage leaf scars* 2–2.9 cm broad, 2–2.5 cm wide, broadly obovate, rhombic or transversely elliptic, greyish-brown becoming grey on older stem portion. LEAF: *prophyll* about 17 cm long; *petiole* 25–40 cm long, 0.5–0.7 cm diam. at apex, sulcate adaxially with \pm sharply angled margins, rounded abaxially, sheath 3.5–11 cm long; *leaf blade* triangular- to ovate-sagittate, rarely subhastate, margins entire, rarely repand, overall length (18–)20–46(–53) cm, overall width (10–)15–26(–34) cm, upper surface dark to mid green, glossy, lower surface paler, duller; *anterior division* 18.5–30 cm long, 16–26 cm wide, apex subacute to acute, *primary lateral veins* (5–)6–7 per side, arising at angle of 30–80° to midrib, somewhat paler than blade on both surfaces, finest parallel veins paler than blade on upper surface; *posterior divisions* 6–16 cm long, 0.24–0.34 \times overall blade length, 8.5–13 cm wide, basal ribs denuded for (0.9–)1.8–4 cm, tip acute to subacute, rounded at extremity, primary acroscopic veins (1–)2(–3), primary basiscopic veins 0–3. INFLORESCENCE: *peduncle* 7.5–17(–22) cm long; *spathe* 10.5–15.5(–16.5) cm long, ca. 3.5–5.5 cm diam. at middle, somewhat constricted, decurrent for 2.5–3.5 cm, at anthesis outer surface green becoming yellowish- or white-membranous at margins, inner surface creamy white; *spadix* 9.2–9.9(–11) cm long overall, fertile male zone (3.0–)3.5–4 cm long, (1.3–)1.9–2 cm diam., subclavate, white, sterile male zone 3.3–5.5 cm long, (1.3–)1.7–2 cm diam., cylindric,

female zone 1.8–2.5 cm long, (1.0–)1.4–1.5 cm diam. near base, tapering upwards. FLOWERS: *stamens* 5–5.5 mm long, 0.6–1.2 mm diam. at apex, tapering slightly towards base; *staminodes* 4.2–5.1 mm long, 0.7–1.4 mm diam. at apex, tapering somewhat towards base, prismatic, truncate; *gynoecium* 3–4 mm long, ovary 1.5–2.2 mm diam., \pm cylindric or barrel-shaped, *locules* 3–6, *ovules* 1–4(–5) per locule, inserted from near base to somewhat above middle of locule, \pm distant, style body somewhat narrower than crown, raphides abundant around stylar canals and in ovary axis, compitum not penetrating ovary, style crown as broad as ovary, densely tanniniferous, lobes well-developed, central dome lacking, stylar canals entering locules sub-apically, stigma 1.5–2.7 mm diam., completely covering style lobes, \pm lacking tannin hairs. FRUIT: *berry* many-seeded, 1.0–1.2 cm long, 0.6–0.9 cm diam., \pm cylindric, white to beige, with delicious mango-like flavour, stigma remnant blackish; *seed* 2.8–3.5 mm long, 1.6–2 mm diam., ovoid. Figs. 3A–B, 4C, 8A–B, 16C, Map 2B.

HABITAT. In flushes and marshes in open, upland grasslands ('campo'), in shade of gallery forests or gallery forest margins, along streams; alt. 975–1360 m approx.

BRAZIL. Distrito Federal: Rio Gema, c. 5 km S of Brasília on road to Belo Horizonte, 21 Sept. 1965, *Irwin et al.* 8526 (infl., F! K! MO! NY! S! UB! US!); near Sobradinho, c. 7 km E of Brasília, 30 Sept. 1965, *Irwin et al.* 8839 (infl., G! GH! NY! U! UB! US!); 3 km S of Planaltina, 7 Nov. 1965, *Irwin et al.* 10047 (infl., F! L! NY! UB! US!). Minas Gerais: Grão Mogol, Rio Itacambirucú, cult. Paraná state on 18 Nov. 1983, *Hatschbach* 47113 (infl., MBM, K!); Diamantina, km. 185 on road from Conselheiro Mato to Diamantina, 4 Feb. 1987, *S. Mayo et al.* 712 (K! SPF!); Trinta Reis, between Sêrro and Diamantina, 3 Feb. 1987, *S. Mayo et al.* 711 (K! SPF!); c. 23 km SW of Diamantina, road to Gouveia, 18 Jan. 1969, *Irwin et al.* 22218 (immature infr., C! F! NY! UB! US!); Serra do Cipó, 20 Feb. 1972, *Anderson et al.* 36389 (infl. infr., F! K! NY! UB! US!); Serra do Cipó, c. 145 km N of Belo Horizonte, 21 Feb. 1968, *Irwin et al.* 20622 (infr., F! K! MO! NY! S! UB! UC! US!); Serra do Cipó, above Hotel Chapeu do Sol on road to Conceição do Mato Dentro, 1–2 Feb. 1987, *S. Mayo et al.* 700 (K! SPF!).

