A REVISION OF MONSTERA (ARACEAE)

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The genus *Monstera,* as here interpreted, comprises 22 species and 3 varieties of scandent epiphytes, including some of the most magnificent and conspicuous climbers of the neotropics, easily recognized by their huge, perforated leaves. Though common and abundant in the wild, *Monstera* species are poorly represented in herbaria, principally because the large fleshy parts are too big for plant presses, difficult to dry, and because the plants usually flower out of reach.

This study had its genesis in an unsuccessful attempt to identify some Mexican monsteras, which revealed the lack of a useful monograph of the genus and the chaotic application of names to specimens in herbaria. Although *Monstera* was monographed by Engler and Krause in 1908, neither author was able to study the plants in the wild and their treatment reflects the inadequacy of herbarium specimens in studies of Araceae. The revision here presented is based on 18 months of field work in Central and South America, encompassing study of about 400 populations representing 17 species. In addition, over 3000 herbarium specimens were examined.

ACKNOWLEDGEMENTS

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HISTORY OF THE GENUS

In 1693, *Monstera* first appeared in western literature in an account of the vegetation of Martinique by the French botanist, Charles Plumier. Plumier provided a generous illustration of a plant (as *Arum hederaceum, amplis foliis perforatis*) which is clearly *Monstera adansonii.* The accompanying text included observations on the dimorphism of roots, the structure of the leaves and inflorescence, and the use of the plant by natives as a snake-bite remedy. Plumier's description and illustrations were cited by Linnaeus (1753) as the basis for *Dracontium pertusum* L. The Linnaean genus *Dracontium* included aroids with perfect flowers, numerous seeds, and five perianth parts. His placement of Plumier's plant in this genus suggests that Linnaeus erroneously considered it to have flowers with a perianth, as Plumier supplied no observations on this point.

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During the decade following the publication of *Dracontium pertusum*, the species was illustrated and described in several works by Philip Miller (1754, 1760, 1763). It was said to be cultivated in England and Holland as a stove plant and Miller described the method of sending cuttings from the West Indies embedded in bales of damp hay. He also provided a good illustration of its flowers from cultivated material and was the first to note the absence of a perianth.

In 1763 the name *Monstera* was first used by Adanson in his *Familles des Plantes*. It is not clear what concept he intended by *Monstera;* the combination of characters associated in his description represents no known species of plant. Apparently he was attempting to redescribe the genus *Dracontium* L. giving it a new name. In the text, he mentioned a *Monstera* with a tuberous root and spiny petioles, evidently referring to *Dracontium spinosum* L. He also mentioned a *Monstera* with perforated leaves, and it is undoubtedly this single characteristic which later led authors to use the name *Monstera* in its present sense, which otherwise disagrees with Adanson's description in several respects: perianth absent (vs. "calice-5 feuilles"), stamens 4 (vs. "7"), and seeds one, rarely two (vs. "plusieurs"). In his publication, Adanson listed *Dracontium* L. as a synonym, thereby rendering the name *Monstera* superfluous. The conservation of the name is discussed below.

Monstera was next taken up by Aublet (1775). In describing an *Anthurium* from French Guiana (as *Dracontium pentaphyllum*), he gave as a common name "la Monstère de la Guiane." There is no indication that Aublet was using the name *Monstera* in relation to Adanson's use of it; most likely he was using it simply as a variant of the names dragon, draco, etc., as part of a general practice of referring to aroids as snakes, serpents, dragons, and monsters. This is an association which is found in many cultures, and even in ancient Greece *dracunculus,* "little dragon," is given by Theophrastus as the name for a Mediterranean aroid. This association is apparently most commonly based on the snake-like appearance of the mottled petioles and peduncles. It seems most probable that *Monstera,* as used by Adanson, is a latinized French equivalent of *Dracontium,* and is not, as Schott (1858) suggested, based on the apparent monstrosity of the holes in the leaves.

During the 70 years following Adanson's publication of *Monstera,* the West Indian species spread in cultivation to botanical gardens and conservatories throughout Europe, where it was duly noted in seed catalogues and plant lists as *Dracontium pertusum* L.

A new phase in aroid classification began in 1830 with the publication of the first of a series of monographic works on the family by H. W. Schott of Vienna. Schott laid the foundation of the generic classification of the Araceae, based largely on floral morphology, and his studies culminated in the *Genera Aroidiarum* (1858) and *Prodromus Systematis Aroidiarum* (1860) which included descriptions of 104 genera and

972 species. In addition, he commissioned the preparation of more than 3000 illustrations of aroids which rank among the finest botanical illustrations known. They are housed in the Museum of Natural History in Vienna and many serve to typify the Schott species.

Schott (1830) revived the name *Monstera* Adans., though the concept delimited by Schott was quite different from that of Adanson, which was essentially identical to Linnaeus' *Dracontium.* The only *Dracontium* included was *D. pertusum* L. and the other ten *Monstera* species were transferred from *Pothos* L. They represent plants now considered to belong to *Rhaphidophora, Epipremnum,* and *Scindapsus* (all Asian) as well as two species of *Philodendron.* The generic description mentioned a persistent spathe, a two-locular ovary with two basal ovules per loculus, and the operculate fruit characteristic of the group. Since the new combination *Monstera pertusa* (Roxb.) Schott was made based on *Pothos pertusus* Roxb., *Dracontium pertusum* L. was given the new name *Monstera adansonii* Schott.

Two years later, Schott (1832) subdivided *Monstera,* separating the Asian species as the genus *Scindapsus,* with the technical distinction of a unilocular ovary in *Scindapsus* and a bilocular ovary in *Monstera.* The description of the spathe in both genera was changed from *persistens* to *decidua.* This left only three species in *Monstera: M. adansonii* Schott, *M. lingulata* (L.) Schott, and *M. cannaefolia* (Rudg.) Schott, the latter two being philodendrons.

By 1840, *Monstera* had been in the European literature for 150 years, and its known range extended from the West Indies to Brazil, but only the one species, *M. adansonii,* was recognized. (The juvenile of *Monstera dubia* was in cultivation as *Marcgravia dubia* but had not yet been identified as an aroid.) In the 1840's *M. deliciosa* was discovered independently by Liebmann in Mexico and Warszewicz in Guatemala, who brought live material to Copenhagen and Berlin respectively. The introduction of this species was a horticultural triumph, and its cultivation quickly spread throughout Europe. It remains today one of the most extensively cultivated plants in both tropical and temperate countries.

Following the introduction of *Monstera deliciosa* into Europe, there was a rush to discover and describe other new species, and by 1860, when Schott produced the first monograph of *Monstera,* he included 35 species. Six of these were placed in a separate genus, *Tornelia,* on the basis of their having pinnatisect leaves.

Schott's concept of species was a narrow one. Faced with an influx of new collections, he attempted to record the diversity he encountered by giving each variant specific status. Thus many of his species are distinguished by slight differences in leaf shape and texture and later authors have placed the names in synonymy. Nonetheless, Schott's monograph serves as an important record of the early collections of *Monstera,* and the plates at Vienna illustrating the Schott species remain a valuable reference.

Following Schott's death in 1865, Adolf Engler of the Berlin Botanic Garden succeeded him as the world specialist on the Araceae. Engler twice monographed the family in its entirety: first, in 1879 as volume two of DeCandolle's *Monographiae Phanerogamarum*, and second, from 1905 to 1920 as a series of volumes of *Das Pflanzenreich*. Engler's first treatment of *Monstera* was in the *Flora Brasiliensis* (1878) where he provided a key to all the species. This was the first key written for the genus (Schott had not produced any) and the number of recognized species was reduced from Schott's 35 to 12.

In 1882, Hemsley revised the Central American species of *Monstera*, synonymizing some species distinguished by Engler. Hemsley was the first to recognize that several species described in the genus *Marcgravia* were really juvenile plants of *Monstera*.

Engler's studies of *Monstera* culminated in a monograph written with K. Krause and published in *Das Pflanzenreich* (1908), a treatment representing considerable progress over earlier efforts. Twenty-seven species were recognized, and 33 others listed in synonomy. The descriptions are ample and a number of collections are cited. However, the key is inconsistent and unworkable. Specimens are very difficult, if not impossible, to determine by using it. While a number of the distinctive species were, by this time, well demarcated, the complex of species centering on *M. adansonii* remained confused.

In the last fifty years, various accounts of *Monstera* have appeared in floristic works. For the most part, these are simply extracts from the Engler and Krause monograph, but two exceptions are: the *Flora of Suriname* (Jonker-Verhoef & Jonker, 1952); and *Commentary on Mexican Araceae* (Bunting, 1965). They include a number of new observations and emphasize the need for a revision of the genus. However, both are hampered by their geographically limited outlook.

As mentioned earlier, the name *Monstera* was superfluous at publication since *Dracontium* L. was cited as a synonym. Bunting (1962b) proposed the conservation of *Monstera* Schott against *Monstera* Adans., but this proposal was rejected (McVaugh, 1967). Subsequently, Nicolson (1968a) proposed the conservation of *Monstera* Adans. with the designation of *M. adansonii* Schott as the lectotype species; this was accepted by the Committee for the Conservation of Generic Names (McVaugh, 1970).

GENERIC RELATIONSHIPS

The tribe Monstereae of the Araceae is a well-defined and easily recognized group of about 200 species which have a number of features in common. All are scandent or subscandent epiphytes of wet tropical forests and contain in their vegetative and flowering parts numerous needle-like or H-shaped trichosclereids. The leaves have two pulvini, one at each end of the petiole, and the lamina often exhibits natural perforations. The spadix consists of perfect flowers, each with four stamens and lacking a perianth, and the spathe is deciduous after anthesis. The Monstereae are unique among the aroids in having meridiosulcate foveolate pollen (Thanikaimoni, 1969) and, for the few species studied, chromosome numbers of $2n$=60 or $2n$=120 (Marchant, 1970).

The present-day distribution of the Monstereae is Indomalaysian and neotropical, with two species in West Africa. The tribe is represented by fossil seeds in a number of tertiary deposits and was apparently a common element of a Paleogene Boreotropical flora (Madison & Tiffney, 1976).

The apportioning of the extant species into genera has been disputed for more than 100 years (e.g., Koch, 1856; Schott, 1858; MacBride, 1936; Steyermark, 1957; Bakhuizen van den Brink, 1958; Bunting, 1962a; Nicolson, 1968b; Hotta, 1970). Extreme positions are the recognition of 12 genera (Schott, 1860) or the inclusion of all of the species in one or two large genera (Koch, 1856; Bakhuizen van den Brink, 1958). The differences among these treatments reflect differences in philosophies of classification rather than in the kinds of characters used. All of these authors refer to the same few generic characters: placentation (axile, parietal, or basal); septation of the ovary (unilocular or bilocular); and geography (Asian or neotropical). Seed morphology, a character overlooked previously, was investigated by Madison and Tiffney (1976) and proves useful in generic classification. Seeds of the Monstereae are of several distinct types, the extremes of which are fusiform seeds 1 mm. long with abundant endosperm, and highly curved seeds 20 mm. long and lacking an endosperm.

In revising this group, I have tried to delimit the genera in a manner consistent with the generic classification of the rest of the family, and at the same time to provide a treatment which reflects the occurrence of groups of species which in their geography, morphology, and ecology show affinities and appear to be closely related. Seven genera are recognized which are defined by a combination of character states of placentation, septation of the ovary, and seed morphology. The genera are either neotropical or paleotropical in distribution except for *Scindapsus,* which is primarily Asian but has one species in South America. Several of the genera have definitive vegetative characters, but I have found no character to consistently separate *Epipremnum, Rhaphidophora,* and *Monstera* other than floral and seed morphology. Nonetheless, these genera are readily distinguished if the relevant features are examined.

Placentation, septation of the ovary, and seed morphology are interrelated factors of which the evolutionarily significant aspect is probably the number and size of seeds produced in the fruit. Seed size and number are subject to selective forces related to dispersal, seedling ecology, intraspecific competition, weediness, and rate of fruit maturation (Harper *et al.*, 1970). The mode of action of these forces in the evolution of the Monstereae is not altogether clear, though several aspects of it may be noted. The genus *Stenospermation* consists of true epiphytes, the seeds of which normally germinate on the surfaces of trees. Species of this genus have apparently entered a new adaptive zone (the other Monstereae germinate terrestrially) where small seed size is a critical factor for germination and establishment (Madison, 1977). It is noted elsewhere in this paper that in *Monstera* there has been selection favoring an increase in seed size related to host tree location by stoloniferous seedlings. The fossil seeds of Monstereae, mostly described in the genus *Epipremnum*, are intermediate in size, and it seems likely that evolution of seed size in the tribe has been simultaneously toward smaller seeds (in *Stenospermation* and *Rhaphidophora*) and larger seeds (in *Monstera* and *Scindapsus*).

MORPHOLOGY

Stem. Phillip Miller, in 1760, described the stem of *Monstera adansonii* as varying from "the thickness of a goose quill to that of a man's thumb." If all of the species are considered, the diameter of mature stems ranges from about 2 mm. in *M. obliqua* to 8 cm. in *M. deliciosa.* The most notable features of the older stems are the leaf scars, the axillary buds, and the adventitious roots.

Vegetative shoots of *Monstera* are normally unbranched, though lateral buds may be released in very old portions of a stem or in injured stems. Flowering is always accompanied by cryptic sympodial branching; the inflorescence is terminal and the continuation shoot arises in the axil of the leaf preceding the leaf which subtends the inflorescence. During development of the continuation shoot, the inflorescence is displaced to the side and appears axillary as illustrated for *M. dubia* in Figure 1.

The stems of *Monstera* have a distinct dorsiventrality and are usually flattened front to back. The portion facing the trunk produces adventitious roots, and the leaves are borne distichously on the opposite face. In some species the two ranks of leaves are nearly opposite (e.g., *M. lechleriana, M. dilacerata*), but in species of section Marcgraviopsis the angle of divergence of the two ranks (measured from the widest point of the leaf scar) is closer to 120°, and in *M. membranacea* and *M. gracilis* it approaches 90°.

In *Monstera lechleriana* and *M. dilacerata* the leaves are borne in a tight cluster at the top of the stem with the leaf bases overlapping. In other species the leaves are spread further apart on the stems, as is true of all species in section Marcgraviopsis. The length of the internodes is fairly constant within a species and is a reliable taxonomic character.

Also constant and taxonomically useful are the shapes of the leaf scars and the axillary buds. The axillary bud is located in a depression which may extend along the internode as a sulcus.

In all species the young stems are green and presumably photosynthetic; with time they may turn brown. The internodes of species in sections Monstera and Tornelia are smooth, whereas the species of sections Marcgraviopsis and Echinospadix usually have the stem roughened by the presence of numerous hard papillae about 1 mm. across and 0.5 mm. high. In these latter two sections the cuticle is quite thick and

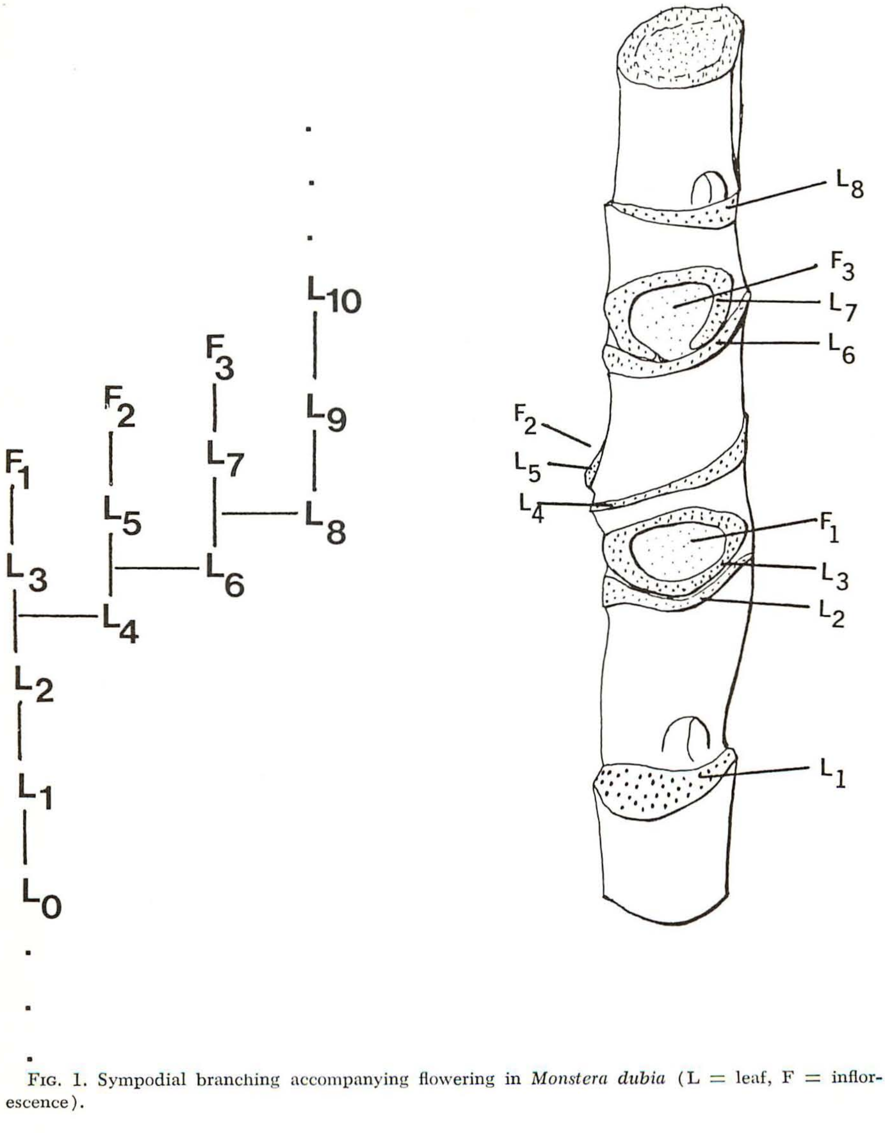


FIG. 1. Sympodial branching accompanying flowering in *Monstera dubia* (L = leaf, F = inflorescence).

yellow-brown in color; with a twisting of the stem it is shed in large flakes.