Material of this species has long been identified as *P. brasiliense*. However, *P. uliginosum* differs from *P. brasiliense* in the following characters: – the intra-vaginal squamules are much smaller and narrower, the leaf blade is somewhat smaller, the stamens and staminodes are longer, the ovary locules fewer, the style body is narrower than the ovary and the style lacks a central dome. The two species are certainly closely related and together with *P. dardanianum* and *P. tweedianum* form a distinctive group of emergent aquatic species with entire, cordiform to sagittate leaves. The four species are distributed within eastern and southern Brazil in a series of non-overlapping ranges from north to south (Maps 2A, B, G, 3C).

Collections from further north in Minas Gerais state near Diamantina and Grão Mogol have repand to sinuately lobed leaf margins (*Anderson et al.* 35477) or larger leaves with rather acute posterior divisions and a longer spadix (Fig. 16C, *Hatschbach* 47113). These variations are not considered sufficient to warrant taxonomic recognition.

13. *Philodendron undulatum* Engler in A. & C. De Candolle, Monog.

Phanerog. 2: 428 (1879) & in Bot. Jahrb. 26: 555 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 133 (1913); Chodat & Vischer in Chodat, Vég. Paraguay 3: 342, figs. 253, 255, 256, 257, 258 (1920); Hauman in Physis 8 (28): 102 (1925); Grau in Lilloa 34: 30, fig. 7W (1983); Croat & Mount in Spichiger, Fl. Paraguay 25 (1988). Type: Paraguay, cult. Asunción, Jul. 1875, *Balansa* 576 (infr., G holo. not seen, P! iso., K! F! photos).

P. eichleri in Bot. Jahrb. 26: 556 (1899); Krause in Engler, Das Pflanzenreich 60 (IV.23Db): 133 (1913). Types: Brazil, Minas Gerais state, Carandaí, cult. Brazil, 15 Nov. 1887 at Quinta da Boa Vista, Rio de Janeiro as no. 67, *Glaziou* 16503 (infl., B! syn.; sterile, P! isosyn.), *Glaziou* 17332, (sterile, B syn. not seen; C! K! P! isosyn.).

Vernacular names: 'Guembé' (Argentina), 'Guembe espinoso' (Argentina), 'Imbe de flor vermelha' (Brazil).

STEM: erect or decumbent, trunk-like and stout, up to 2.5 m tall, 9–20 cm thick, lower part grey: *adventitious roots* running \pm down stem, not spreading widely, about 1.4 cm diam., with rugose, \pm corky epidermis and prominent lenticels; *internodes* very short; *prophyll scars* similar in length to internodes; *intravaginal squamules* 2–8 mm long, 3–4 mm wide at base, \pm flattened, triangular, sometimes falcate, acute-acuminate, common to numerous, persistent and quite conspicuous; *foliage leaf scars* transverse-elliptic to subrhombic, \pm oblique, c. 3 cm long, c. 5–7 cm wide. LEAF: 8–10 per crown; *prophyll* up to 60 cm long, pale yellowish green; *petiole* 35–63(–100) cm long, subequalling or longer than leaf blade, c. 1 cm thick at apex, sulcate with sharply angled margins; *leaf blade* triangular-sagittate in outline, upper surface dark dull green, margins sinuately lobed, overall length (30–)40–80 cm, overall width (21–)29–65(–72) cm, usually widest below petiole attachment; *anterior division* (19–)26–55 cm long, (20.5–)25–65(–70) cm wide, apex acute, more rarely acute-acuminate, subacute or rounded; *primary lateral lobes* 4–7(–8) per side, subtriangular to hemispheric, usually \pm oblique and pointing slightly towards leaf apex, tips rounded, basal primary lateral lobes 1.5–6.5(–14) cm, shorter towards apex of division; *primary lateral veins* 4–7(–8) per side, \pm regularly spaced, paler than lamina abaxially, arising at an angle of 30–90°; *posterior divisions* 11–25 cm long, 0.2–0.4 \times overall blade length, (10–)13–30(–36) cm wide, basal ribs denuded for 1–5(–6.5) cm, tip subacute to rounded, primary acroscopic lobes (1–)2–3, primary basicopic lobes (0–)2–5, much shallower than acroscopic lobes, basicopic lamina area nearly always well developed, sinus between posterior divisions usually \pm oblong, sometimes broadly parabolic. INFLORESCENCE: *peduncle* (4–)7–15 cm long, 0.8–2 cm diam. at apex; *spathe* (11.5–)12.5–25 cm long, c. (1.9–)2.5–5 cm diam. at middle, subcylindric, decurrent for (1.5–)2.8–6 cm, green or reddish-green or dull purplish green basally on outer surface, white or crimson on inner surface; *spadix* (9.5–)13–19.5 cm long, fertile male zone 3.5–5.5(–8) cm long, (0.9–)1.3–3 cm diam., subcylindric, sterile male zone (3.5–)5.5–7 cm long, usually longer than fertile male zone, (0.9–)1.2–2.5 cm diam., thicker basally, female zone (1.5–)4–5 cm long, (1.0–)2–3.5 cm diam. FLOWERS: *stamens* 3.5–4.8(–6) mm long, (0.5–)0.7–1 mm diam. at apex; *staminodes* 3–6(–7.7) mm long, longest at base of sterile zone, at apex (0.6–)0.8–1.2(–1.4) mm diam., clavate, usually flattened, tapering gradually and then abruptly to base; *gynoeceum* 5–6.5 mm long, ovary flask-shaped to subcylindric, 3–4 mm diam., raphides common

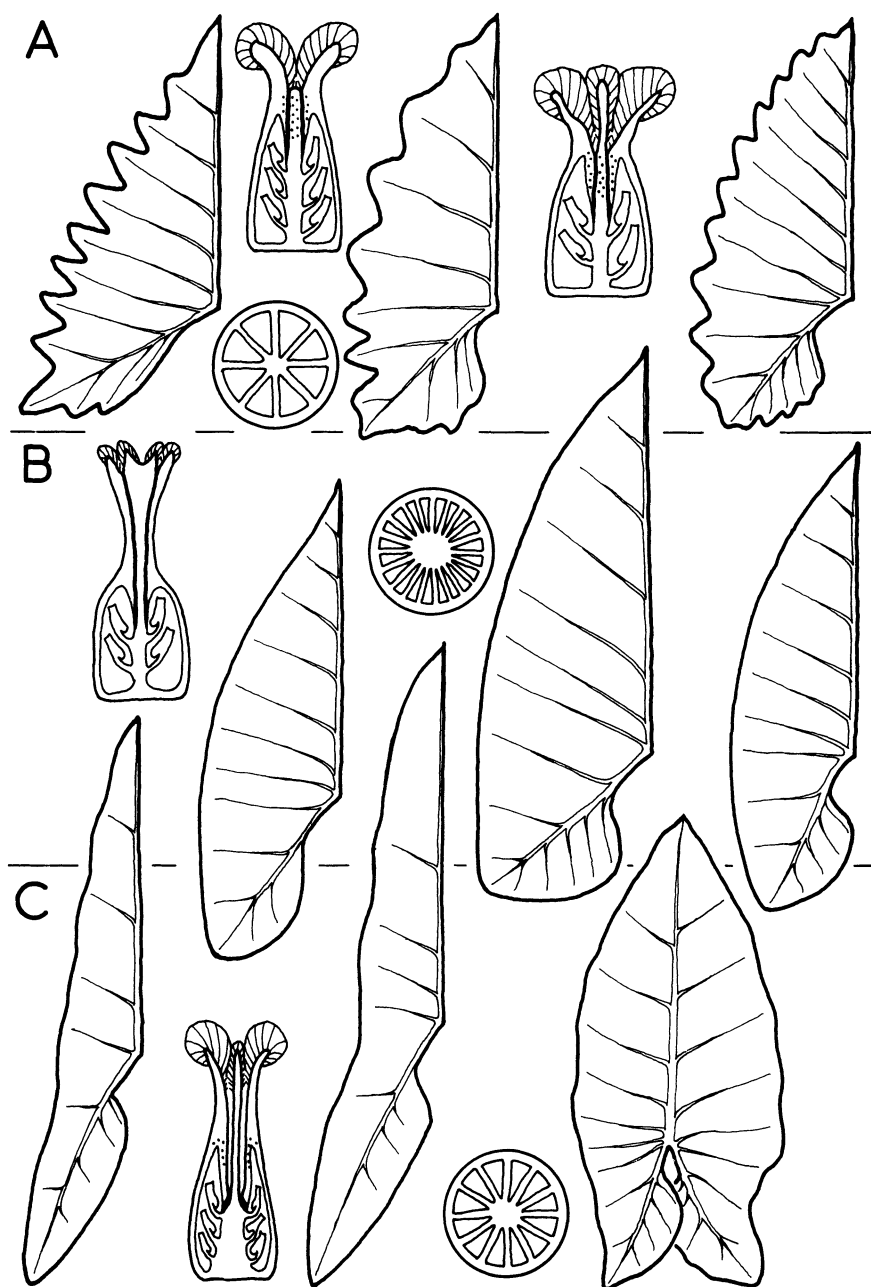


FIG. 17. A–C. *Philodendron* subgen. *Meconostigma*. Leaf blade and gynoeceum (semi-diagrammatic, not to scale); TS of ovary shows approximate mean number of locules; oblique hatching represents stigmatic tissue, thick lines show the course of stylar canals, stippling shows a zone of abundant raphide idioblasts. **A** *P. undulatum*. Left to right: leaf blade (Glaziou 17332); LS gynoeceum (Burkart et al. 30669); TS ovary; leaf blade (Martinez Crovetto 10864); LS gynoeceum (Eiten & Eiten 2330); leaf blade (Eiten & Eiten 2330); **B** *P. venezuelense*. Left to right: LS gynoeceum (Madison et al. 6944); leaf blade (Steyermark & Bunting 102504B); TS ovary; leaf blades (Liesner 3497, Liesner 6438); **C** *P. williamsii*. Left to right: leaf blade (Sucre 5728); LS gynoeceum (Williams s.n.); leaf blade (Burle Marx BM VI); TS ovary; leaf blade (Harley et al. 18501).