Roots. In many climbing plants the functions of anchorage, and water absorption and conduction have been divided between different kinds of roots. This root dimorphism has been observed in many lianescent species of dicots, monocots, and ferns (Went, 1895; Schenk, 1892; Lieurau, 1888). Its occurrence in *Monstera* has been discussed by Van Tieghem (1866), Lieurau (1888), and Engler and Krause (1908).

In *Monstera* the radicle elongates to a length of several centimeters at germination, but forms only a limited root system which is apparently short-lived. Most of the plant's root system is adventitious. The terrestrial seedling stages produce roots only at the nodes of the stem; these early roots are usually about 1 mm. thick and rarely exceed 20 cm. in length. The dimorphism of adventitious roots appears only after the plant has begun to climb, and usually when it is more than 1 m. above the ground and the stem is 7–10 mm. thick.

Went (1895) refers to the two kinds of adventitious roots as feeder roots and anchor roots ("Nährwurzeln" and "Haftwurzeln"). The feeder roots arise only at the nodes, generally one per node and more or less opposite the center of insertion of the leaf. These roots are positively geotropic and may either hang in the air or grow attached to the substrate. They are generally unbranched until they reach the ground, which may be a distance of 20–30 meters. But once they penetrate the soil, they branch profusely. Engler and Krause (1908) hypothesized that these roots are the major water-conducting organ of the plant rather than the stem. This seems likely because in older plants the stem may lose all connection with the ground through decay or mechanical injury without the plant wilting or showing other signs of water stress.

The anchor roots which serve to attach the plant to its substrate are produced along the internodes, though they may arise at the nodes as well. They are not positively geotropic, but grow in any direction over the substrate, often following the course of a fissure or irregularity in the surface. Where I have seen *Monstera* growing on a very smooth trunk or sheer rock, the anchor roots grew perpendicular to the stem. They may be 2–50 cm. long, but are usually 10–20 cm. long. The anchor roots adhere to the substrate by means of root hairs which terminate in a sort of suctorial disc (Went, 1895).

The anchor roots seem to require substrate contact for their continued growth after they have been initiated. When a climbing stem loses contact with its substrate, for instance by reaching the top of a stump, the production of roots in the subsequent internodes is decreased in number, and those that are elaborated become hard and cease growing when only about 1 cm. in length. Hanging stolons as well as pendent fertile shoots of those species which normally hang lack feeder roots altogether and bear only a small tuft of aborted anchor roots at each node.

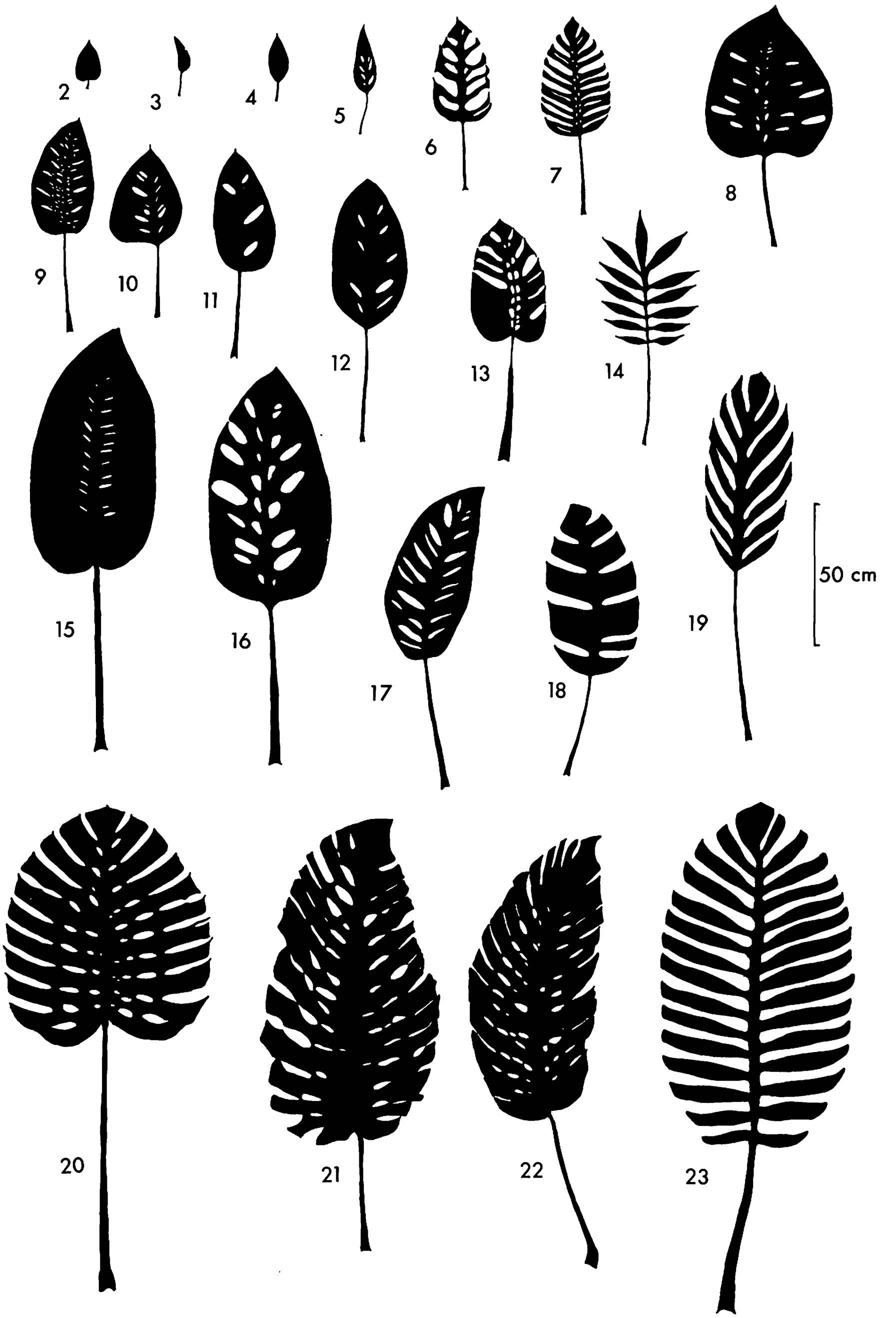
Leaf. The leaves of monocotyledons are normally described as consisting of a sheath, petiole, and lamina, but in the Araceae a different terminology is used (Schott, 1860; Engler & Krause, 1908 and others). The sheath and petiole together are called the petiole, which is described as being vaginate, winged, or canaliculate, or having a sheathing base or portion. For the sake of consistency this terminology is used in the present treatment, and the term petiole thus encompasses all of the leaf from its articulation at the stem to the lamina base.

The nature of the sheathing portion of the petiole, which protects the next developing leaf and terminal bud, is taxonomically useful in *Monstera.* The sheath may be restricted to the lower part of the petiole, or it may extend to the lamina base. At its upper end it terminates bluntly or is widely auriculate or is extended into a ligule. In *M. tuberculata* the ligule is about equal in length to the petiole. After the next leaf has expanded, the sheath may remain green and persist, or it may be marcescent or deciduous. The petioles of *Monstera* leaves have a swollen portion or pulvinus at each end; the upper one, located at the base of the lamina, is called the geniculum and is often conspicuously curved.

Although *Monstera* leaves arise distichously, their insertion is often not readily apparent because they may move to a different position subsequent to unfolding. The result of this movement is that the leaves are fanned out rather than placed one above the other, which is perhaps an adaptation to avoid the shading of the lower leaves by the upper ones. Observation of a large *M. deliciosa* growing in cultivation supports the assumption that this arrangement is a response to variation of light incidence. The plant, which was receiving approximately unilateral light from a window, was rotated 180°. There followed an extensive rearrangement of the leaves, occurring over a period of about two weeks and apparently resulting in less shading than immediately after rotation of the pot. This rearrangement was accompanied by a considerable flexion in the region of the pulvini, even in leaves more than two years old.

The leaf laminae of many species of *Monstera* exhibit perforations, one of the most characteristic features of the genus. Naturally fenestrate leaves also occur in *Epipremnum, Amydrium,* and *Rhaphidophora* in the Monstereae; *Cyrtosperma, Dracontium,* and *Rhektophyllum* in the subfamily Lasioideae (Araceae); and in *Aponogeton fenestralis* (Aponogetonaceae) and *Pentagonia* (Rubiaceae). This phenomenon early attracted the attention of various botanists. A. P. DeCandolle (1827) considered the holes to represent a failure of development and signify a weakness of the plant. August de St. Hilaire (1840), on the other hand, took them as an expression of "une plus grande energie vitale."

The ontogeny of the perforations was first elucidated by Trecul (1854). He observed that early in the development of the lamina, small patches



FIGS. 2–23. Adult leaves of *Monstera* species (to the same scale): 2. M. tuberculata; 3. M. pittieri; 4. M. obliqua; 5. M. xanthospatha; 6. M. gracilis; 7. M. epipremnoides; 8. M. oreophila; 9. M. siltepecana; 10. M. adansonii var. laniata; 11. M. adansonii var. adansonii; 12. M. adansonii var. klotzschiana; 13. M. membranaceae; 14. M. subpinnata; 15. M. lechleriana; 16. M. acacoyaguensis; 17. M. acuminata; 18. M. spruceana; 19. M. dilacerata; 20. M. deliciosa; 21. M. punctulata; 22. M. dubia; 23. M. tenuis.

of cells became discolored and died, and the part of the lamina that they would have developed into failed to develop. The death of these cells began in the mesophyll, and if it started very late in development, an area of mesophyll might be destroyed, but not the epidermis. This situation would result in windows in the leaf, similar to those found in species of *Zantedischia,* with the upper and lower epidermis covering an empty space.

The ontogeny of the fenestrations in *Monstera* leaves was subsequently studied by Schwartz (1878) and Melville and Wrigley (1969), and in *Epipremnum* by Webber (1960), but these authors did not add any substantial observations beyond those of Trecul. Melville and Wrigley (1969) proposed an interpretation of the formation of the holes in terms of Turing's diffusion reaction theory of morphogenesis, but this is so abstract as to be unverifiable.

The significance of the holes is obscure. King (1892) suggested that they allow water to drip through to the roots; otherwise the leaves would act like umbrellas and the roots would be left dry. This is a fanciful interpretation with no basis in reality. It seems possible that the holes may act to break up a still air layer adjacent to the leaf and thereby increase convection and prevent the leaf from overheating when exposed to heavy insolation. Lacerated leaves of *Musa* were shown to have consistently lower temperatures in full sun than equivalent entire leaves (Taylor & Sexton, 1972), and the holes in *Monstera* leaves might well function in the same way as the tears in *Musa* leaves.

If the holes begin to form early enough in development, they may extend to the margin, resulting in a pinnatifid leaf. Subsequent initiation of a second series of holes may lead to a leaf which is both perforate and pinnatifid. Variations in the shape of adult *Monstera* leaves resulting from these phenomena are illustrated in Figure 2–23.

Reproductive structures. There does not seem to be a pronounced seasonality in the reproductive behavior of *Monstera.* In all species for which more than a few collections are known from a region, flowering individuals may be found in any month of the year. When plants do flower, several inflorescences are usually produced sequentially, each shoot of the sympodium bearing two cataphylls and the inflorescence. The usual number is two to four spadices in a cluster, though six to eight is normal in *M. obliqua* while the inflorescences are usually solitary in *M. lechleriana.*

The spadices of *Monstera* are borne on erect peduncles except in *M. tuberculata* where the peduncle and spadix are pendent. The peduncle is terete or flattened, 5–45 cm. long and 0.2–4.0 cm. thick; it continues to grow after flowering and may increase 50% in length and thickness between anthesis and fruit maturity.

The developing spathe is green and tightly wrapped around the spadix, exceeding it in length. At the time of flowering, the spathe unfurls and becomes colored; depending on the species, it may be white to deep yellow to rose. The spathe often shows a constriction about ⅔ of the way up its length which represents the region where it was closed over the top of the spadix in the bud. When fully expanded the spathe may be nearly globose with only a slit-like opening or it may be hemispherical with the spadix fully in view. The spathe persists for two or three days after opening and then falls off following the formation of an abscission layer at the base. Sometimes the spathe is enmeshed in a cluster of inflorescences and may persist *in situ* for a considerable time after abscission.

The spadix goes through a variety of color changes in development. It may be green or white in the bud, and is usually white to yellow at anthesis. Following anthesis it turns green, and at maturity it may remain green or become white, yellow, or orange. During development of the fruit the spadix may double in thickness and length. The use of spadix size as a character in the taxonomy of the genus has been unsatisfactory because authors give dimensions of 'the spadix' without specifying the stage of development.

The axis of the flowering spadix bears numerous, spirally arranged, perfect flowers, each with four stamens and lacking a perianth. The flowers at the base of the spadix are usually sterile. The flowers are protogynous by one or two days, and maturation of the inflorescence is acropetal. Production of stigmatic drops has ceased by the beginning of anthesis, and thus self-fertilization is not possible within an inflorescence.

The stamens have a broad filament 1.0–1.5 mm. wide with an adaxial ridge. The anthers are not visible until just before anthesis, when they emerge from adjacent pistils by elongation of the filament. The pollen, which is shed through slits in the anthers, is aggregated into sticky threads.

The ovary is bilocular with a perforation at the base of the septum. There are two anatropous basal ovules in each loculus borne to either side of the perforation. The slit-like stylar canal opens into an elongate stigma usually surrounded by a slight ridge. The stylar region contains numerous needle-like trichosclereids, 2–3 mm. long, which are oriented along the axis of the pistil.

Bunting (1965) has suggested that *Monstera* may be wind pollinated, but its syndrome of floral characters definitely suggests insect pollination. At the time of flowering, the spathe turns from green to white, rose, or yellow as does the spadix. These inflorescences are conspicuous in a dark forest, and apparently attract visually-oriented pollinators. I have not observed any odor produced by inflorescences of *Monstera* except a faint, sweet smell in a few cases. The flowers at the base of the spadix are sterile, but produce a large stigmatic drop. These may be functioning as nectaries, as there are no nectaries in the fertile flowers.

A pollination phenomenon, known for many of the Araceae, is an increase in temperature of the spadix. Leick (1915) reported for *Monstera deliciosa* an increase of 15°C over ambient temperature at anthesis. This may attract a heat-seeking insect, or may serve to volatilize a relatively non-volatile scent.

Insect visitors to *Monstera* spadices are varied and numerous. In a single inflorescence I have observed several species of beetles, hemiptera, flies, and bees. Of these, the bees are the most mobile and are perhaps the effective pollinators. C. H. Dodson (personal communication) has observed trigonid bees to be the chief pollinators of *M. lechleriana* and *M. dilacerata* in Ecuador. The failure of seed set in isolated plants and in a number of species in cultivation underscores the necessity for a proper pollinating agent and suggests that *Monstera* may be free of the agamospermy which bedevils classification of other aroids, notably *Anthurium.*

Following pollination the spathe abscises and the spadix turns green, apparently becoming photosynthetic and also providing a cryptic coloration to protect the developing seeds. Probably more effective in this regard are the numerous trichosclereids in the stylar region of the pistils, which represent a considerable mechanical barrier around the developing seeds. I have never observed predation of developing *Monstera* fruits.

The fruits mature in a period of 2–15 months, depending on the species, and the protective stylar portion of the pistil is shed, revealing the seeds in a sweet pulp which is usually gray, but may be brightly colored. The seeds are eaten by birds according to observations recorded on herbarium specimens, but I have not observed birds at ripe fruits. It is not uncommon to find, attached to the plant, the axis of an old spadix with all of the seeds gone, suggesting that they may have been picked off and eaten. However, one also frequently finds a large number of seedlings originating in a single spot on the ground below a *Monstera* plant, indicating that either a ripe spadix has fallen or a large number of seeds have fallen or washed off at one time.

Seeds. Although the ovaries of *Monstera* flowers contain four ovules, three usually abort and the fruits are one-seeded; rarely are two-seeded berries encountered. During the development of the seed, the ovule curves and becomes reflexed about the raphe so that the path of the vascular bundle in the raphe is S-shaped. This unusual morphology is illustrated by Madison and Tiffney (1976).

Abundant endosperm is produced early in the development of the seed but is consumed by the growing embryo. In the mature seed, endosperm is absent and the principal storage organ is the swollen hypocotyl of the embryo. Cut, fresh seeds are green or bluish in color within.

In contrast to other Monstereae, the seeds of *Monstera* have a soft seed coat. Seeds of *M. adansonii* and *M. deliciosa,* and probably other species as well, rapidly lost viability if allowed to dry out, but if kept moist may be stored for several months.

Seed shape and size are quite variable in the genus and provide useful taxonomic characters at the specific level. Seeds of a number of species are illustrated by Madison and Tiffney (1976).

Sclereids and Raphides. As with most Araceae, *Monstera* has cells containing bundles of calcium oxalate raphides distributed throughout the tissues of the plant; these are particularly abundant in the fruit and seed coat. In addition, monsteras contain the needle-like trichosclereids characteristic of the subfamily, but these are much less regularly distributed. In most species, they are absent from the roots (except in *M. deliciosa*); they are absent from the leaf lamina in *M. punctulata* and from the stylar portion of the ovary in *M. obliqua*. They are always present in the spathe. Nicolson (1960) found them most consistently in stems and petioles.

The sclereids are usually unbranched as they occur in the ovary, but in the rest of the plant they are often H-shaped and occasionally stellate. Hanstein (1864) considered the H-shaped forms to be the result of 'copulation' of two adjacent fibers, but ontogenetic studies by Van Tieghem (1886), Block (1946), and others have not supported this hypothesis.