in subepidermal tissue of upper ovary walls and style body, *locules* 6–9(–10) per ovary, ovules 2–3(–4) per locule, inserted from base to upper third of ovary axis, distant, evenly spaced, style body distinctly narrower than ovary or style crown, packed with raphide cells around stylar canals, compitum not penetrating ovary, style crown consisting of well-developed spreading, usually tanniniferous style lobes, central dome lacking or very short or very slender, clavate and slightly overtopping crown lobes, stylar canals entering locules subapically or in upper third of locules, stigma (2·5–)3–4·5 mm diam., covering entire style crown including dorsal surfaces of style lobes, tannin hairs numerous or lacking. FRUIT: *fertile berry* c. 1·2 cm long, 0·7–0·8 cm diam., cylindric (yellow fide Croat & Mount 1988); *seed* galled in all but one collection seen, 2·6–3 mm long, 1·3–1·5 mm diam., subcylindric. Fig. 17A, Map 2H.

HABITAT. Most collections lack ecological details; Chodat & Vischer (1920) give a detailed habitat description for Paraguay, where *P. undulatum* grows as an emergent aquatic in open marshes and also thrives in damp marshy woodlands where the stem becomes much taller; it seems not to be restricted to marsh habitats, however, since Schinini & Bordas (21251) collected the species growing on rocks in the Cordillera de Altos of Paraguay. In Brazil three collections give the habitat as riverine marshes (*Duarte* 3526, *Eiten* & *Eiten* 2330, *Zappi* & *Mayo* 77).

ARGENTINA. Prov. Entre Rios: Dep. Concordia, cult. Instituto Darwinion, 26 Dec. 1974, *Burkart et al.* 30669 (infl., F!).

BRAZIL. Mato Grosso do Sul: near Campo Grande, 27 Sep. 1940, *M. B. & R. Foster* (sterile, US!); 60 km W of Miranda (Camp of Military Engineers), 28 Jan. 1979, *Krapovickas & Cristobal* 34435 (infr., CTES!). Minas Gerais: Carandaí and Tiradentes, margins of Rio Carandaí and Rio das Mortes, 28 Oct. 1952, *Duarte* 3526 (infl., MO!). São Paulo: município of Moji-Guaçu, 2·8 km NNW of Padua Sales 22·11–22·18S, 47·7–47·10W, c. 27 km NW of Moji-Mirim, 19 Sept. 1960, *G. & L. T. Eiten* 2330 (infl., UB! US!); road between Campos do Jordão and junction with the Dutra highway to São Paulo, 1 Oct. 1988, *Zappi* & *S. Mayo* 77 (K! SPF!).

PARAGUAY. Dep. San Pedro, San Estanislao, 20 Jun. 1977, *Krapovickas & Schinini* 32585 (infr., C! CTES! F! G! MO! WIS!); Dep. Central, San Bernardino, Dec., *Hassler* 1713 (infl. only, G!); Dep. Cordillera, Cerro de Tobati, Cordillera de Altos, 11 Oct. 1981, *Schinini & Bordas* 21251 (infl., CTES! K!); Villarica, Dec. 1931, *Jorgensen* 4599 (infl. infr., C! F! MO! S!).

CULTIVATED. Argentina: Prov. Corrientes, Dep. Capital, Corrientes, Dec. 1976, *Martinez Crovetto* 10864 (infl., CTES!); San Marcos cresco, 7 March 1899, *Stuckert* 6597 (infl., G!); Brazil: cult. Burle Marx, Sítio Santo Antônio da Bica, Barra de Guaratiba, Rio de Janeiro state, 15 Feb. 1983, *Burle Marx* BM VIII (infr., K!); 'Serra da Babylonia, Minas Gerais', 30 June 1869, *Glaziou* D.182 (sterile, P! S! US!); 'Rio Janeiro et Minas', 1887, *Glaziou* 16503 (infl., B!, leaf P!); 'En culture sous le no. 67 á Quinta 15 xi 1887 RJ' (= cult. Rio de Janeiro, Quinta da Bôa Vista), 1888, *Glaziou* 17332 (leaf, B ?destroyed, C! K! P!). Paraguay: Asunción, July 1875, *Balansa* 576 (immature infr., P!); cult. Asunción, originally from Cerro Tobatí, 4 Sept. 1976, *Schinini* 13458 (sterile, CTES!).

With some circumspection, I have reduced *P. eichleri* to synonymy, since there appear to be no consistent characters to distinguish this taxon, which

consists of Brazilian populations in Minas Gerais and São Paulo states, from *P. undulatum*, previously recognized only in Paraguay and Argentina. With the exception of a single Paraguayan collection the species is characteristic of riverine marsh habitats. The sinuately lobed leaf blade is a constant feature, and though the primary lateral lobes are sometimes shallow enough to fall within the range of variation shown by *P. tweedianum*, the much shorter peduncle of *P. undulatum* serves to distinguish these two species clearly enough.

The gynoeceium varies in the presence or absence of a style dome, but in general style domes are more frequently lacking in this species; when present they are either very short or extremely slender (Fig. 17A). The slender form occurs in the Brazilian material, but in the Paraguayan and Argentinian specimens only very short central domes were observed. Gynoecea lacking style domes are common in the Brazilian specimens, making their presence an unreliable character even within a single spadix.

Duarte's collection (Duarte 3526) from Carandaí, Minas Gerais, Brazil, is from the same locality as Glaziou's types of *P. eichleri* and is notable for having a crimson inner spathe surface. It is not clear what value this character may have, since the field notes of *Eiten & Eiten* 2330 from São Paulo make no mention of red spathe colour; this character appears to vary between populations. Grau (1983) describes purple spathes in material cultivated at Tucuman, Argentina, suggesting that this polymorphism also occurs in the Paraguayan – Argentinian part of the range.

Further collection and field study in the drainage system of the Rios Paraná and Paraguay is needed to clarify the definition of *P. undulatum*. It would be interesting to investigate the possibility of a hybrid origin of this taxon from crossing between *P. tweedianum*, *P. brasiliense* and *P. bipinnatifidum*. Glaziou 16503, one of the syntypes of *P. eichleri*, despite having mature gynoecea, has malformed staminodes and stamens, suggesting an arrested ontogeny of these zones. A similar phenomenon has been observed in material of *P. × evansii*, a hybrid between *P. speciosum* and *P. bipinnatifidum* which has leaves very similar to those of *P. undulatum*.

A sterile collection from Mato Grosso do Sul, Brazil (Foster & Foster 1098) has longer primary lateral lobes than other material seen. Possibly it represents a distinct taxon, but further material is needed. The collectors recorded 2 inflorescences at the base of each petiole.

14. *Philodendron venezuelense* Bunting in Acta Bot. Venezuelica 10(1–4): 315 (1975) & in Rev. Fac. Agron. (Maracay) 10:250 (1980). Type: Venezuela, Territorio Federal Amazonas, Departamento Casiquiare, environs of Yavita on the Rio Temi and near the Yavita-Pimichín road as far as 5 km towards Pimichín, 6–19 Jul. 1969, Bunting *et al.* 3864 (infl. infr., MY holo., not seen, U not seen).

[*P. speciosum* sensu Madison in Aroideana 2(3): fig. 11 (1979)].

Vernacular names: 'Guambe lejito', 'Juambe', 'boo-taw-he-noo' (Makuna), 'oo-waw-ne' (Maku).

STEM: erect, short, stout, c. 8 cm thick, obscured by petiole bases and prophylls. LEAF: *prophyll* 30–84 cm long, 6–8 cm wide at base, yellow-green, drying to brown, rigid and hard when young, persistent; *petiole* 60–124 cm long, apex 1–1.3 cm diam., densely verruculose-regulose, ± ridged centrally on upper surface, margins angled, sheath 14–18 cm long, sheath margins

eventually deciduous; *leaf blade* sagittate, margins entire to somewhat repand, overall length 80–110 cm long, overall width 56–66 cm, upper surface dark glossy green with yellow-green primary lateral veins; *anterior division* 56–67 cm long, 56–66 cm wide, apex subacute to obtuse with acuminate to cuspidate tip, *primary lateral veins* (5–)6–7 per side, arising at an angle of 45–85°, cross veinlets between finest parallel veins very distinct throughout blade on upper side in dried material; *posterior divisions* often somewhat introrse, (15–)23–30 cm long, 0·3 × overall blade length, 25–30 cm wide, basal ribs denuded for 4–8·5 cm, tip rectilinear to obtuse and rounded at extremity, primary acroscopic veins 3–4, primary basiscopic veins 3–6, basiscopic lamina areas well-developed, sometimes overlapping. INFLORESCENCE: 1(–2) per leaf, innermost inflorescence (when in pairs) subtended by prophyll; *peduncle* 4–12 cm long, c. 1·5 cm diam. at apex; *spathe* 14–23 cm long, (2·5–)3–4·5 cm diam. at middle, decurrent for 2–3 cm, outer surface glossy green to whitish-yellow, red-maculate, reddish towards apex, inner surface ivory white; *spadix* 13–17(–21) cm long overall, fertile male zone 3·5–6·5 cm long, (1·1–)1·5–2·7 cm diam., subcylindric to ellipsoid, acute, sterile male zone 6–8·5 cm long, 1·5–3·3 cm diam., subcylindric, tapering slightly towards apex, female zone 4–5 cm long, 1·7–2·5 cm diam., tapering towards apex. FLOWERS: *stamens* 3·5–4·8 mm long, 0·6–1 mm diam. at apex; *staminodes* c. 7 per flower, 3·3–6 mm long, 0·8–1·5 mm diam. at apex, shorter in apical portion of sterile zone, clavate, truncate at apex, prismatic in section, tapering gradually to base; *gynoecium* 5·5–14·5 mm long, ovary ± cylindric, 3–8·5 mm long, 3–5 mm diam., raphides frequent to common in axis, *locules* 17–22 per ovary, ovules 2(–3) per locule, chalaza prominent, hemispheric, darker coloured, raphe produced as an appendage overtopping micropyle, integuments containing raphides, ovules well-spaced from one another and inserted on basal half to two thirds of ovary axis, style body much narrower than ovary and greatly elongated, 2·5–7 mm long including crown, becoming toughened and tanniniferous in lower region, softer and lacking tannin apically, scattered raphide cells present, compitum shallow, not penetrating ovary, as deep as style lobes, style crown 2·5–4 mm diam., distinctly lobed, non-tanniniferous, with conspicuous layer of druse cells immediately bordering stigmatic epidermis, central dome present, lobed, broad, equalling or overtopping style lobes, usually somewhat excavated centrally, stylar canals very long, probably entering locules just above insertion of uppermost ovule in each locule, stigma not seen in well-preserved state. FRUIT: *submature berry* 1·2–1·4 cm long, 0·7–1·1 cm diam., whitish-yellow, suffused and spotted with dark salmon red, bright red when mature with pineapple odour, style persistent, dark brown; *seed* 2·4–3 mm long, 1–1·2 mm diam., cylindric-ellipsoid. Fig. 17B, Map 4D.