In the earlier literature the trichosclereids were sometimes referred to as 'raphides,' initiating a confusion which has persisted to the present. For instance, the scratchy and acrid nature of unripe *Monstera* fruits has been widely attributed to raphides of calcium oxalate, but the stylar portion of the fruit is abundantly supplied with trichosclereids which visibly penetrate the skin when the fruit is handled. This portion of the ovary is deciduous and is not normally eaten, so it remains unclear whether the reported prickly nature of the unripe fruits is due to raphides or trichosclereids.

GROWTH HABITS

Species of *Monstera* are hemi-epiphytes adapted to growing on the lower to middle trunks of trees below the canopy. Germination is terrestrial and the young plants creep along the ground until they encounter a tree and begin to climb. Eventually, as the older portions of the stem die and decay, the plant may lose connection with the ground by its stem although retaining a terrestrial connection by long adventitious roots.

Plants of this habitat and habit have been referred to as 'shade epiphytes' (Walter, 1971) or 'small climbers' (Richards, 1952). They are mostly monocotyledons and ferns and in the neotropics the majority of them belong to a relatively few genera of the families Araceae, Cyclanthaceae, and Polypodiaceae.

The principal advantage of this habit of growth is usually considered to be the interception of a greater amount of sunlight without the necessity of building a self-supporting structure to reach the light. The data of Schulz (1970) show an approximate doubling of total incident light per day between 15 cm. above ground and 2.5 m. above ground in a rain forest in Surinam. Other possible advantages to these species are the evasion of strictly terrestrial predators and the placement of flowers and fruits in a conspicuous situation.

The principal adaptive radiation in *Monstera* has been a diversification of growth habits within the shade epiphyte habitat, involving differences in the kinds of trees on which species grow and the way they grow on them. This combination is so distinctive that most species can be recognized from a distance. In addition, specialization of growth habits has occurred in the seedling and juvenile stages, and in some species evolutionary divergence of the juvenile and adult phases has resulted in marked heterophylly.

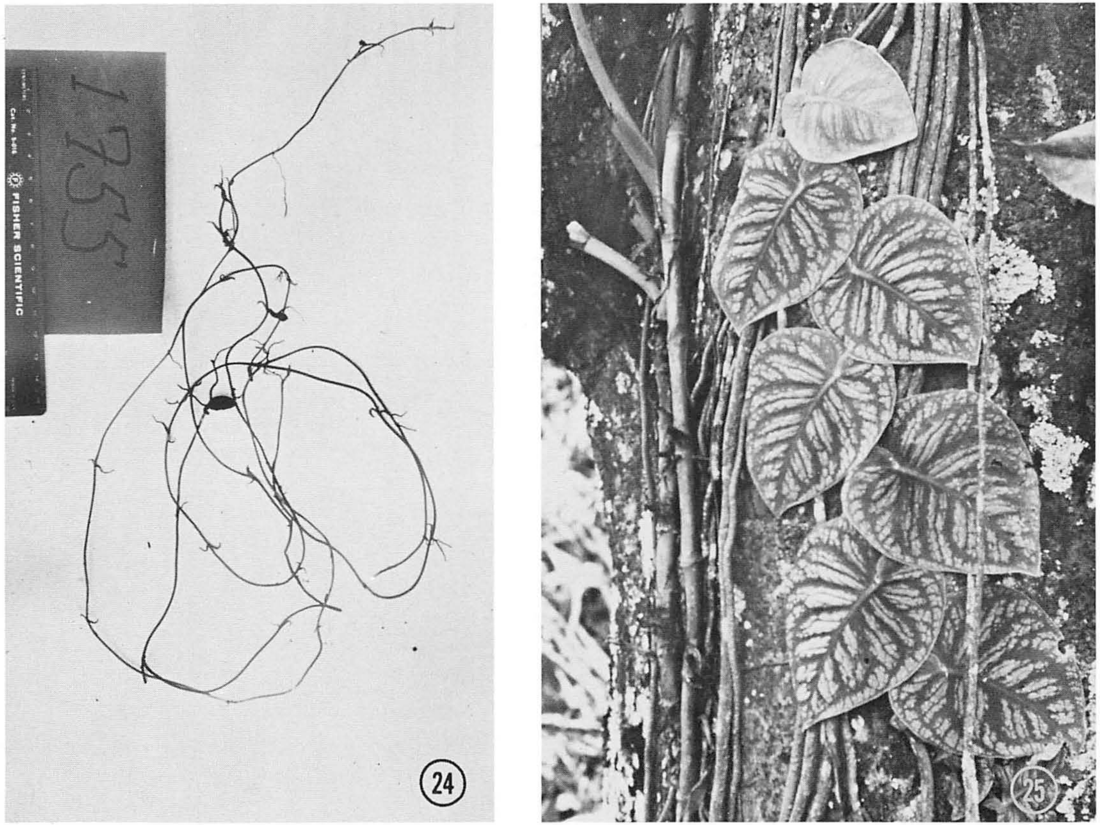
The discussion that follows will consider separately the growth habits of the seedling, juvenile, and adult phases. The term seedling here refers to the portion of the plant which grows, at least in part, on the resources stored in the seed, generally for the first several months of growth. The juvenile is the post-seedling stage before the production of adult foliage, and includes the earliest stages of climbing. The adult phase is that which has leaves typical of flowering individuals. In species where development is by a gradual increase in size, this division is somewhat artificial, but in other species it is clearly marked by well-defined changes in morphology.

In field and geenhouse studies of *Monstera,* I have observed no deviation from the seedling and juvenile type characteristic of each species. The growth habits of adults are more variable, and the types here described represent the modal habits of species rather than definitive categories.

Seedlings. *Monstera* seeds are apparently dispersed by birds, and germinate on the ground. The seedlings and juveniles grow as terrestrial plants until they encounter a tree and begin to climb. Field observations indicate that, where *Monstera* seedlings are found growing on a slope, they almost always grow uphill. This tropism may be fairly effective in locating a tree, since the microrelief of the forest floor generally includes slopes toward the bases of trees because of the accumulation of litter.

Strong and Ray (1975) studied, in the wild, seedlings of a species they refer to by the ambiguous name *Monstera gigantea,* which is probably *M. tenuis* or *M. dubia.* According to their observations the seedlings grow directly toward darkness, a phenomenon which they term 'skototropism.' Since potential host trees represent a dark sector of the horizon, growth toward darkness could be an effective mechanism for tree location by the seedling.

In plants of section Monstera the first two leaves of the seedling are cataphylls, followed by foliage leaves. The plant shows a gradual increase



FIGS. 24–25. 24. Stolon-like seedling of *Monstera acuminata* (*Madison 1755*, GH); 25. Shingle plant, *M. dubia*.

in size of the leaves and diameter of the stems throughout its development. In the subsequent discussion I refer to this type of growth as unspecialized.

In plants of sections Marcgraviopsis and Echinospadix the germinating seed produces a green stolon about 1 mm. in diameter with internodes 4–10 cm. long (Fig. 24). Cataphylls or minute scale leaves are borne at the nodes. This stolon grows along the surface of the ground for a distance of up to two meters without increase in diameter. The seedling normally begins to produce foliage leaves only after it has begun to climb. In the subsequent discussion I refer to this type of growth as specialized.

Seedlings of species in section Monstera, the unspecialized type, are difficult to find in the field. Even in very small and probably young plants the seed coat is not evident. However, I have encountered seedlings of *M. lechleriana* and *M. adansonii* in the wild; in these the seed coat was empty and shriveled and its resources apparently exhausted by the time the third foliage leaf was produced. A similar situation was found in seedlings of *M. adansonii* grown in cultivation, where the seed coats were empty and shriveled by the time the stem had elongated 3–8 cm. from the place of germination.

In contrast, the stolon-like seedlings of species in sections Marcgraviopsis and Echinospadix are fairly commonly encountered in the wild, and are always found attached to the plump seed. Seedlings of this type can elongate for a distance of 1–2 m. on the resources stored in the seed. They are green and photosynthetic where exposed to light, but often they grow under leaf litter and are white in color. These stolon-like seedlings seem to be an adaptation for rapid location of a tree. The species which grow in this way are evading competition as terrestrial plants by reaching an epiphytic habitat as seedlings.

The probability that a stolon-like seedling will successfully reach a tree is a function of the length it can grow, which in turn depends on the energy stored in the seed. This situation would favor an evolutionary increase in seed size for species with stolon-like seedlings, offset by an increased energetic cost per seed, usually resulting in fewer seeds produced per plant. In the size range of *Monstera* seeds (6–22 mm.) increased size also probably involves a decrease in dispersibility. The mean seed weight of FAA-preserved seeds of species with stolon-like seedlings is 255 mg. compared to 140 mg. for species with unspecialized seedlings ($p < .05$).

Juvenile Plants. The *Monstera* species with unspecialized seedlings also have unspecialized juveniles. The terrestrial and climbing plant shows a gradual increase in leaf size and stem diameter toward the adult condition.

The species with stolon-like seedlings, however, have a highly modified juvenile. When the plant begins climbing a tree, it produces asymmetric foliage leaves which are flattened against the tree so as to overlap one another and completely cover the stem (Fig. 25). The petiole is very short and the sheathing portion, which protects the next developing leaf, is extended into a ligular outgrowth. This tightly appressed type of shoot with overlapping leaves is known in the horticultural literature as a 'shingle plant.' The shingle plant grows up the trunk producing successively larger leaves until it reaches a critical size, when in the course of a few nodes it changes abruptly to the adult form with large exserted leaves.

The shingle plant habit appears in several unrelated genera of climbers, e.g., *Marcgravia, Ficus, Metrosideros, Drynaria, Hoya, Scindapsus, Conchophyllum, Teratophyllum.* Goebel (1900) and Karsten (1925) suggest that in *Monstera* it is an adaptation to protect the young adventitious roots from dessication, as they are covered by the appressed leaves. It would also seem that transpirational water loss would be decreased by this habit, since the stomata, which are limited to the abaxial surface, are in contact with a still layer of moist air against the trunk of the tree, and are protected from drying winds.

It is plausible that the shingle plant is an adaptation to water stress when one considers the nature of the seedling. In section Monstera with unspecialized juveniles, a plant which is beginning to climb a trunk has a stem 5–10 mm. in diameter which in its horizontal terrestrial portion has numerous nodes, each with adventitious roots. The shingle plant, which is beginning to climb, is attached to a horizontal stem only 1–2 mm. in diameter, with relatively few nodes and few adventitious roots. Consequently, the young shingle plant has a much smaller terrestrial water-gathering system than those with an unspecialized climbing shoot of section Monstera, and it is more likely to be subject to water stress.

The stem of the growing shingle plant increases in diameter with each successive node, to the point where it can elaborate adventitious roots. These roots range from 4–10 mm. in diameter and usually extend to the ground. The adventitious roots increase the water-gathering capacity of the individual to the extent that it can undergo a phase change to the adult condition.

Thus the stolon-like seedling and the shingle plant juvenile combine to form a complex in which the shingle plant is an adaptation to water stress related to the small root system of the stolon-like seedling, which in turn is an adaptation for rapid location of a suitable substrate.

Adult Plants. The seedlings and juveniles of *Monstera* show two contrasting morphologies, the unspecialized gradual increase in size of plants of section Monstera and the stolon-like seedlings and shingle plant juvenile of sections Marcgraviopsis and Echinospadix. In the adult phase there has been a much greater diversification of growth habits, involving differences in the size of trees on which species grow, as well as the way they grow on them.

There is a correlation in *Monstera* between size of the mature plant and size of the tree on which it grows. The largest species (*M. tenuis, M. acuminata, M. punctulata,* and *M. lechleriana*) are found as reproductive individuals only on the largest forest trees. Smaller trees either do not provide a sufficient length of clear bole for these climbers to mature on, or else lack the strength to support a massive epiphyte. These *Monstera* species sometimes become established on small trees, but on reaching the first few branches, the stem grows away from its support and the pendant tip grows back to the ground.

Smaller species of *Monstera* can grow to maturity on smaller trees though they also colonize larger trees where they mostly grow among buttress roots and on the lower trunk, seldom climbing above 5 meters. *Monstera obliqua, M. xanthospatha,* and *M. minima* are the smallest species of the genus, with stems 2–10 mm. thick and leaves 10–25 cm. long. They can grow to maturity on nearly any woody substrate from the largest trees to twigs of shrubs or small saplings. Compared to the large monsteras, the small species occupy a more abundant but ephemeral habitat.

The size of *Monstera* species is correlated with growth rate and life span as well. Plants of several species were tagged in the field and inspected 12–18 months later. The small *M. obliqua* showed an annual stem elongation of 2–5 m., representing 30–70 new leaves with a total area of 0.2–0.4 m^2. Applying this rate of growth to plants which could be traced back to an apparent germination site suggested that individuals may flower within 1½ years after germination. At the other extreme, adult plants of *Monstera lechleriana* showed an annual rate of stem elongation of 12–20 cm. and a production of 4–8 leaves with a total area of 1.2–2.0 m^2. Individuals of this species apparently do not flower until about 6–8 years of age.

Considering the genus as a whole, the species of *Monstera* show a continuum ranging from small, rapidly elongating and early maturing species which occupy abundant but ephemeral habitats (twigs and small branches) to massive species with a slow rate of stem elongation and late maturation which occupy rare but stable habitats (boles of large forest trees).

Related to differences in elongation rate and host tree size preference, other differences of *Monstera* species are in which might be called the general aspect or attitude of the plants. *Monstera lechleriana* and *M. dilacerata* elaborate a tight head or cluster of 10–15 spreading leaves at the top of the stem. *Monstera punctulata* and *M. tenuis* have a more open habit of growth, with the arching leaves separated by long internodes. *Monstera acuminata* and *M. dubia* have long internodes and the leaf laminae are pendent from the petioles, and hang parallel to the trunk of the host tree. Individuals of the last two species often clothe the entire bole of a large tree to a height of 25 meters.

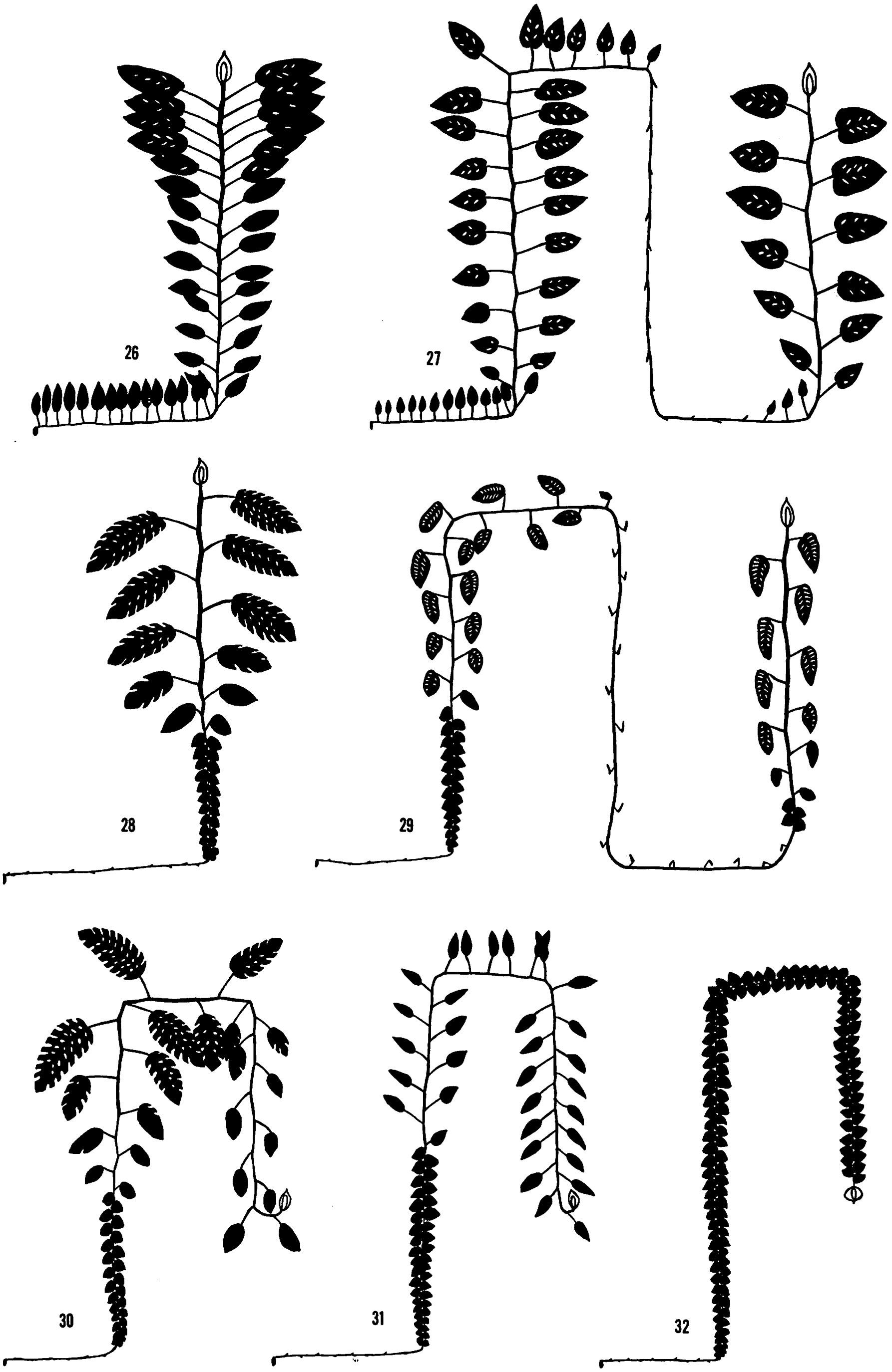
In species having long internodes, the leaves are spaced well apart and the shading of a leaf by the one above is diminished, but fewer leaves can be produced on a trunk before reaching the canopy. When a plant of *Monstera acuminata* reaches branches above the bole of the host tree, the stem is altered into a hanging stolon. This stolon has internodes to 30 cm. long and bears only cataphylls or highly reduced sickle-shaped foliage leaves at the nodes. It drops to the ground and grows horizontally, often for a distance of 10–20 m. until it encounters a tree and begins to climb. This represents a second type of tree searching activity in addition to that of the seedlings. While these stolons ('flagelliform shoots' of Engler and Krause, 1908) are encountered occasionally in most species, they are especially common in *M. acuminata, M. siltepecana,* and *M. obliqua.*

A second type of hanging shoot is found in *Monstera dubia,* a species having internodes 6–12 cm. long and large semi-pendent leaves. When the shoot reaches the first or second forking of branches in a tree, it turns 180° and begins growing downward as a hanging shoot. Unlike the hanging stolons described above, the hanging shoots of *M. dubia* produce full size stems and leaves, just as do the climbing shoots, except in this case the adventitious roots mostly abort. This manner of growth doubles the useful length of the bole of the host tree. When the hanging shoot eventually reaches the ground, it may root and grow up the trunk again as a climbing shoot. Flowering occurs in either ascending or hanging shoots.

Several species *(Monstera luteynii, M. pittieri* and *M. tuberculata)* always produce hanging shoots and flower only in the pendent portions. They all have small coriaceous leaves and thick cuticles, apparently xeromorphic adaptations to the greater water stress of free-hanging rootless shoots as compared to attached shoots with numerous adventitious roots. The hypothetical neotonous origin of *M. tuberculata* from an *M. dubia*-like ancestor is shown in Figures 26–32.

Monstera acuminata, with four radically different kinds of shoots, represents an extreme of heteroblastic development (Fig. 29). The seedling is a thread-like creeper which elongates rapidly while locating a host tree. The second stage is a shingle plant with xeromorphic features encompassing the transition from terrestrial growth to the more xeric epiphytic habitat. Several meters above the ground, an abrupt change to the adult form takes place. This results in a massive sub-canopy epiphyte with exserted leaves, which is the major energy-gathering phase of the life cycle. In addition to the abundant production of fruits and seeds, the adult elaborates shoots of a fourth type—hanging and creeping leafless stolons—which colonize additional trees or serve the individual as a means of recovery after establishment on an unsuitable host.

The elaboration of several different kinds of shoots by a single species has been a source of confusion in the classification and identification of monsteras, and the shingle plant juveniles of section Marcgraviopsis have even been described as new species of the dicotyledonous genus *Marcgravia.* Yet once the life cycles are understood, they furnish an insight



FIGS. 26–32. Schematic diagrams of heteromorphic shoots in *Monstera;* in nature the seedlings and juveniles have died and decayed by the time the adult is flowering: 26. *M. lechleriana,* showing unspecialized development; 27. *M. siltepecana,* with a hanging stolon; 28. *M. punctulata,* with a stolon-like seedling, shingle plant, and adult; 29. *M. acuminata,* like *M. punctulata* with the addition of hanging and creeping stolons; 30. *M. dubia;* 31. *M. pittieri;* 32. *M. tuberculata.* Figs. 30, 31, and 32 illustrate a hypothetical reduction series leading to *M. tuberculata,* a vegetatively neotonous form flowering on a shoot which is morphologically a shingle plant.

into the systematic relationships of the species and in this revision provide the basis for the subgeneric classification.

GEOGRAPHY

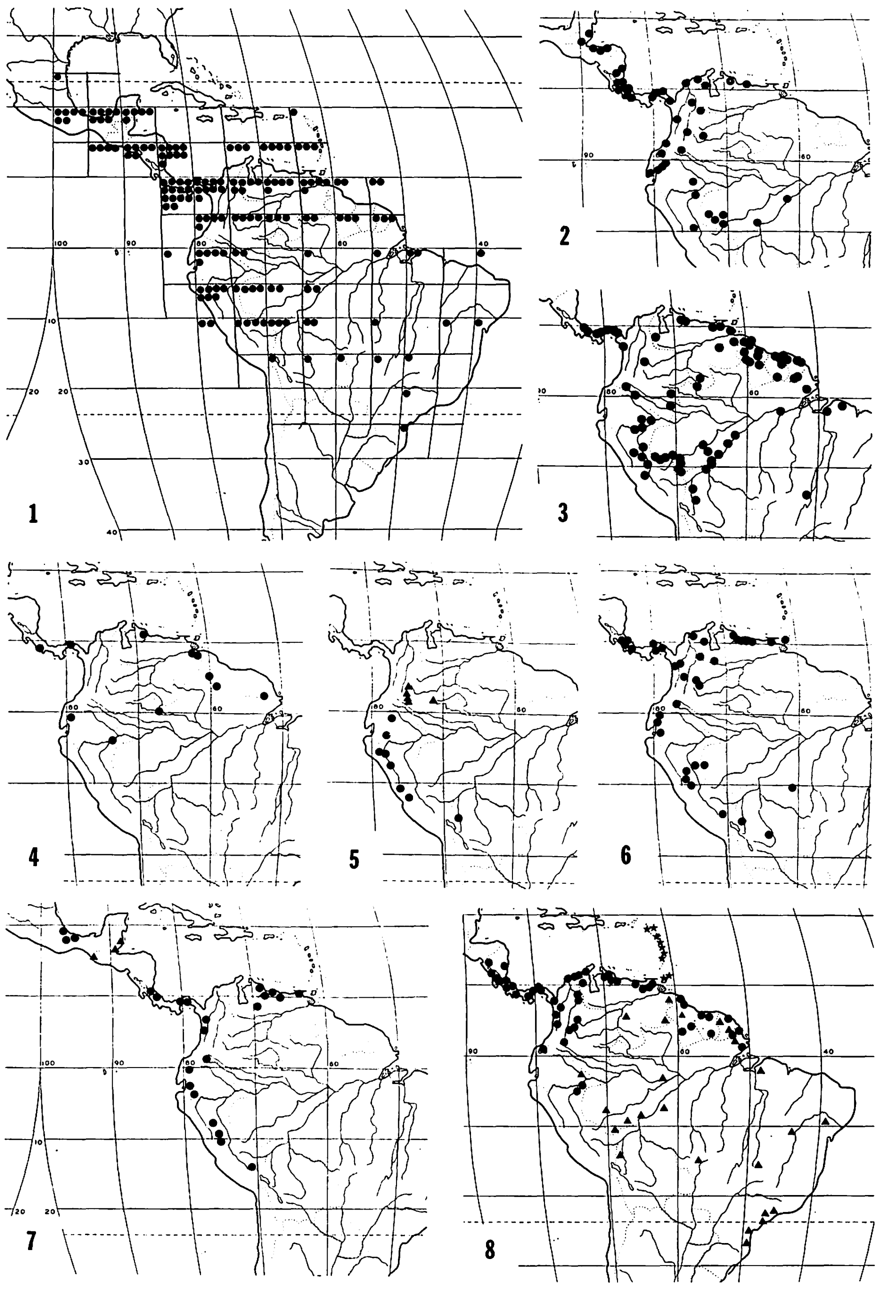
The center of species diversity in *Monstera* is in Costa Rica and Panama, with secondary centers in Mexico and the northern Andes (Map 1). Only a single weedy species, *M. adansonii,* has colonized the Caribbean Islands and coastal Brazil. The absence of endemic species in the Guiana highlands and southern Brazil emphasizes the essentially north-Andean distribution of the genus in South America.

The genus most closely related to *Monstera* and, considered by several authors to be congeneric, is *Epipremnum,* which is found at present in Indomalaya and the Pacific. *Epipremnum* is represented in the Tertiary by fossil seeds first appearing in Eocene deposits, although more common and diverse in Oligocene deposits. These fossils are found from England to western Siberia and occur as far north as 55° latitude (Madison & Tiffney, 1976). The Paleogene boreotropical flora, with which the fossils are associated, was fairly uniform in the eastern and western hemispheres, largely due to the availability of migration routes across the north Atlantic and Beringia (Wolfe, 1975). A possible interpretation of the present distribution of *Epipremnum* and *Monstera* is that they are both derivatives of an ancestral complex in the Paleogene boreotropical flora and have subsequently diverged in geographic isolation.

Wolfe (1975) and Raven and Axelrod (1974) suggest that the North American portion of the Eocene tropical flora was largely extinguished following the onset of climatic deterioration in the late Oligocene; surviving elements are seen in some of the dry Caribbean flora and mesothermal montane floras of Central America.

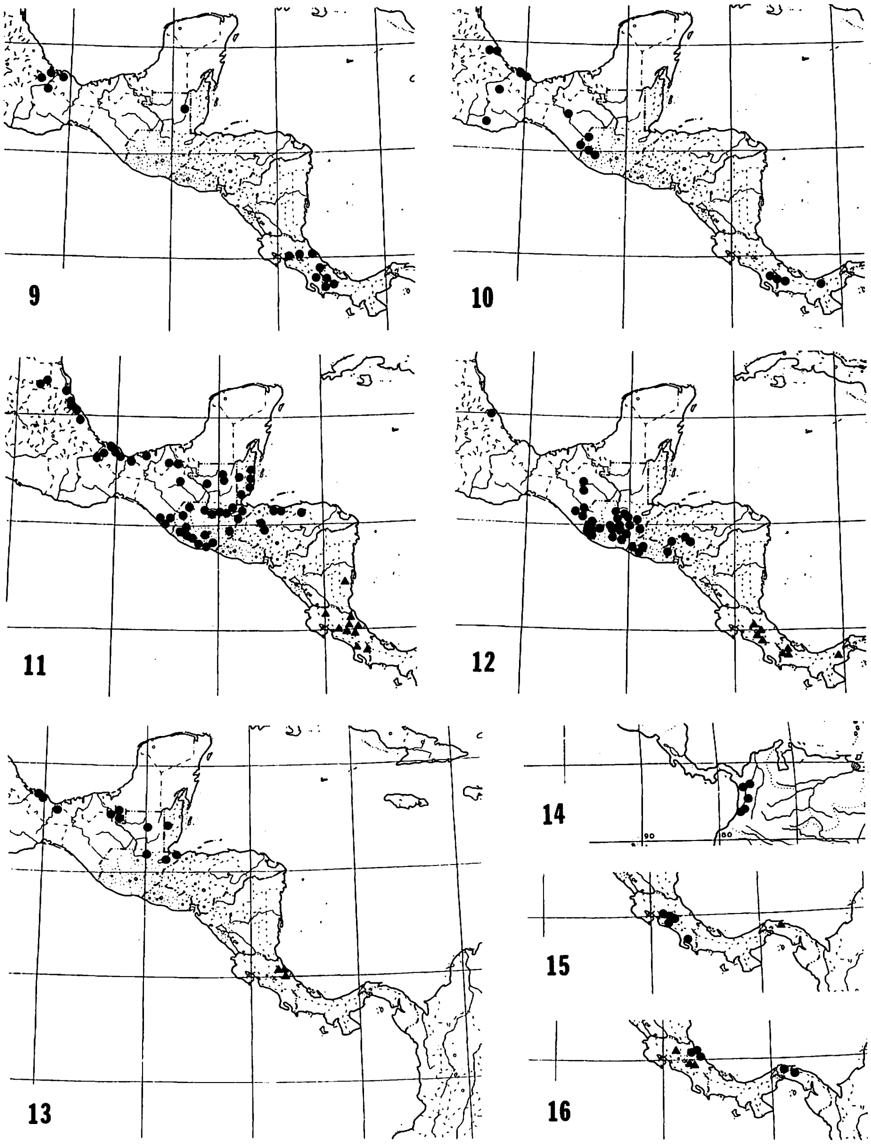
Several lines of evidence suggest that *Monstera* may represent a remnant of this Paleogene tropical flora which has persisted in North America, subsequently spreading into South America in Neogene times. One is the distribution of isolated or relict taxa in the genus. All four sections are represented in Mexico, but only two in South America. The species found in South America all either occur in Central America or show close affinities to Central American species. On the other hand, *M. membranacea* and *M. deliciosa,* which are morphologically isolated and show no close affinities to other species, are confined to Central America and Mexico.

A second is the distribution of species in relation to seed size. The size of *Monstera* seeds spans a critical range for dispersal by birds, the apparent mechanism of dispersal in this genus. The smallest seeds are about 5 mm. long and are probably easily dispersed by most frugivorous birds. However, the largest seeds (20–22 mm. across) have a much more restricted pool of potential dispersal vectors. The largest-seeded species



Maps 1–8. 1. Density distribution of *Monstera* species; for each square of 5° latitude by 5° longitude the number of dots equals the number of species of *Monstera* occurring in that region. 2–8. Distribution of *Monstera* species: 2. *M. dilacerta;* 3. *M. obliqua;* 4. *M. spruceana;* 5. *M. subpinnata* (dots) and *M. gracilis* (triangles); 6. *M. dubia;* 7. *M. lechleriana* (dots) and *M. acacoyaguensis* (triangles); 8. *M. adansonii* var. *adansonii* (stars), var. *laniata* (dots), and var. *klotzschiana* (triangles).

occur in Mexico, and there is a cline of decreasing seed size both within and between species toward South America. All of the South American species have seeds less than 10 mm. long, and one could argue that the species in South America are simply the most disperable



MAPS 9–16. Distribution of *Monstera* species: 9. *M. punctulata;* 10. *M. deliciosa;* 11. *M. acuminata* (dots) and *M. tenuis* (triangles); 12. *M. siltepecana* (dots) and *M. oreophila* (triangles); 13. *M. tuberculata* var. *tuberculata* (dots) and var. *brevinodum* (triangles); 14. *M. xanthospatha;* 15. *M. membranacea* (dots) and *M. minima* (triangles); 16. *M. pittieri* (dots) and *M. luteynii* (triangles).

(and dispersed), assuming the genus to have had a North American origin.

An additional relevant line of evidence is the range of climatic tolerance in *Monstera*. Although strictly tropical in natural distribution, *M. deliciosa, M. adansonii,* and *Epipremnum aureum* grow vigorously, flower, and set fruit in central Florida where they are annually exposed to frost. This moderate cold-hardiness, coupled with a degree of drought tolerance, suggests that *Monstera* species could have survived periods of unfavorable climate in the late Paleogene followed by diversification and dispersal into South America in the Neogene.

Distributions of individual *Monstera* species are shown in Maps 2–16. A pattern found in several species is that of a disjunct distribution of Mexico-Guatemala and Costa Rica-Panama. Three species of montane habitats show this distribution: *M. punctulata* (Map 9), *M. deliciosa* (Map 10), and *M. lechleriana* (Map 7). The latter two exhibit morphological differentiation between the southern and northern populations, indicating that this disjunction has persisted long enough to allow some evolutionary divergence. *Monstera siltepecana* and *M. oreophila* are two closely related montane species which may represent geographical speciation based on this disjunction. The barrier between these two regions for montane species seems to be the absence of high and wet mountains in the region of Nicaragua and Honduras, where the mountain ranges are lower than those to the north and south. The mountains of this intervening area are covered with mesic oak-pine forest.

A similar disjunction is found in *Monstera tuberculata* (Map 13), a lowland species of the Atlantic coastal plain not known to occur above 200 m. elevation. The Mexican and Costa Rican populations are separate taxonomic varieties, well differentiated by the morphology of their fruits. At present, a wet tropical forest is continuous along the Atlantic coast from Costa Rica to Mexico. The absence of *M. tuberculata* from Nicaragua and Honduras may represent the extermination of these species in the middle region of a once continuous distribution because of periods of drier climate in the Pleistocene, as suggested by the Raven and Axelrod (1974). The only *Monstera* species distributed continuously through this region, *M. dilacerata* (Map 2), has seeds about one-half the size of the disjunct species. This feature may increase its rate of dispersal to the point that it is the first species to have reinvaded the area after a period of dry climate.

In South America, *Monstera* is distributed primarily in a broad arc extending from Peru to the Guianas, thus reflecting the distribution of the lower montane slopes which are the chief habitat of most species. The only *Monstera* species which is abundant in the Amazon Basin is *M. obliqua,* a tiny creeper inhabiting the margins of waterways. The massive monsteras which form such a characteristic element of wet Central American vegetation are mostly absent from the Amazon region.

SPECIES CONCEPT

In considering the overall pattern of speciation in *Monstera,* two distinct elements may be separated. The species of sections Marcgraviopsis, Tornelia, and Echinospadix are clearly demarcated in terms of their morphology, growth habits, and habitat preferences, and intermediates between species are absent. Thus, even though *M. acuminata* and *M. dubia* are quite variable, they are easily recognized and it is not difficult to distinguish them from other species. This pattern suggests an early speciation followed by the extinction of intermediates.

In contrast, the species of section *Monstera* are connected by numerous intermediates and the delimitation of species is difficult. Quite diverse elements may be joined by a series of intergrading forms, and nearly all of the species intergrade with *M. adansonii,* which is itself polymorphic. In addition, there are broad geographic clines found with respect to several characters, among them fruit color, style length and seed size.

In Mexico, species of section Monstera have white fruits; further south the same or related species have pale yellow fruits, in Colombia medium yellow, and deep yellow or orange in the Guianas and Amazonia. A second cline is in the shape of the style, which is prismatic in Mexico. It is more conical and attenuate to the south, resulting in rather spiny appearing spadices in Brazil in contrast to the smooth spadices found in Mexico. Seed size is greatest in Mexico and decreases to the south and east. Each cline is found within and between species in section Monstera.

The existence of these clines and of large numbers of intermediates suggests that barriers to genetic exchange between these species are weak and that hybridization and introgression are correspondingly common. Thus, for example, the genes for yellow fruit color have spread through the South American populations of all species in section Monstera but are absent from the Mexican populations. This results in the confusing situation where fruit color in populations of *Monstera lechleriana* of Venezuela more closely resemble *M. adansonii* in Venezuela than they do populations of *M. lechleriana* in Mexico.