HABITAT. Terrestrial in open savannas on wet sandy soils on rock outcrops and in 'caatingas' of the Rio Negro drainage basin, or hemi-epiphytic in rainforest; alt. 100–200 m approx.

BRAZIL. Amazonas: Rio Negro, caatinga at Porto Camanaus, 19 Oct. 1978, *Madison et al.* 6944 (infl., INPA (as PFE 444)! K! SEL!).

COLOMBIA. Amazonas-Vaupes: Rio Apaporis, Raudal de Jirijirimo, 27 Nov. 1951, *Schultes & Cabrera* 14605 (infr., US!); Rio Apaporis, Jinogojé, mouth of Rio Piraparaná, 0°15S 70°30W, 15 Jun. 1952, *Schultes & Cabrera* 16747 (infra., NY! US!).

VENEZUELA. Territorio Federal Amazonas: Piedra Catipan, left bank of rio Yatua, 1°35'N, 66°25'W, 9 Apr. 1970, *Steyermark & Bunting* 102504-B (sterile, MO!); E of San Carlos de Rio Negro, 1°56'N, 67°04'W, 14 Nov. 1977, *Liesner* 3497 (infl., MO!); 7 km NE of San Carlos de Rio Negro, c. 20 km S of confluence of Rio Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 10 Apr. 1979, *Liesner* 6438 (infl. infr. MO!)

I have seen neither of the specimens cited by Bunting in the original description where, as well as the type, he cites *Bunting, Akkermans & van Rooden* 3972 (MY), collected from the same region. I have, however, examined other material authenticated by Bunting. No detailed description of the stem can be given in the absence of more complete information or material and I have relied on Bunting's descriptions for some details of form, colour and range of size measurements.

The elongated style body (Fig. 17B) is a remarkable feature, outwardly similar to the style of *P. williamsii* but differing greatly in internal structure. Bunting (1980) notes that *P. venezuelense* differs from *P. solimoesense* by its broader leaves and long, persistent prophylls ('cataphylls'), which together with the petiole bases obscure the stem.

Madison (notes to *Madison et al.* 6944) states that the seeds are good to eat.

15. *P. williamsii* *J. D. Hooker* in *Bot. Mag.* 97: t.5899 (1871); Engler in *Martius, Fl. Bras.* 3(2): 166 (1878) & in *A. & C. De Candolle, Monog. Phanerog.* 2: 426 (1879) & in *Bot. Jahrb.* 26: 555 (1899); Krause in Engler, *Das Pflanzenreich* 60 (IV.23Db): 130 (1913); Mayo in *Mori et al. in Bot. Rev.* 49(2): 210 (1983) & in *Anais XXXIV Congresso Nacional de Botânica, Porto Alegre, Brazil* 2: 215–227 (1984). Type: Plant cultivated at Kew in August 1870, originally from Brazil, Bahia, region of Salvador, *Williams* s.n. (holotype K!).

Vernacular name: 'Milho de caboclo' (*Williams* in litt.).

STEM: erect to decumbent, branching in horizontal portion, erect portion 50–120 cm tall, stout and trunk-like, 5–8.5 cm thick; *adventitious roots* c. 1.5 cm thick; *internodes* less than 1 mm long; *prophyll scars* longer than true internodes, c. 5 mm long; *intravaginal squamules* 1–2 mm long or less, c. 1–2 mm broad, triangular or multitoothed, inconspicuous, persistent; *foliage leaf scars* subcircular to transverse-elliptic, c. 4 cm long, 4–5 cm wide, lighter than rest of stem surface. LEAF: *prophyll* subequal to petioles of new leaves, yellow-green; *petiole* 50–92 cm long, 0.8–1.5 cm diam. at apex, broadly sulcate adaxially with sharply angled to rounded margins and sometimes with slight central ridge, sometimes minutely verruculose, sheath 8–16 cm long; *leaf blade* elongate-sagittate, margin repand, overall length 62–100 cm, overall width (24–)28–44 cm, upper surface mid green with paler green primary lateral veins, lower surface paler green with yet paler and pinkish flushed primary lateral veins; *anterior division* 39–70 cm long, 16–44 cm wide, widest at base, apex acute to obtuse with acuminate tip, *primary lateral veins* 3–5(–6), usually 4 per side, more spaced out towards leaf apex, arising at an angle of 50–90°, cross veinlets between finest parallel veins often quite distinct in dried material; *posterior divisions* 20–34 cm long, 0.3(–0.4) × overall blade length, (12–)14–21 cm wide, retrorse to slightly introrse, basal ribs denuded for (3–)4–6.5 cm, tip acute and ± rounded at extremity, primary acroscopic