A number of the species of section Monstera have broad geographic ranges. They are species found at forest margins, along waterways, and in clearings rather than in deep forests. Apparently they have adapted readily to the great increase in habitats resulting from disturbances by man, and *Monstera adansonii* has become a common neotropical weed on fence posts and telephone poles. This has perhaps contributed to the breakdown of ecological or geographic barriers that formerly separated species of this section and accounts in part for the numerous intermediates between species.

The application of binomial nomenclatûre to this situation is not straightforward. In this revision, I am treating as species groups of individuals which are ecologically and morphologically similar. The degree of similarity requisite for the inclusion of two individuals in a species depends on the amount of variability known to occur within populations and individuals, and on the relative abundance of intermediates between unlike forms. The resulting classification is a broad one and emphasizes similarities rather than differences, though in the description of each species I have tried to indicate the extent of its variability. I am sympathetic to the possibility that a taxonomist of different temperament, using the same data and approach, might accept 40 or 45 species where I recognize 22. It is likely that some of the species recognized in section Monstera are in reality groups of sibling species, but while suspecting this I have been unable, with the information available, to recognize additional taxonomic entities. In addition, there are specimens which, while not fitting any of the known species, are insufficient as the basis for the description of new taxa. I predict that further species of *Monstera* are most likely to be found in section Monstera and to come from Costa Rica and Panama, particularly the mountainous regions.

Several previous authors have recognized infrageneric taxa in *Monstera.* Miquel (1844) divided the genus into two sections: section Monstera, with the flowers at the base of the spadix imperfect and carpelate; and section Heteropsis, with all the flowers perfect. Carl Koch (1857) included the genera *Scindapsus, Alloschemone,* and *Rhaphidophora* in Monstera which he divided into six subgenera. Three of his subgenera include species of *Monstera* as here delimited. These were distinguished on the basis of leaf shape: one included species with entire margins; a second with the leaves pinnatifid but not perforate; and a third with the leaves pinnatifid and perforate. Schott (1860) separated the pinnatifid-leaved species of *Monstera* as a separate genus, *Tornelia.*

I consider these subdivisions of the genus to be artificial, and propose a new classification in which the genus is divided into four sections. The majority of the species are placed into two sections on the basis of their patterns of development. In section Monstera the seedlings have exserted foliage leaves and develop to the adult stage by a gradual increase in size. In section Marcgraviopsis, the species exhibit heteroblastic development with three distinct phases: the seedling is a stolon-like creeper, the juvenile is a shingle plant, and the adult has large exserted leaves. Two unusual species are relegated to monotypic sections on the basis of characters discussed in the description of those sections.

This treatment separates into different sections species which as adults may be rather similar, but have very different developmental histories (e.g., *Monstera dilacerata* and *M. tenuis*). On the other hand, species which show a very similar heteroblastic development in early stages, but differing morphologies as adults, are included in the same section.

TAXONOMIC TREATMENT

TRIBE MONSTEREAE ENGLER

Monstereae Engler, Nov. Act. Akad. Leopold. 39:143 (1876).
Anepsideae Engler, Nov. Act. Akad. Leopold. 39:143 (1876).
Rhaphidophoreae Engler, Nov. Act. Akad. Leopold. 39:143 (1876).
Scindapseae Nakai, Ordines Familia 216 (1943).
Stenospermationeae Nakai, Ordines Familia 216 (1943).
Rhodospatheae Nakai, Ordines Familia 216 (1943).
Callae Schott subtribus Monsterinae Schott, Prod. Syst. Aroid. 346 (1860).

Scandent epiphytes lacking laticiferous elements; trichosclereids usually present in spathe and spadix; the leaves entire, pinnatifid, or foraminate, the latter two conditions resulting from the death of small groups of laminar cells early in development; the petiole geniculate; the primary lateral veins of the lamina parallel, the secondary lateral veins parallel or reticulate. Spathe naviculiform, deciduous after flowering (rarely persistent in *Rhaphidophora*); spadix cylindric, without an appendix; flowers perfect, sometimes sterile near the base of the spadix; stamens 4, extrorse; perianth lacking; ovary 1–2(–6) locular, ovules 1–∞, anatropous or amphitropous; fruit a berry, usually with the stylar portion deciduous; pollen meridiosulcate, foveolate.

TYPE: *Monstera* Adans.

KEY TO GENERA OF THE TRIBE MONSTEREAE

A. Needle-like trichosclereids present in the spathe and spadix.
B. Ovary unilocular or incompletely bilocular, paleotropical (1 species Brazil).
C. Ovule amphitropous, solitary, basal; seeds lacking endosperm. . . 1. *Scindapsus.*
C. Ovules anatropous, more than one; seeds with endosperm.
D. Ovules 2–4(–6) at the base of a single intrusive parietal placenta; seeds curved, 3–7 mm. long, 1.5–4 mm. wide. .... 2. *Epipremnum.*
D. Ovules numerous, superposed on two (rarely three) parietal placentae; seeds fusiform, straight, 1.3–3.2 mm. long, 0.6–1.0 mm. wide. .... 3. *Rhaphidophora.*
B. Ovary 2–6 locular, neotropical.
E. Seeds globose to oblong, 6–22 mm. long, the raphe S-shaped, endosperm absent; ovules 2 per loculus; leaves pinnatifid, foraminate, or entire. ...... 4. *Monstera.*
E. Seeds fusiform, claviform, or lenticular, less than 3 mm. long, endosperm present; ovules (2–)3–∞ per loculus, leaves entire.
F. Placentation basal, seeds fusiform to claviform, 2.0–2.5 mm. long; leaves thickly coriaceous. .... 5. *Stenospermation.*
F. Placentation axile, seeds lenticular and flattened, curved 180°, 1.0–1.6 mm. across; leaves not coriaceous. .... 6. *Rhodospatha.*
A. Needle-like trichosclereids absent from the spathe and spadix; ovary unilocular with one intrusive placenta bearing two ovules near the base, seeds lacking endosperm, Malaysia. .... 7. *Amydrium.*

1. **Scindapsus** Schott, Melet. I:21 (1832). TYPE: S. *officinalis* (Roxb.) Schott (*Pothos officinalis* Roxb.).

Cuscuaria Schott, Bonplandia 5:45 (1857). TYPE: *C. marantifolia* Schott (*Pothos cuscuaria* Aublet).

Alloschemone Schott, Genera Aroid. App. (1858). TYPE: *A. poeppigiana* Schott, *nom. illegit.* (*Scindapsus occidentalis* Poepp., *A. occidentalis* (Poepp.) Engler & Krause).

Leaves entire in the Asian species, pinnatifid in the Brazilian species, never perforate. Secondary lateral veins running parallel to the primary lateral veins. Spadix sessile; ovary unilocular, ovule amphitropous, basal, solitary; seed strongly curved, somewhat flattened, 3–9 mm. long, 3–7 mm. wide, 2.0–4.5 mm. thick, testa smooth, hard; endosperm absent.

About 25 species, India and Sikkim to the Solomon Islands, one species in Amazonian Brazil. For a discussion of the Brazilian species see Madison 1976.

2. **Epipremnum** Schott, Bonplandia 5:45 (1857). TYPE: *E. mirabile* Schott.

Leaves entire or pinnatifid, coriaceous; secondary lateral veins parallel or reticulate. Spadix sessile; ovary unilocular with a single intrusive placenta bearing 2–4(–6) ovules at its base; seeds strongly curved, asymmetric, 3–7 mm. long, 1.6–5.0 mm. wide; testa hard, smooth, pitted or rugose; endosperm present, embryo curved.

About 15 species, Burma to Samoa and the Marshall Islands.

This genus has been merged with *Rhaphidophora* by several authors, but in its seed morphology and vegetative characters it is much closer to *Monstera.*

3. **Rhaphidophora** Hassk. Flora 25 (Beibl. 1):11 (1842). TYPE: *R. lacera* Hasskarl, *nom. illegit.* (*Pothos pertusus* Roxb., *R. pertusa* (Roxb.) Schott).
Afroraphidophora Engler, Natur. Pflanzenfam. II:31 (1906). LECTOTYPE: *A. africana* (N. E. Brown) Engler (*Rhaphidophora africana* N. E. Brown).

Leaves entire, pinnatifid or perforate; secondary lateral veins parallel to primary. Spadix sessile or stipitate; ovary unilocular, divided by 2 (rarely 3) intrusive parietal placentae bearing numerous superposed ovules; seeds elongate, fusiform or flattened, straight or very slightly curved, 1.3–3.2 mm. long, 0.6–1.0 mm. wide, smooth; endosperm present, embryo axile, straight or slightly curved.

About 60 species, West Africa, India and Ceylon, Nepal to Samoa, Formosa.

4. **Monstera** Adans., Fam. des Plantes II:470 (1763). LECTOTYPE: *M. adansonii* Schott (*Dracontium pertusum* L.).
Tornelia Guttierez ex Linnaea, Linnaeae 26:282 (1853). TYPE: *T. fragrans* Guttierez ex Linnaea.
Serangium W. Wood, Salisb. Gen. Pl. Frag., p. 5 (1866). TYPE: *Dracontium pertusum* L.

Leaves entire, pinnatifid, or perforate; secondary lateral veins usually reticulate. Spadix sessile; ovary bilocular, the septum perforate at its base, two basal ovules per loculus; berries mostly one-seeded, seeds sub-globose to oblong, 6–22 mm. long, 4–12 mm. wide, the funiculus S-shaped, testa soft; endosperm absent.

Twenty-two species, Mexico to Brazil, Lesser Antilles.

5. **Stenospermation** Schott, General Aroid. t. 70 (1858). LECTOTYPE: S. *mathewsii* Schott.

Leaves entire, ovate to lanceolate, thickly coriaceous. Stem terete, usually less than 1 m. in length and not closely attached to the substrate. Spadix white, often stipitate; ovary bilocular, ovules numerous and basal; seeds elongate, fusiform to claviform, 2.0–2.5 mm. long, 1.0 mm. wide, long raphe present; abundant endosperm, embryo axile, straight or slightly curved.

About 20 species, western neotropics from Nicaragua to Bolivia.

6. **Rhodospatha** Poepp., Poepp. & Endlicher Nov. Gen. et Spec. III:91 (1845). LECTOTYPE: *R. latifolia* Poepp.

Atimeta Schott, Genera Aroid. t. 71 (1858). TYPE: *A. videniana* Schott.
Anespsias Schott, Genera Aroid. t. 73 (1858). TYPE: *A. moritzianus* Schott.

Leaves entire; secondary lateral veins closely parallel to primary; lamina membranaceous, developing leaves red or pink. Spadix sessile or stipitate, fruiting spadix often red; ovary bilocular, rarely 3–6 locular, ovules numerous, superposed in several series on the septum; seeds reniform to lenticular, strongly compressed, 1.0–1.6 mm. across, 0.5 mm. thick; endosperm present.

About 15 species, Mexico to Brazil.

7. **Amydrium** Schott, Ann. Mus. Lugd. Bat. **I**:127 (1863). TYPE: *A. humile* Schott.
Epipremnopsis Engler, Das Pflanzenreich IV 23(B):1 (1908). TYPE: *E. media* (Zoll. & Mor.) Engler (*Scindapsis medius* Zoll. & Mor.).

Trichosclereids lacking. Leaves entire, pinnatifid, or foraminate; secondary lateral veins reticulate. Spathe yellow; spadix stipitate or sessile; ovary unilocular with a deeply intrusive parietal placenta bearing two ovules; seeds reniform, about 9 mm. wide, 7 mm. long; endosperm absent.

Four species, Malaysia.

EXCLUDED GENERA

Anadendrum and *Heteropsis* are intermediate in character between the subfamilies Monsteroideae and Pothoideae. They were included in the Monstereae by Hutchinson (1959) but placed in the Pothoideae by Engler and Krause (1908).

Anadendrum has a perianth of connate tepals in contrast to the naked flowers of the Monstereae. It lacks the characteristic trichosclereids and has inaperturate pollen rather than the meridiosulcate pollen of the Monstereae (Thanikaimoni, 1969). Engler and Krause (1908) mention perforate and pinnate leaves in the generic descriptions of *Anadendrum*, but all the species they describe have entire leaves. If perforate leaves do occur in *Anadendrum* this would suggest a greater affinity to the Monstereae; on the other hand, this condition is also found in *Rhektophyllum* and *Cyrtosperma* of the Lasiodeae, and thus is not definitive. This genus seems best retained in the Pothoideae.

Heteropsis differs from the typical Monstereae in several respects. It has entire, subsessile leaves which apparently lack a geniculum. Trichosclereids are absent. Species of *Heteropsis* exhibit monopodial growth, in contrast to the strictly sympodial growth of the Monstereae. I follow Engler and Krause (1908) in relegating this genus to a separate tribe of the Pothoideae.

MONSTERA ADANS., NOM. CONSERV.

Monstera Adans., Fam. des Plantes **II**:470 (1763). LECTOTYPE: *M. adansonii* Schott (*Dracontium pertusum* L.) see Nicolson (1968a) on typification.
Tornelia Guttierez ex Linnaea, Linnaea **26**:282 (1853). TYPE: *T. fragrans* Guttierez ex. Linnaea.
Serangium W. Wood, Salisb. Gen. Pl. Frag., p. 5 (1866). TYPE: *Dracontium pertusum* L.

Scandent epiphytes of wet tropical forests, climbing by adventitious roots. *Seedling:*

germination hypogeal, the seedling producing two cataphylls and then exserted foliage leaves, or producing a green stolon-like shoot 1–2 mm. in diameter with internodes 4–10 cm. long, bearing scale leaves at the nodes, this stolon to 2 m. long. *Juvenile:* a terrestrial or climbing creeper with exserted leaves, or a climber with a flattened stem and ovate to orbicular leaves tightly appressed against the substrate, overlapping one another and covering the stem, these leaves with a petiole less than one-half the length of the lamina and the sheath extended into a ligular outgrowth about the length of the petiole. *Adult stem:* green or brown, smooth or tuberculate to warty, 2–80 mm. thick, with internodes 1–12 cm. long (to 30 cm. long in stolons), leaves produced distichously, the angle of divergence between the two ranks from about 90° to 180°. *Adventitious roots:* of two types, positively geotropic feeder roots produced at the nodes and extending to the ground, and ageotropic clasping roots produced along the internodes and attaching the plant to the stem. *Petiole:* 4–110 cm. long with a pulvinus at each end, vaginate for 1/6 to all its length, the sheath wings deciduous or persistent. *Lamina:* membranaceous to coriaceous, ovate to lanceolate, 10–120 cm. long, 4–75 cm. wide, the base cordate to acute or cuneate, often oblique, the apex various, usually acute; margins entire or pinnatifid, the lamina perforate or not, the perforations in 1–4 series per side; primary lateral veins indistinct or distinct and 6–40 in number per side, usually white and prominent abaxially, the secondary lateral veins parallel to the primary or reticulate. *Peduncle:* terete or flattened, 2–40 mm. thick, 1–40 cm. long. *Spathe:* white, cream, yellow to deep yellow, or rose at maturity, coriaceous, hemispherical to naviculiform, 5–35 cm. tall, 3–15 cm. across when open, opening widely or only by a narrow slit, deciduous after anthesis. *Flowering spadix:* sessile, white to yellow, cylindric, 5–30 mm. thick, 4–33 cm. long, sterile near the base, the fertile flowers perfect, with four stamens opening extrorsely, ovary bilocular with two basal anatropous ovules per loculus, the pistils prismatic, truncate at the apex or with a curved or straight conical style. *Fruiting spadix:* green, white, or yellow to orange, cylindric, 1.0–9.5 cm. thick, 5–42 cm. long, the stylar portion of the berries deciduous to expose the seeds in a gray or orange pulp, or the berries indehiscent. *Seeds:* globose to oblong, 5–22 mm. long, 3–12 mm. across, the raphe S-shaped by curvature of the seed in development; the testa brown and soft, the embryo macropodial and green or blue.

KEY TO SECTIONS OF MONSTERA

A. Plants in the earliest climbing phase with exserted leaves, the petioles more than ⅔ the lamina length.
  B. Pistils 10–18 mm. across in fruit, seeds 16–22 mm. long. ..... Section *Tornelia.*
  B. Pistils 5–8 mm. across in fruit, seeds 5–13 mm. long. .... Section *Monstera.*
A. Plants in the earliest climbing phase with leaves tightly appressed to the substrate, the petioles less than ½ the lamina length.
  C. Flowering spadix erect, adult leaf with a short ligule or ligule lacking. .... Section *Marcgraviopsis.*
  C. Flowering spadix pendent, adult leaf with a ligule about equal in length to the petiole. .... Section *Echinospadix.*

KEY TO SPECIES OF MONSTERA

A. Lamina regularly pinnatifid (rarely on one side only).
  B. Lamina lacking perforations.
    C. Pinnae 15–30 in number per side, flowering spadix 3.5–5.0 cm. thick (Nicaragua to Panama). .... 18. *M. tenuis.*
    C. Pinnae 4–12 per side, flowering spadix 1–3 cm. thick.
      D. Lamina broadly cordate at the base, secondary lateral veins reticulate, pistils 10–18 mm. across in fruit. .... 22. *M. deliciosa.*
      D. Lamina truncate to acute at the base, secondary lateral veins parallel, pistils 5–8 mm. across in fruit.
        E. Peduncle equal to or shorter than the spadix.
          F. Pistils truncate, flowering spadix 12–25 cm. long, lamina pinnae not constricted at the base. .... 17. *M. spruceana.*

F. Pistils with a conical style, flowering spadix 8–12 cm. long, pinnae usually constricted at the base. . . . . 8. *M. subpinnata.*
E. Peduncle more than 4 cm. longer than the spadix.
G. Flowering spadix 4–6 cm. long, 1.0–1.2 cm. thick, stem 5–10 mm. thick, peduncle 5–8 mm. thick (Colombia). . . . . 9. *M. gracilis.*
G. Flowering spadix 7–16 cm. long, 1.5–2.5 cm. thick, stem 15–40 mm. thick, peduncle 10–16 mm. thick. . . . . 7. *M. dilacerata.*
B. Lamina with perforations.
H. Secondary lateral veins parallel.
I. Pinnae 8–12 per side, petiole sheath deciduous, flowering spadix 4–6 cm. long, peduncle 8–18 cm. long, below 1000 m. (Colombia). . . . . 9. *M. gracilis.*
I. Pinnae 12–20 per side, petiole sheath persistent, flowering spadix 9–12 cm. long, peduncle 20–30 cm., above 1600 m. (Costa Rica). . . . . . . 10. *M. epipremnoides.*
H. Secondary lateral veins reticulate.
J. Petiole sheath green and persistent, lamina membranaceous, spathe decurrent on the peduncle for 3–8 cm. (Costa Rica). . . . . 6. *M. membranacea.*
J. Petiole sheath deciduous or at least marcescent, lamina coriaceous to subcoriaceous, spathe not decurrent on the peduncle.
K. Lamina shorter than the petiole, less than 1⅓ times longer than broad, pistils in fruit 10–18 mm. across. . . . . 22. *M. deliciosa.*
K. Lamina exceeding the petiole, more than 1⅓ times longer than broad, pistils in fruit 5–8 mm. across.
L. Petiole white-spotted, lamina bright green, peduncle more than 12 cm. long, dried pistils with a golden-colored cap. . . . . 16. *M. punctulata.*
L. Petiole and lamina dull green, peduncle less than 11 cm. long, dried pistils brown or black, not capitate. . . . . 15. *M. dubia.*
A. Lamina with the margins entire, or with a few lacerations but not regularly pinnatifid.
M. Lamina with perforations.
N. Petiole 5–18 cm. long, peduncle more than twice the length of the spadix, stems 2–10 mm. thick, spathe deep yellow abaxially.
O. Flowering spadix 5–10 mm. thick, mature berries globose, below 1000 m. elev. . . . . 12. *M. obliqua.*
O. Flowering spadix about 20 mm. thick, mature berries prismatic, above 1400 m. (Colombia). . . . . 11. *M. xanthospatha.*
N. Petiole longer than 18 cm., peduncle less than twice the length of the flowering spadix, stem 10–60 mm. thick, spathe not deep yellow abaxially.
P. Secondary lateral veins reticulate.
Q. Petiole sheath persistent, lamina thinly membranaceous, peduncle 13–17 cm. long (Costa Rica). . . . . 6. *M. membranacea.*
Q. Petiole sheath deciduous, lamina subcoriaceous to coriaceous, peduncle 5–12 cm. long.
R. Spathe 16–25 cm. tall, flowering spadix 10–13 cm. long, fruiting spadix green (Mexico to Honduras). . . . . 4. *M. siltepecana.*
R. Spathe 6–12 cm. tall, flowering spadix 5–10 cm. long, fruiting spadix pale yellow (Costa Rica to South America). 15. *M. dubia.*
P. Secondary lateral veins parallel (rarely reticulate near the margin).
S. Peduncle 4–10 cm. shorter than the spadix, juvenile a shingle plant (Mexico to Honduras). . . . . 14. *M. acuminata.*
S. Peduncle equal to or exceeding the spadix, juvenile with exserted leaves.
T. Primary lateral veins 5–10 mm. apart, above 1600 m. elev. (Panama and Costa Rica). . . . . 5. *M. oreophila.*
T. Primary lateral veins more than 15 mm. apart.
U. Flowering spadix less than 13 cm. long, fruiting spadix less than 17 cm. long. . . . . 1. *M. adansonii.*
U. Flowering spadix more than 15 cm. long, fruiting spadix more than 20 cm. long.
V. Leaf base abruptly truncate or subcordate (16–)20–40 primary lateral veins per side, flowering spadix 2.5–3.5 cm. thick. . . . . . 2. *M. lechleriana.*

V. Leaf lamina with a broadly cuneate portion at the base, 12–16 primary lateral veins per side, flowering spadix 1.5–2.0 cm. thick (Mexico and Guatemala). .... 3. *M. acacoyaguensis.*
M. Lamina entire, without perforations.
W. Lamina 13–120 cm. long, peduncle 1–4 cm. thick.
X. Fruiting spadix 2–4 cm. thick, seeds 5–8 mm. long, petiole sheath deciduous. .... 1. *M. adansonii.*
X. Fruiting spadix 4.0–6.5 cm. thick, seeds 10–20 mm. long, petiole sheath persistent.
Y. Lamina 35–65 cm. long, peduncle 7–13 cm. long, seeds 16–20 mm. long, internodes 6–12 cm. (Mexico to Honduras). .... 14. *M. acuminata.*
Y. Lamina 70–120 cm. long, peduncle 20–40 cm. long, seeds 10–13 mm. long, internodes 4–6 cm. .... 2. *M. lechleriana.*
W. Lamina less than 35 cm. long, peduncle 2–9 mm. thick.
Z. Peduncle equal to or shorter than the spadix, pendent epiphyte flowering on hanging stems, stems with a thick tan cuticle, often flaking off in dried specimens.
AA. Lamina more than 20 cm. long and 15 cm. wide. .... 15. *M. dubia.*
AA. Lamina less than 20 cm. long and 15 cm. wide.
BB. Petiole less than 4 cm. long, spadix pendent. .... 21. *M. tuberculata.*
BB. Petiole more than 7 cm. long, spadix erect.
CC. Lamina 2–5 times longer than broad, veins obscure (Costa Rica and Panama). .... 19. *M. pittieri.*
CC. Lamina 1–2 times longer than broad, veins prominent in dried leaves (Costa Rica). .... 20. *M. luteynii.*
Z. Peduncle longer than the spadix, attached epiphyte flowering in the climbing portion, stems green, lacking a thick flaky cuticle.
DD. Peduncle 1½–2 times the length of the leaves (lamina and petiole) (Panama). .... 13. *M. minima.*
DD. Peduncle shorter than the leaves.
EE. Spathe deep yellow abaxially, flowering spadix less than 8 cm. long, petioles 5–18 cm. long, stem 2–10 mm. thick.
FF. Flowering spadix 5–10 mm. thick, mature berries globose, below 1000 m. elevation. .... 12. *M. obliqua.*
FF. Flowering spadix about 20 mm. thick, mature berries prismatic, above 1400 m. (Colombia). .... 11. *M. xanthospatha.*
EE. Spathe pale yellow or cream abaxially, flowering spadix more than 10 cm. long, petioles more than 20 cm. long, stems 10–30 cm. thick. . . 1. *M. adansonii.*

MONSTERA section MONSTERA

TYPE SPECIES: *Monstera adansonii* Schott
SYNONYM: *Monstera* section Heteropsis Miq., Linnaea 18:79 (1844)
TYPE SPECIES: *Monstera obliqua* Miq.

The species of section Monstera have seedlings with exserted foliage leaves, and development to the adult stage is by a gradual increase in the size of successive leaves without pronounced heterophylly. The peduncle is longer than the spadix in these species except for *M. siltepecana* and *M. subpinnata.*

The species in this section are connected by many intergrading forms, making their delimitation difficult. Most of the species intergrade with *Monstera adansonii,* which is itself polymorphic. *Monstera membranacea* is rather isolated in the section, showing no close relationship to other species.

1. **Monstera adansonii** Schott

Scandent epiphyte 2–4(–6) m. tall. *Juvenile:* terrestrial creeper, stem smooth, green, terete, internodes 1–6 cm. long; petiole vaginate for ⅓ to ⅚ its length, the lamina widely ovate to narrowly elliptic, entire or perforated at a very early stage when only 5–10 cm. long. *Adult stem:* subterete, green, smooth, 1.5–3.0 cm. thick, the internodes 3–10 cm. long; leaf scars shallow, 3–10 mm. wide at the widest point, the ends of each leaf scar overlapping for 3–6 mm.; axillary buds longer than wide, located in a depression which is not extended into a sulcus. *Petiole:* smooth, 20–60 cm. long, somewhat shorter than the lamina, vaginate to the geniculum, the wings of the sheath deciduous or persistent, the geniculum 3–5 cm. long. *Lamina:* subcoriaceous, glossy adaxially, very widely ovate to elliptic, 25–70 cm. long, 15–45 cm. wide, the base cuneate to broadly truncate, sometimes oblique and unequal, being cuneate on one side and truncate to subcordate on the other side, the tip acute or shortly mucronate; margin entire, rarely irregularly laciniate, perforations absent to numerous in several series on each side of the midrib; primary lateral veins parallel, 8–16 in number, secondary lateral veins parallel to the primary. *Peduncle:* smooth, green, subterete to flattened, 9–22 cm. long, 1.0–1.4 cm. thick, 1.1–2.0 cm. wide. *Spathe:* cream to pale yellow, coriaceous, 12–28 cm. tall, 10–25 cm. around, acuminate, opening widely at maturity. *Flowering spadix:* cream to yellow, cylindric, 8–13 cm. long, 1.1–2.6 cm. thick, the pistils 4–7 mm. long, truncate or acute at the apex, the lower 6–8 rows of flowers sterile. *Fruiting spadix:* green, becoming yellow to deep yellow at maturity, 10–17 cm. long, 2–4 cm. thick, the stylar portion of the pistil containing trichosclereids, deciduous, revealing the seeds in a gray pulp. Berries mostly one-seeded, the seeds brown or black, 5–7 mm. long, 4–6 mm. wide, 2–3 mm. thick.

KEY TO VARIETIES

Petiole sheath with wings deciduous; leaf base unequal with one side truncate to subcordate and the other side cuneate to acute, the lamina less than twice as long as wide; lateral veins on at least one side arising from the midrib at an angle greater than 60°; Nicaragua to Peru, Venezuela, the Guianas, and Brazil (Amapá). . . . . 1 b. var. *laniata.*

Petiole sheath with wings persistent; leaf base subequal, cuneate to bluntly acute, the lamina more than twice as long as wide; lateral veins on both sides arising at an angle less than 60°.

Pistils truncate at the apex, cream to pale yellow in flower; Lesser Antilles. . . . . 1 a. var. *adansonii.*

Pistils acute at the apex, medium yellow in flower; Venezuela, the Guianas, Brazil, Peru. . . . . 1 c. var. *klotzschiana.*

1 a. **Monstera adansonii** Schott var. **adansonii**

FIG. 33, MAP 8

Monstera adansonii Schott, Wiener Zeitschrift fur Kunst, Literatur & Mode 4:1028 (1830) based on *Dracontium pertusum* L., Species Plantarum p. 967 (1753) non *Monstera pertusa* (Roxb.) Schott, Wiener Zeitschrift fur Kunst, Lit. & Mode 4:1028 (1830). *Calla dracontium* Meyer, Prim. Flor. Essequebo p. 197 (1818). *Calla pertusa* (L.) Kunth, Synopsis 1:129 (1822), *Monstera pertusa* (L.) deVriese, Hort. Sparm. Bergens p. 40 (1839). TYPE: Martinique, Fort St. Pierre, May: R. P. Charles Plumier, Description des Plantes de l'Amérique, t. LVI, LVII (1693). REPRESENTATIVE COLLECTION: Martinique, Fort St. Pierre, May 1820, *Plee 687* (BH,P,US).

Monstera jaquinii Schott, Oest. Bot. Woch. IV:66 (1854). *Monstera pertusa* (L.) deVriese var. *jacquinii* (Schott) Engler, in Martius, Flora Brasiliensis III (2):113 (1878). TYPE: cultivated, Hortus Schoenbrun.: Jacquin, Plant Rar. Hort. Schoenbr. II: t. 184, 185 (1797). REPRESENTATIVE COLLECTION: habitat in America meridionalis, Herbarium Jacquin, 1778 (S).

Monstera imrayana Schott, Oest. Bot. Zeit. 9:40 (1859). TYPE: Dominica, *Imray 330*

FIG. 33. *Monstera adansonii* var. *adansonii.* From Plumier, Descriptions des Plantes de l'Amerique, pl. LVI. Paris, 1693.

(holotype K; drawing of holotype = Schott Aroideae No. 2269, W, *non vidi,* photo BR,C,GH,NY,S,US).

Monstera macrophylla Schott, Prodr. Syst. Aroid. p. 362 (1868). TYPE: Guadeloupe, *Perotet* (W, destroyed; drawing of holotype = Schott Aroideae No. 2275, W, *non vidi,* photo BH,BR,C,GH,NY,S,US). REPRESENTATIVE COLLECTION: Guadeloupe, 1843, *L'Herminier s.n.* (P).

Juvenile: leaves falcate, the lamina 3–4 times longer than broad. *Adult stem:* 1.5–2.5 cm. thick, internodes 2–3 cm. long. *Petiole:* 25–40 cm. long, the sheath wings persistent. *Lamina:* ovate to elliptic, 14–20 cm. wide, 35–50 cm. long, the length more than twice the width, midrib somewhat falcate, lateral veins mostly arising at an angle less than 60° with the midrib, the leaf base cuneate to bluntly acute; the margin entire; perforations 1 to 5 in number on each side, ovate to elliptic, 2.0–3.5 cm. wide, 5–8 cm. long. *Peduncle:* subterete, about 1.1 cm. thick, 15–22 cm. long. *Spathe:* pale yellow, 16–23 cm. long, twice the length of the spadix or more. *Flowering spadix:* cream to pale yellow, 1.1–1.5 cm. thick, 8–11 cm. long; pistils prismatic, truncate at the apex, 4.0–4.5 mm. long. *Fruiting spadix:* pale yellow, 1.8–2.2 cm. thick, 10–13 cm. long.

ETYMOLOGY. After Michael Adanson (1727–1806), French botanist and author of the name *Monstera.*

COMMON NAMES. Bois de couleuvre, Caracol, Siguini (Guadeloupe).

DISTRIBUTION. Lesser Antilles, Saba to Trinidad.

REPRESENTATIVE SPECIMENS. **Saba:** mountain, 800 m., 16 July 1906, *Boldingh 1811* (U). **St. Kitts:** Buckley Estate, September 1901, *Britton & Cowell 204* (NY). **Antigua:** Wallings, Sept. 1938, *Box 1530* (BM,US). **Guadeloupe:** Basse Terre, Ravine de Belost, 20 m., June 1935, *Stehle 1973* (US); Basse Terre, Dec. 1938, *Quentin 1072* (US); Marne Gommier, 1896, *Duss 3304* (NY,US); Route Gourbeyre, 200 m., Oct. 1937, *Questal 405*(P,US); 1843, *L'Herminier s.n.* (P); Rivières Gourbeyre, 1893, *Duss 3297* (US). **Dominica:** 1843, *McPhail s.n.* (BM); Laiou Valley, June 1888, *Ramage s.n.* (K); Rivière, Sept. 1936, *Stehle 3048* (P); Roseau Valley, 1903, *Lloyd 563* (NY); Hatton Garden Estate, near bridge over St. Mary's River, April 1940, *Hodge & Hodge 3006* (GH); 1903, *Othmer s.n.* (M). **Martinique:** Case Pilote, 1871, *Hahn 1020* (BM,GH,K, P,US); Fort St. Pierre, May 1820, *Plee 687* (BH,P,US); Absalon, 1880, *Duss 522* (NY). **St. Vincent:** damp forest, 500–2000 ft., May–July 1890, *H. H. & G. W. Smith 37* (K); Botanic Gardens, Feb. 1932, *Fairchild 2754* (UC,US). **Tobago:** Mason Hall Bridge, April 1914, *Broadway 4835* (S,US); Castara road, Jan. 1953, *Hunnewell 19920* (GH). **Trinidad:** Mayaro, March 1922, *Bailey 668* (BH).

1 b. **Monstera adansonii** Schott var. **laniata** (Schott) Madison, *comb. nov.*

Tornelia laniata Schott, Oest. Bot. Zeit. 8:179 (1858). *Monstera pertusa* (L.) deVriese var. *laniata* (Schott) Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: Costa Rica, Candelarta, *Orsted 15795* (C; isotype B, *non vidi*).

Heteropsis ovata Miq., Hort. Amstelod. Delect. Sem. (1853). *Monstera ovata* (Miq.) Schott, Oest. Bot. Zeit. 8:387 (1858). TYPE: Surinam, Wildparkstation, cultivated material from this locality given to Koch by Miquel, *Carl Koch s.n.* (holotype B, *non vidi,* fragment of holotype at K).

Monstera holtoniana Schott, Oest. Bot. Zeit. 9:40 (1859). TYPE: Colombia, La Paila, 17 February 1853, *I. F. Holton 217* (holotype K, photo SEL; isotypes PH no. 610479, NY; drawing of holotype = Schott Aroideae no. 2318, W, *non vidi,* photo BR,C,GH,NY,S,SEL,US).

Monstera friedrichsthalli Schott, Oest. Bot. Wochen. 4:65 (1854). TYPE: Nicaragua, Niquinohomo, *Friedrichsthal 1206* (W, destroyed; drawing of holotype = Schott Aroideae No. 2245, W *non vidi,* photo BR,C,GH,NY,S,SEL,US). REPRESENTATIVE COLLECTION: Nicaragua, Dept. Matagalpa, 6–10 km. northeast of Matagalpa on road to El Tuma, 1000 m., 14–16 Jan. 1963, *Williams, Molina & Williams 24033* (F).