veins (1–)2–3(–4), primary basiscopic veins (0–)1–4(–5), basiscopic lamina area well developed, \pm overlapping. INFLORESCENCE: *peduncle* 8.5–14(–30?) cm long, 2–4 cm diam. at apex, either enclosed almost entirely in petiole sheath or (fide Hooker) as long as spathe: *spathe* 20–30 cm long, 4–8 cm diam. at middle, decurrent for 2.5–5 cm long, outer surface glossy green with darker fine veins, dotted here and there with minute pale brown extra-floral nectaries, inner surface pale yellowish-white; *spadix* 18.5–30 cm long, white, fertile male zone 5.5–6.5 cm long, 2–2.8 cm diam., subellipsoid, sterile male zone 8–8.5 cm long, 1.4–3 cm diam., upper region sometimes narrower than adjacent fertile male zone, female zone 3.5–5 cm long, 2.2–3.5 cm diam. FLOWERS: *stamens* 7–7.3 mm long, 1–1.4 mm diam. at apex; *staminodes* 6.5–7.5 mm long, 2.2–3.8 mm diam. at apex, always \pm clavate, apex sometimes rounded, usually flattened, narrowing abruptly just below apex or tapering gradually; *gynoecium* 9–15.5 mm long, ovary \pm flask-shaped. 4.5–5.5 mm long, 3–4.8 mm diam., raphides very numerous in septa and inner walls, at least in apical part of ovary, or extending also to base, *locules* 12–13 per ovary, *ovules* 3–4 per locule, inserted from base to about middle of axis, evenly spaced, style body lacking since compitum penetrates well down into ovary axis, style crown very elongated, extending for up to 9–10 mm beyond ovary locules, \pm lacking tannin, style lobes at apex weakly or not at all evident externally but running down inside as distinct ridges covered with stigmatic papillae almost to base of compitum, central dome present, extending to apex of style crown or slightly less, stylar canals very short, entering locules about halfway down, stigma 4.2–6 mm diam., sometimes with many tannin hairs, covering style crown lobes when these are well-developed (*Williams* s.n.) or \pm confined to style funnel when lobes are not well-developed (*Harley et al.* 18501). FRUIT: *berry* shortly compressed-cylindric, 1.6–1.7 cm long, 1.3–1.5 cm diam., pale orange, style fleshy and persistent; *seed* ovoid-subcylindric, 5–5.5 mm long, 2.8–3.1 mm diam., pointed at micropylar end, buff white testa very fleshy, forming a \pm opaque sarcotesta surrounding subcylindric inner body containing endosperm and embryo. Fig. 17C, Map 2D.

HABITAT. Hemi-epiphytic in rainforest, rupicolous, or terrestrial in restinga coastal vegetation on sandy soils. The most complete fertile field collection seen (*Harley et al.* 18501) was in fruit in early February; alt. 0–500 m approx.

BRAZIL. Bahia: 5 km SE of Maraú at junction with road N to Ponta do Mutá, 14.08S, 39.00W, 2 Feb. 1977, *Harley et al.* 18501 (infr., CEPEC! K! RB! SEL! US!). Espírito Santo: Reserva de Sooretama, near headquarters buildings in musurunga forest, 22 Jul. 1969, *Sucre* 5728 (sterile, RB!); N of Santa Teresa, valley of the Conão, 7 Nov. 1953, *Duarte* 3673 & *J. C. Gomes* 431 (infl. fragment, RB!).

CULTIVATED. Brazil: collected in Espírito Santo state, Brazil, cult. R. Burle Marx, Sítio Santo Antônio da Bica, Barra de Guaratiba, Rio de Janeiro state, 15 Feb. 1983, voucher by S. Mayo, *Burle Marx* BM VI (sterile, K!). United Kingdom: cult. Kew, collected near Salvador, Bahia state, Brazil, vouchers by J. D. Hooker, Aug. 1870 and N. E. Brown 9 June 1876, *Williams* s.n. (infl., K! holo). United States of America: Florida, Dade County, South Miami, cult. A. Fernandez, 21 Apr. 1983, *Plowman* 13002 (young infl., F!).

The most complete collection seen (*Harley et al.* 18501) is a very good match with the type specimen of *Williams*, and comes from an area fairly close to

Salvador, the assumed type locality. The material from Espírito Santo state differs in having narrower and relatively more elongated leaves (Fig. 17C), but in the absence of fertile specimens it is impossible to assess fully the distinctions between these two populations. It is to be expected, however, that more than one taxon may be involved in view of the suggestion of a phyto-geographic boundary in Espírito Santo between vicariant species pairs in several families (Prance 1979). The plant most commonly cultivated in the USA and elsewhere as *P. williamsii* resembles the Espírito Santo population rather than the type.