Juvenile: leaves ovate, the lamina 1½–2 times longer than wide, entire or perforate with 1–4 elliptic perforations per side. *Adult stem:* elliptic in cross section, 1.5–2.5 cm. across, 1.2–1.6 cm. thick, internodes 2.5–8.0 cm. long. *Petiole:* 20–45 cm. long, the sheath wings neatly deciduous. *Lamina:* ovate to broadly ovate, 15–40 cm. wide, 22–55 cm. long, the length less than twice the width; the base unequal, one side truncate to subcordate, the other side cuneate to acute; primary lateral veins at least on one side arising at an angle greater than 60° with the midrib; perforations absent to numerous in several series, elliptic to elongate, smaller than in the other varieties. *Peduncle:* subterete, 1.0–1.6 cm. thick, 10–18 cm. long. *Spathe:* cream to pale yellow, 12–28 cm. tall, 10–25 cm. around, 1½–2 times longer than the spadix. *Flowering spadix:* pale yellow, 1.4–2.5 cm. thick, 8–13 cm. long; pistils prismatic, truncate at the apex. *Fruiting spadix:* 2.0–3.6 cm. thick, 10–16 cm. long, pale yellow.

COMMON NAMES. Chirrivaca (Costa Rica); Halloquaballa (Arawak, Guyana); Hierba de puerco, Pasmo (Panama); Patquina (Peru); Piñanona (Costa Rica); Saca-frío (Venezuela); Sipó tracuá, Tracuá (Brazil); Ventanillo (Costa Rica, Nicaragua).

DISTRIBUTION. Nicaragua to northeastern Peru, Curacao, Tobago, Venezuela, the Guianas, and Brazil (Amapá and Pará).

REPRESENTATIVE SPECIMENS. **Nicaragua. Jinotega:** Cerro Sialci, 1200–1400 m., July 1947, *Standley 10476* (F). **Zelaya:** vicinity of El Recreo, on Río Mico, 30 m., May 1949, *Standley 19528* (F); vicinity of Rama, 50 m., Sept. 1972, *Madison 716* (GH). **Chinandega:** Ameya, near sea level, June 1923, *Maxon, Harvey & Valentine 7131* (US); vicinity of Chichigalpa, 90 m., July 1947, *Standley 11513* (F). **Managua:** Managua, May 1926, *Chaves 204* (US); Sierra de Managua, 600–900 m., April, *Garnier 768* (US); Casa Colorada & vicinity, 850 m., June 1923, *Maxon, Harvey & Valentine 7370* (US). **Matagalpa:** 6–10 km. northeast of Matagalpa, road to El Tuma, Jan. 1963, *Williams, Molina & Williams 24033* (F). **Granada:** Volcán Mombacho, Feb. 1903, *Baker 2335* (K). **Without locality:** 1853–56, US north Pacific Exploring Expedition, *Wright s.n.* (GH,US). **Costa Rica. Guanacaste:** vicinity of Tilaran, 500–650 m., Jan. 1926, *Standley & Valerio 46587a* (US); vicinity of Santa Rosa, 280–600 m., Sept. 1972, *Madison 721* (CR,GH); vicinity of Cañas, June 1970, *Daubenmire 814* (F); near La Cruz, 200 m., May 1968, *Burger & Stolze 4841* (F); Punta Mala, March 1892, *Tonduz 6807* (CR). **Alajuela:** Zarcero, 5500 ft., Jan. 1938, *Smith H 161* (F); vicinity of Atenas, June 1971, *Gentry 780b* (MO); vicinity of Los Chiles, Río Frío, 30–40 m., Aug. 1949, *Holm & Iltis 780a* (A,BM). **Heredia:** Río Puerto Viejo, 2 km. upstream from confluence with Río Sarapiqui, 100 m., Jan. 1968, *Burger & Stolze 5780* (CR,NY); 10°27′N × 84°07′W, 110 m., May 1973, *Madison 1522* (GH). **Puntarenas:** lower end of road to Monteverde, Jan. 1972, *Wilbur, Almeda & Luteyn 15862* (DUKE); Cabo Blanco Reserve, 9°35′N × 85°56′W, 0–200 m., Dec. 1969, *Burger & Liesner 6614* (F); 8 km. north of Dominical, 10 m., Oct. 1972, *Madison 759* (GH). **San José:** Río Paquita, 1–3 m., Aug. 1936, *Dodge & Goerger 9763* (CR,F,MO); La Verbena, near Alajuelita, 1000 m., Aug. 1894, *Tonduz 8837*(CR,US); San José, 1135 m., April 1890, *Pittier 2839* (CR); basin of El General, 675–900 m., Mar. 1940, *Skutch 4824* (CR,F,US); Las Pavas, 1070 m., Feb. 1924, *Standley 36071* (US); Cerro de las Mercedes, near Desamparados, Sept. 1941, *Alfaro 10* (CR,F); vicinity of El General, 850 m., July 1936, *Skutch 2664* (MICH,US); Las Vueltas, Tucurrique, 635 m., Nov. 1898, *Tonduz 12789* (US). **Cartago:** La Estrella, March 1924, *Standley 39516* (US); Turrialba, July 1965, *Croat 257* (MO). **Panama. Chiriqui:** Quebrada Punta de Piedra, 2 mi. SW of Puerto Armuelles, 0–100 m., Mar. 1973, *Croat 22458* (MO); Puerto Armuelles, 0–75 m., July 1940, *Woodson & Scherry 903* (MO); 16 km. from David on road to Boquete, 400 m., Oct. 1972, *Madison 761* (GH); Guabalá, 50 m., Oct. 1972, *Madison 762* (GH). **Bocas del Toro:** Shepherd Island, Aug. 1964, *McDaniel 5165* (MO); Water Valley, Oct. 1940, *vonWedel 984* (GH, MO,US). **Veraguas:** 5 mi. west of Santa Fé, 800–1200 m., Mar. 1973, *Croat 23053* (MO). **Los Santos:** Guaniquito, 10 mi. north of Tonosi, 100–200 m., July 1970, *Luteyn & Foster 1359* (DUKE); several miles south of Pedasi, July 1967, *Stimson 5303* (DUKE,NY). **Coclé:** 6 mi. north of El Valle, Aug. 1970, *Luteyn & Kennedy 1635* (DUKE); Penonome, 50–1000 ft., Feb.–Mar. 1908, *Williams 571* (NY). **Colon:** Fato, near sea level, July–Aug. 1911, *Pittier 3841* (US); Maria Chiquita on road to Porto Bello, July 1970, *Croat 11359* (MO); near Guasimo, April 1970, *Croat 9986* (MO). **Panama:** Río Pita, 1–3 mi. above Río Maestra, Oct. 1961, *Duke 4748* (BH,GH,NO,US); Perlas Archipelago, San José Island, Fald Hill, April 1945, *Johnston 806* (GH,US); near Arraijan, 15 m., July 1938, *Woodson, Allen & Seibert 1339* (F,GH,MO); Río

Tapia, Dec. 1923, *Standley 28133* (US); 5 mi. west of Chepo, Sept. 1972, *Tyson 6720* (MO). **Canal Zone:** Ancon, 20–80 m., Feb. 1911, *Pittier 3954* (US). **Darien:** Puerto St. Catherine, July 1962, *Dwyer 2299* (MO); 1–4 mi. N of Pucro, June 1967, *Duke 13051* (MO); road from El Real to Pinogana, July 1962, *Duke 5135* (GH,MO, US). **Curacao:** woods of Trinidad, June 1963, *Arnoldo 3025* (US). **Colombia. Atlantico:** region of Baranquilla, Megua, July 1934, *Elias 1217* (F,US); Tubara, 200–250 m., Jan. 1946, *Dugand & Jaramillo 4055* (US). **Magdalena:** Santa Marta, Don Amo Viejo, 2000 ft., June 1899, *Smith 2308* (F,GH,K,MICH,MO,NY,P,PH,US,VT); near Las Nubes, NW slope of Sierra Nevada de Santa Marta, 800 m., Mar. 1973, *Madison 1247* (GH); Parque Tayrona, Canaveral, 45 m., May 1974, *Plowman & Davis 3733* (GH). **Cesar:** Rincon Honda, Aug. 1924, *Allen 258* (F,MO). **Guajira:** Serrania La Macuira, cerro Manzano, 1500–2300 ft., Mar. 1963, *Saravia 2418* (US); 12 km. south of Carraipia, 450 m., July 1944, *Haught 4279* (US). **Cordoba:** near Planeta Rica, 100 m., Nov. 1972, *Madison 787* (GH). **Bolivar:** vicinity of Turbaco, 200–300 m., Nov. 1926, *Killip & Smith 14304* (GH,NY,US). **Chocó:** Río Truando at junction Q. Buche, 40 m., April 1968, *Duke 15752(3)* (US). **Antioquia:** Puerto Berrio, 250 m., May 1949, *Scolnik, Molina & Barkely 19An534* (US); Zaragoza, between Tirana Creek and the hydroelectric plant, 500 m., Feb. 1971, *Soejarto & Villa 2731* (GH); 10 km. W of Venecia, 800 m., Nov. 1972, *Madison 819* (GH). **Cundinamarca:** La Vega, camino a Nocaima, 950–1200 m., Jan. 1942, *Barriga 10651* (US). **El Valle:** Hacienda Valparaiso, Zarzal, 1020 m., July 1939, *Arvelaez & Cuatrecasas 6411* (US); Río Bugalagrande, 1400 m., June 1930, *Dryander 442* (US). **Meta:** Sierrana Macarena, northern end, 600 m., Nov. 1972, *Madison 856* (GH); Río Meta, Cabuyaro, 235 m., Oct. 1938, *Cuatrecasas 3601* (US). **Caqueta:** Morelia, 150 m., Nov. 1941, *von Sneidern s.n.* (S). **Putumayo:** region of Mocoa, 430 m., Dec. 1972, *Madison 874* (GH). **Ecuador. Esmeraldas:** San Lorenzo, Aug. 1967, *Sparre 18076* (S); Hacienda Timbre, April 1967, *Sparre 15446* (S). **Peru. Loreto:** Iquitos and vicinity, July 1967, *Martin, Plowman & Lau-Cam 1629* (ECON); Leticia, Sept. 1929, *Williams 3044* (F). **Venezuela. Zulia:** Dtto. Colon, Caña Dulce, July 1963, *Lescarboura 30* (VEN); El Palmar, 150 m., Aug. 1957, *Medina 910* (VEN). **Lara:** La Miel, Dec. 1966, *Smith V427* (VEN). **Yaracuy:** E of Nirgua, 650 m., Nov. 1967, *Steyermark, Bunting & Wessels-Boer 100329* (VEN). **Miranda:** vicinity of Caucagua, June 1967, *Aristiguieta 2862* (VEN). **Aragua:** Los Cantaños, *Fernandez 110* (VEN). **Anzoátegui:** Río Neveri, 800–1200 m., Mar. 1945, *Steyermark 61388* (F,S). **Monagas:** La Hormiga area, E of Maturin, 14–50 m., Sept. 1955, *Wurdack & Monachina 39402* (NY,S). **Delta Amacura:** between La Margarita and Puerto Miranda, Río Acure, 80–100 m., Nov. 1960, *Steyermark 87816* (NY,VEN). **Apuré:** Reserva Forestal San Camilo, El Nula, 280–300 m., March 1968, *Steyermark, Bunting & Blanco 94966* (VEN). **Bolivar:** Cerro Pichaco, 45 km. N of Tumeremo, 100–300 m., Feb. 1961, *Steyermark 89207* (NY,VEN). **Guyana:** Rupununi River, Sept. 1948, *WB 48* (NY); Waini River, 8°20′N × 59°40′W, April 1923, *De La Cruz 3764* (F,GH,MO,NY,PH,US); Assakatta, 7°45′N × 59°05′W, Sept. 1923, *De La Cruz 4327* (F,GH,MO,NY,PH,US). **Surinam:** lower slopes of Juliana Top, 500–600 m., Aug. 1963, *Irwin et al. 54777* (NY); vicinity of Paramaribo, Peperpot, Jan. 1961, *Kramer & Hekking 2631* (C,K,U); Jagtlust, Aug. 1844, *Focke 830* (U). **French Guiana:** Cayenne, June 1914, *Benoist 21* (P); Iles du Salut, Aug. 1854, *Sagot s.n.* (P); Toukouchipann, 500 m., Aug. 1972, *deGranville 1307* (US). **Brazil. Amapá:** 1°45′N × 50°58′W, Aug. 1962, *Pires & Cavalcante 52495* (MG,NY). **Pará:** Monte Alegre, region of Formosa, Sept. 1953, *Froes 30455* (NY).

1 c. **Monstera adansonii** Schott var. **klotzschiana** (Schott) Madison, *comb. nov.*

Monstera klotzschiana Schott, Oest. Bot. Woch. 4:419 (1854). *Monstera pertusa* (L.) deVriese var. *klotzschiana* (Schott) Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: Brazil, Rio de Janeiro, *Luschnath s.n.* (holotype B, *non vidi;* isotype LE).

Monstera velloziana Schott, Oest. Bot. Woch. 4:66 (1854). *Arum pertusum* Vellozo, Flora Fluminense IX, t. 117 (1835). TYPE: Brazil, *Vellozo,* Flora Fluminense IX t. 117 (1835).

Monstera modesta Schott, Genera Aroidiarum: 75 (1858). *Monstera pertusa* (L.) deVriese var. *modesta* (Schott) Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: *Schott,* Genera Aroidiarum t. 75 (1858). In the *Prodr. Syst. Aroid.* (1860) p. 360, Schott amplifies this as "v.v. cult. ex Mexico australis," but this is probably an incorrect location.

Monstera oblongifolia Schott, Prod. Syst. Aroid. p. 369 (1860). TYPE: Brazil, Rio de Janeiro, a cultivated specimen illustrated by Schott Aroideae No. 2305 (W, *non vidi,* photo BR,C,GH,NY,S,US).

Monstera gaudichaudii Schott, Prod. Syst. Aroid. p. 368 (1860). TYPE: Brazil, Rio de Janeiro, 1834, *Gaudichaud 351* (holotype G, *non vidi;* drawing of holotype = Schott Aroideae No. 2268, W, *non vidi;* photo BR,C,GH,NY,S,US; isotypes B, *non vidi,* L,P).

Monstera lanceaefolia Schott, Prod. Syst. Aroid. p. 368 (1860). TYPE: Brazil, Rio de Janeiro, "v.v. cult." the description is the type.

Monstera maximiliana Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: Brazil, Bahia, *Expeditio archiducis Maximiliana* (W, destroyed, the description is now the type).

Monstera brownii Moore, Trans. Linn. Soc. London, 2nd Ser. **IV**:502 (1895). TYPE: Brazil, Mato Grosso, near Santa Cruz, September, *Moore 351* (holotype BM, photo BH,SEL; isotype B, *non vidi,* photo BH,GH,US).

Monstera coriacea Engler, Bot. Jahrb. 37:118 (1905). TYPE: Brazil, Acre, Jurua Miry, August 1901, *Ule 5730* (B, *non vidi,* photo BH,US).

Monstera peckoltii Krause, Engler Bot. Jahrb. 54, Beibl. **118**:124 (1916). TYPE: Brazil, Rio de Janeiro, *Peckolt 37* (B, *non vidi,* photo BH,GH,US).

Juvenile: leaves ovate to elliptic, 2–4 times longer than broad, entire, rarely with 1-2 elliptic perforations. *Adult stem:* internodes short, 1–4 cm. long, sometimes the petiole bases overlapping and hiding the stem. *Petiole:* 25–50 cm. long, the sheath wings persistent. *Lamina:* coriaceous ovate to elliptic, 18–30 cm. wide, 35–65 cm. long, about twice as long as wide; the base cuneate to bluntly acute; primary lateral veins arising at an angle less than 60° with the midrib; perforations 1 to 8 per side in a single series on each side, ovate to narrowly elliptic, 1–2 cm. wide, 5–12 cm. long. *Peduncle:* subterete to flattened, 14–22 cm. long, 1¼–2 times longer than the spadix. *Flowering spadix:* pale to medium yellow, 2.0–2.6 cm. thick, 8–13 cm. long; the pistils turbinate to acuminate at the apex. *Fruiting spadix:* yellow to orange, 3–4 cm. thick, 12–17 cm. long.

ETYMOLOGY. Named for the botanist Johann Friedrich Klotzsch (1805–1860).

COMMON NAMES. Corcamilla, Picatón (Venezuela); Imbe, Palma de S. Sebastião (Brazil).

DISTRIBUTION. Amazonian Peru and Bolivia, southern Venezuela, the Guianas, and Brazil south to Paraná.