C. H. Williams, the collector of the type specimen, was resident at Salvador, the capital of Bahia state and generally known as "Bahia" in the last century. Williams was an active correspondent of J. D. Hooker between 1863 and 1869, as evidenced by letters in the Kew archive. During this period he exchanged plants regularly with Kew. His letters describe an aroid which is probably the same as that which Hooker eventually described in 1871 as *P. williamsii*. Hooker's description in the Botanical Magazine says only that '... This noble aroid has been for years a well known ornament of the aquarium near the Palm House at Kew... It was sent to Kew by Mr Williams, of Bahia, many years ago...' Williams states in a letter to Hooker (28 Feb. 1865, Vol. 218 no. 348): 'I am also preparing, that is drying, seeds of a very curious Aroideae, which gives a head like Indian corn, full of pulpy grains very sweet and pleasant to the taste, and considered a great delicacy here. It is not cultivated, but found wild – and is known as "Milho de caboclo" Indian's mais – also grows near water, around tanks...' A later letter (13 March 1865) mentions that he is sending the seeds, and on 10 May 1865 he wrote '... In it [the consignment] you will also find some seedlings of the aroid you thought like the "Tornelia fragrans"...' and he listed '8. Tornelia fragrans? 8 plants' as included in the consignment. Hooker had clearly made the comparison between the infructescence of Williams' plant and that of the edible *Monstera deliciosa* (syn. *Tornelia fragrans*).

Engler (1899) and Krause (1913) both cite a collection from Ilhéus, Bahia, made by Archduke Ferdinand Maximilian no. 728, formerly held at Vienna (W). This was destroyed in the Second World War, but a pencil drawing at W prepared under Schott's direction (Schott Icones Aroideae no. 2553, see Schott 1984) shows two leaves which are probably of *P. williamsii*. It is possible, however, that these leaves could be of the large form of *P. corcovadense* found in the coastal rainforest of Bahia; Schott himself did not identify the drawing to species.

INCOMPLETELY KNOWN SPECIES

1. *Philodendron petraeum* Chodat & Vischer in Chodat, Vég. Paraguay 3: 357, 376, fig. 262, 263 (1920). Type: Paraguay, Tobaty between Tobaty and Barrero Grande, Chodat & Vischer 349 (?G, not seen).

P. petraeum Chodat & Vischer var. *petraeum* ['var. *genuinum*'].

P. petraeum Chodat & Vischer var. *tobatiense* Chodat & Vischer in Chodat, Vég. Paraguay 3: 377 (1920). Type: Paraguay, Chodat & Vischer 350 (G, not seen).

P. petraeum Chodat & Vischer var. *triangulare* Chodat & Vischer in Chodat, Vég. Paraguay 3: 379 (1920). Type: Paraguay, Chodat & Vischer 347 (G, not seen).

P. petraeum Chodat & Vischer var. *valenzuelae* Chodat & Vischer in Chodat, Vég. Paraguay 3: 379 (1920). Type: Paraguay, near Valenzuela, Chodat & Vischer 357 (G, not seen).

I have not studied the type material of any of these taxa, which except for var. *petraeum* are known only from sterile plants. The species has sagittate leaves, a rupicolous habit, the spathe as long or longer than the peduncle and a 6-locular ovary according to the description. In var. *tobatiense* the leaves are larger, up to 50 cm long and 40 cm broad. Vars. *triangulare* and *valenzuelae* both have smaller glaucous leaves which are triangular in the former and relatively narrow in the latter.

The available information suggests that *P. petraeum* is a distinct species, since it does not appear to fit any other described taxon. Though superficially similar to *P. corcovadense*, Chodat & Vischer's fig. 262, shows stems with very contracted internodes. These taxa are cited in Croat & Mount's recent treatment of Paraguayan *Araceae* (Croat & Mount 1988).

2. *Philodendron pseudoundulatum* Grau in Lilloa 36: 31, t. 7v (1983). Type: cultivated plant, Argentina, Tucumán, San Miguel de Tucumán, Grau 19 (LIL, holo., not seen).

This species was described from cultivated material which probably came from the region of Santa Cruz in Bolivia, according to the author. His description and figure show a large plant with stems up to 1.5 m tall and leaf blades up to 1 m long which are broadly sagittate with repand to irregularly undulate margins. The inflorescences are large, the peduncle is 10–15 cm long, the spathe 20–25 cm long, and the spadix 20 cm long. The ovary is 8–10-locular and the stamens 6–8 mm long.

As far as it is possible to tell from the description, this plant does not conform to any previously described species. In view of the few collections that exist from Bolivia, it would not be surprising if further study of this interesting taxon confirmed that it is indeed a distinct species.

3. *Philodendron* sp. A

This Brazilian species (Map 3B) is known only from a single sterile specimen (Espírito Santo state, Reserva de Sooretama, Lagoa de Macuco, 16 Jul. 1969, Sucre 5613 [RB!]). The collection includes habit photographs showing that the plant is an erect, emergent aquatic of open habitat in lake margin swamps. The leaf blade is about 50 cm long and sinuately lobed with about 4 primary lateral veins per side in the anterior division.

A somewhat similar aquatic plant but with smaller leaves occurs in Minas Gerais state at Diamantina (Pereira 2841 & Pabst 3677 [HB! RB!]).

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