REPRESENTATIVE SPECIMENS. **Peru. Loreto:** Mishuyacu, near Iquitos, 100 m., May–June 1930, *Klug 1532* (F). **Bolivia.** Isapuri, 1500 ft., October 1901, *Williams 676* (in part) (NY). **Venezuela. Bolivar:** Cerro Marimarota, Cerro Le Puerta, 100–250 m., Jan. 1956, *Wurdack & Monachina 41385* (F,NY,VEN); Chimanta Massif, near Río Tirica, 1000 m., May 1953, *Steyermark 75581* (F,NY). **Amazonas:** upper Río Yaciba, 120–150 m., Jan. 1954, *Maguire, Wurdack & Bunting 37444* (NY,VEN). **Guyana.** Upper Mazaruni River, Kurupung, Nov. 1922, *Leng 139* (NY); Kaieteur Falls, Potaro River, Oct.–Nov. 1923, *De La Cruz 4485* (NY). **Surinam.** Savanna I, Zanderij, Oct. 1944, *Maguire & Stahel 25505* (F,NY,US,VEN); Emmaketen 800 m., Sept. 1959, *Daniels & Jonker 1153* (U). **French Guiana.** Grand Inini, Saut. Emerillon, Aug. 1970, *deGranville 661* (US). **Brazil. Rio Branco:** Walde des Quellgebietes, von Mniam, Feb. 1910, *Ule 8484* (MG). **Amapá:** Rio Araguari, Serra do Navio, Sept. 1961, *Pires, Rodrigues & Irvine 51214* (NY). **Amazonas:** Rio Livramento, Humayta, Nov. 1934, *Krukoff 6769* (NY); Alto Purus, Ponto Alegre, April 1904, *Huber 4520* (MG); Manaus, km. 3 da Estrada BR–17, Sept. 1955, *Francisco, RB no. 99990* (RB). **Pará:** BR–22, km. 98, vicinity of Cachoeira, Aug. 1964, *Prance & Silva 58797* (F,GH,MO, NY,S,U,US,W); Belém, Conceição do Aura, May 1952, *Smith 7124* (R,US). **Acre:** Rio

Acre, San Francisco, April 1911, *Ule 9242* (MG); 9°20′S × 69°W, Aug. 1933, *Krukoff 5646* (A,NY). **Ceará:** without locality, *Allemão & deCysneiros 1578* (R); Serra de Baturite, Sept. 1910, *Ule 9002* (L). **Mato Grosso:** near Santa Cruz, *Moore 351* (B,BM, *non vidi*). **Minas Gerais:** without locality, 1816–1821, *Saint-Hilaire 1039* (P). **Bahia:** Rio Preto, 1913, *v. Lutzelburg 361* (M); Rio Sergy, bei S. Bento des Lages, Aug. 1912, *v. Lutzelburg 15102* (M,NY,R). **Rio de Janeiro:** Lidice, July 1969, *Braga 55* (RB); Tres Irmãos, May 1920, *Lampaio 3292* (R). **Guanabara:** Jurujuba, July 1888, *Schwacke 6299* (RB); Sumare, Serra da Carioca, 200–400 m., Nov. 1928, *Smith & Vieira 1297* (F,GH,S,US,). **São Paulo:** Ilha de Sto. Amaro, May 1932, *Hoehne 29667* (NY); Maresias, betw. São Sebastião and Santos, 100 m., July 1967, *Lindeman & de Haas 5626* (US). **Paraná:** Rio do Cedro, 50–100 m., Feb. 1969, *Hatschbach 21184* (C,S,US); Guaratuba, 3 m., Feb. 1952, *Reitz 4372* (US). **Santa Catarina:** S. Francisco do Sul, 100 m., Dec. 1950, *Reitz 3677* (UC).

Synonyms of *Monstera adansonii* Schott of uncertain varietal affinity:

Heteropsis surinamensis Miq., Hort. Amstelod. Delect. Sem. p. 3 (1853).

Monstera surinamensis (Miq.) Schott, Oest. Bot. Zeit. 8:386 (1858). TYPE: Surinam, material cultivated by Miquel, illustrated by Schott Aroideae No. 2326, 2327 (W, *non vidi*, photo BR,GH,NY,S,US).

Monstera fenestrata Schott, Oest. Bot. Woch. 5:290 (1855). TYPE: Venezuela, "Appun. v.v. cult." illustrated by Schott Aroideae No. 2244 (W, *non vidi*, photo BH,BR,C,S).

Monstera milleriana Schott, Oest. Bot. Zeit. 8:386 (1858). TYPE: Surinam, *Hostmann 845* (K).

Monstera crassifolia Schott, Oest. Bot. Zeit. 9:40(1859). TYPE: Venezuela "v.v. cult." illustrated by Schott Aroideae No. 558, 2230, 2233, 2234, 2235 (W, *non vidi*, photo BH,BR,C,GH,NY,S). REPRESENTATIVE COLLECTION: Venezuela, Tovar, 1854–55, *Fendler 1351* (GH,K,NO,NY), determined by Schott.

Monstera seemanii Schott, Oest. Bot. Zeit. 9:40 (1859). TYPE: Taboga, Jan. 1849, *Seeman 1568* (K, isotype BM).

Monstera parkeriana Schott, Oest. Bot. Zeit. 9:41 (1859). TYPE: Guyana, Demerara, *Parker s.n.* (K, photo BH,F,SEL).

Monstera blanchetti Schott, Prodr. Syst. Aroid. p. 367 (1860). TYPE: Brazil, Bahia, *Blanchet s.n.* (holotype G, *non vidi;* drawing of holotype = Schott Aroideae No. 1226, W, *non vidi*, photo BH,BR,C,GH,NY,S,US; possible isotype BM).

Monstera poeppigii Schott, Prodr. Syst. Aroid., p. 365 (1860). TYPE: Peru, Pampayacu, *Poeppig*, illustrated by Schott Aroideae no. 2319; W, *non vidi*, photo SEL.

Monstera ecuadorensis Engler & Krause, Das Pflanzenreich IV 23B:107 (1908). TYPE: Ecuador, in dem Regenwaldern am Fuss der Westcordillere, *Lehman 185* (B, *non vidi*, photo BH,GH,SEL,US).

REPRESENTATIVE SPECIMENS OF UNCERTAIN VARIETAL AFFINITY. **Trinidad.** Coastal hillsides, Maqueripe, March 1920, *Britton, Britton & Hazen 215* (NY,US).**Tobago.** Nov. 1889, *Eggers 5608* (P). **Colombia. Caqueta:** 4 km. south of Florencia, Fan. 1969, *Plowman & Kennedy 2251* (GH). **Peru. Ayacucho:** Río Apurimac Valley, near Kimpitiriki, 400 m., May 1929, *Killip & Smith 22865* (NY,US). **Venezuela. Delta Amacuro:** Río Cuyubini, Sierra Imataca, 100–200 m., Nov. 1960, *Steyermark 87662* (NY,VEN). **Apuré:** Reserva Forestal San Camilo, 280–300 m., March 1968, *Steyermark, Bunting & Blanco 101397* (VEN). **Guyana.** Kanuku Mountains, drainage of Takutu River, 200 m., March 1938, *Smith 3329* (GH,K,NY). **Surinam.** Lucie River, 2–10 km. below confluence of Oost River, 225 m., Sept. 1963, *Irwin et al. 55562* (NY,U). **French Guiana.** Vicinity of Cayenne, July 1921, *Broadway 974* (GH,NY,US). **Brazil. Amazonas:** Serpa, Feb. 1875, *Traill 1132* (P). **Pernambuco:** Tapera, April 1936, *Pickel 4139* (US).

Monstera adansonii was the first species of *Monstera* to be described. Linnaeus named it *Dracontium pertusum* in his Species Plantarum (1753). In 1830 Schott used the generic name *Monstera* Adans. and transferred a number of species previously described in Linnaean genera to it. Among them was *Pothos pertusus* Roxb. which became *Monstera pertusa* (Roxb.) Schott; the epithet *pertusa* was thus preoccupied, and a new name had to be given in *Monstera* for *Dracontium pertusum* L. This nomen novum was *M. adansonii* Schott. Eventually, as generic concepts came to be more clearly defined, *Pothos pertusus* Roxb. was transferred to the genus *Rhaphidophora* Hassk.

Adolf Engler (1878) adopted the name *Monstera pertusa* (L.) deVriese ignoring the fact that this is a later homonym of *M. pertusa* (Roxb.) Schott. The name *M. pertusa* (L.) deVriese thus came to be widely used in floristic and taxonomic works, but it is illegitimate and the correct name for the species is *M. adansonii* Schott.

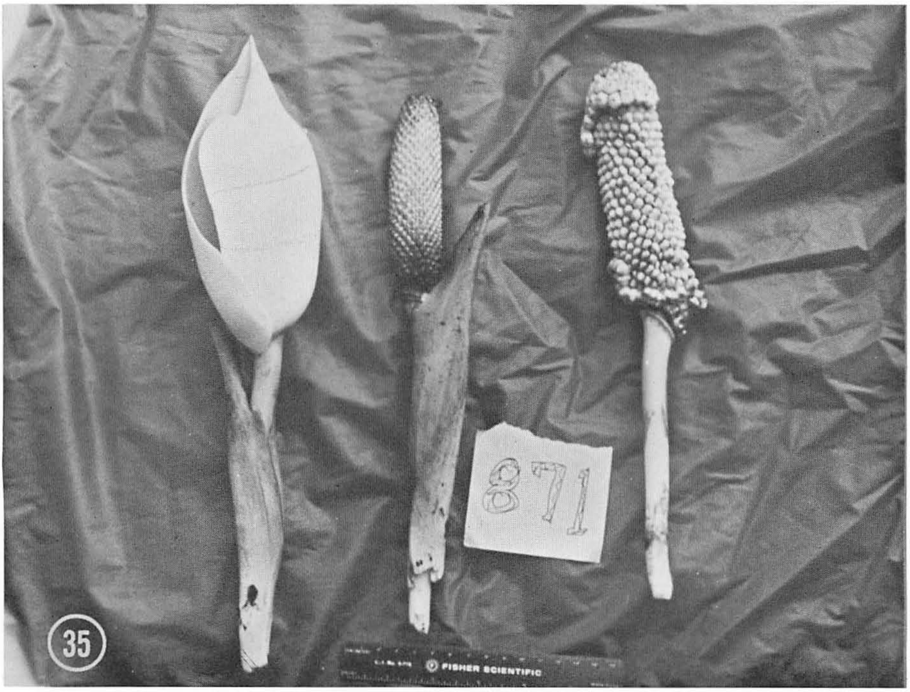
Monstera adansonii is central in a complex of species making up the greater part of section Monstera. These species are extremely variable morphologically and are connected by intermediate forms. Most species of the complex represent morphological and ecological specializations which show connecting links to *M. adansonii;* in addition, transitional forms are found between various combinations of species independent of *M. adansonii.*

Monstera adansonii is the most widespread, most common, most abundant, and most variable species of the complex. Indeed, the range of variation within *M. adansonii* is greater than that existing between some of the other species. Schott, who had very little material to work with, was not presented with the problem of continuous variation between fairly distinct forms; consequently he managed to distinguish 21 species within *M. adansonii* as here delimited. However, a number of his determinations on herbarium specimens are followed by a question mark, suggesting that he recognized some of the problems in his treatment.

Engler and Krause (1908) synonymized most of Schott's species into a "typus polymorphus" *Monstera pertusa* (L.) deVriese, which they subdivided into four varieties. Their varietal division, based largely on the leaf base and the petiole sheath, is rather arbitrary; its artificiality is suggested by the fact that three of the varieties have the same geographical range as the species.

Study of nearly 1,000 specimens of *Monstera adansonii* has led to the recognition of three varieties in the present treatment. These varieties are morphologically and geographically distinct, but in their regions of sympatry they appear to hybridize freely, so that in these areas varietal determinations are difficult or impossible. Thus, much of the material from Venezuela and the Guianas, the main area of sympatry, can only be determined to species.

Monstera adansonii var. *laniata* extends from Nicaragua to northern Peru and across Venezuela and the Guianas to Territoria Amapá in northernmost Brazil. Its most distinctive feature is the very unequal leaf base which is truncate on one side and cuneate to acute on the other. In addition, the petiole sheath is deciduous and the pistils truncate. This



FIGS. 34–35. *Monstera lechleriana:* 34. habit (*Madison 594,* GH); 35. inflorescence, immature fruiting spadix, and mature fruiting spadix in which most of the berries have already shed the stylar portion (*Madison 871,* GH).

variety mostly occurs in open situations: along river banks, in clearings, at forest margins, and in disturbed areas. It has a weedy tendency and is found commonly on fenceposts and roadside trees. I have never encountered it in a deep forest.

Monstera adansonii var. *adansonii* is limited in distribution to the Lesser Antilles. It represents a distinct form which apparently originated in northern South America and invaded the Antillean chain along which it has dispersed as far as Saba. It is intermediate between the other two varieties, combining the floral characteristics of var. *laniata* with the vegetative characteristics of var. *klotzschiana.*

Monstera adansonii var. *klotzschiana* is distributed throughout the Amazon Basin as well as along the southeastern coast of Brazil. In this variety, the leaf bases are cuneate to acute on both sides and the petiole sheath is persistent. The pistils are turbinate to acute and the flowers and fruits are medium yellow or orange, in contrast to the cream or pale yellow color found in the other varieties.

2. Monstera lechleriana Schott

FIGS. 34–35, MAP 7

Monstera lechleriana Schott, Prodr. Syst. Aroid. p. 366 (1860). TYPE: Peru, Gavan, August 1854, *Lechler 267a* (K, photo BH).

Monstera egregia Schott, Seeman Journ. of Botany 2:53 (1864). TYPE: cultivated, of Mexican origin. Schott Aroideae No. 2238, 2239 apparently represent type material. (W, *non vidi,* photo C,BR,GH,NY,S,US). REPRESENTATIVE COLLECTION: Mexico, Vera Cruz, 8 km. south of Misantla, Lauraceae Forest, 750 m., 26 December 1971, *Madison 597* (GH).

Monstera maxima Engler and Krause, Das Pflanzenreich IV 23B:107 (1908). SYNTYPES: Ecuador, Balao, *Eggers 14651* (B, *non vidi,* photo BH,F,GH,US); Ecuador, Gualea, *Sodiro s.n.* (B, *non vidi,* photo BH,SEL). Peru, Prov. Sandia, Chunchusmayo, 900 m., June 1902, *Weberbauer 1182* (B, *non vidi*); Peru, Prov. Huamiles, Río Monzón zwischen Monzón und dem Huallaga, 600–700 m., August 1903, *Weberbauer 3602* (B, *non vidi*).

Monstera standleyana Bunting, Baileya 14:133 (1966). TYPE: cultivated in conservatory of Cornell University, from material of unknown commercial source. November 1964, *Bunting 1534* (holotype BH no. 100111–6; isotypes K,US no. 2521082–4, UC no. 1327778–9, NY). PARATYPES: Costa Rica, Prov. Cartago, vicinity of Pejivalle, 900 m., 7–8 February 1926, epiphytic vine in wet forest, *P. C. Standley & J. Valerio 47245* (US); Prov. Guanacaste, La Tejona, N of Tilaran, 600–700 m., on tree, acaulescent or with short stems, 25 January 1926, *P. C. Standley & J. Valerio 46054* (US).

Epiphyte on the lower trunks of large trees, to 7 m. tall. *Juvenile:* terrestrial creeper, internodes 1–6 cm. long, leaves exserted and erect, petiole vaginate for $\frac{1}{2}$ to $\frac{5}{6}$ its length, the wings persistent; lamina ovate to lanceolate, cuneate at the base, the tip acute to acuminate, coriaceous, glossy adaxially, pale abaxially, slightly unequal. *Adult stem:* subterete, green, smooth, 4.5–6.0 cm. thick, internodes 4–6 cm. long; leaf scars 3.4 cm. across at widest point, the ends of each scar overlapping for 1–2 cm., the lower part terminating behind the axillary bud of the preceding leaf; axillary bud about 1 cm. wide, half as tall, flat, in a depression on the stem. *Petiole:* smooth, 55–120 cm. long, about equal in length or somewhat shorter than the lamina, widely vaginate nearly to the lamina base, on the largest leaves vaginate to within 15 cm. of the lamina base, the sheath wings persistent, their apices blunt or auriculate; the geniculum curved, (5–)7–10 cm. long. *Lamina:* coriaceous, glossy adaxially, ovate, about twice as long as wide, 75–120 cm. long, 35–70 cm. wide, the base somewhat oblique, broadly truncate to slightly cordate, the tip acute; margin entire, perforations lacking or in a single series on each side of the midrib, the perforation elliptic to narrowly elliptic, 1–8 cm. long; primary lateral veins parallel, (16–)20–40 in number, 1–3 cm. distant, the secondary lateral veins parallel to the primary. *Peduncle:* smooth, green toward the apex, white at the base, flattened, 1.5–2.5 cm. thick, 2–4 cm. wide, (16–)20–40 cm. long. *Spathe:* white or pale yellow, thickly coriaceous, 18–44 cm. tall, 15–34 cm. around, constricted above the spadix, i.e., ⅔ to ¾ of the way up, when fully open only exposing the spadix through a narrow slit 1–6 cm. across; tip acute to acuminate. *Flowering spadix:* cream to pale yellow, stigmatic drop orange, (12–)15–20 cm. long, 2.5–4.5 cm. thick, cylindric or slightly tapering, the flowers near the base sterile, the fertile pistils prismatic, truncate at the apex in Mexican specimens, mostly rounded to acute at the apex in material from Central and South America; pistils 8–11 mm. long, 4 mm. across. *Fruiting spadix:* cream to medium yellow (18–) 20–28 cm. long, 4.5–5.5 cm. thick, the berries 16–20 mm. long, 7–9 mm. across, mostly one-seeded; seeds brown, oblong, 10–13 mm. long, 4–6 mm. wide, 3.4 mm. thick.

ETYMOLOGY. After Wilibald Lechler (1814–1856), collector of the type specimen.

COMMON NAMES. Boa Huasca (Peru); Mamurillo, Pantano, Picaton (Venezuela).

DISTRIBUTION. Mexico, Costa Rica to Peru, and Venezuela, mostly at elevations of 800–2100 meters.

REPRESENTATIVE SPECIMENS. **Mexico. Vera Cruz:** 19 km. E. of Catemaco, Bosque Tropical, March 1965, *Quintero 2243* (MICH,US); Zongolica, El Palmar, Campo Experimental de Hule, Nov. 1944, *Santos 3635* (MICH); km. 45 on road Conejo-Huatusco, Barranca de Santa Maria across from Hda. El Mirador, Sept. 1961, *Moore & Bunting 8858* (BH); 8 km. south of Misantla on road to Jalapa, 750 m., Dec. 1971, *Madison 597* (GH). **Oaxaca:** 12–15 mi. from Valle Nacional on road to Oaxaca, 600–1200 m., Aug. 1972, *Madison 634* (GH). **Costa Rica. Alajuela:** Alto Paloma, 1900 m., Jan. 1970, *Lent 1846* (F); S slope of Volcán Arenal, 550 m., Sept. 1972, *Madison 730* (GH). **Panama. Panama:** Cerro Campana, very top of the peak, 1000 m., May 1973, *Madison 1505* (GH); Cerro Jefe, Jan. 1972, *Gentry, Dwyer & Tyson 3499* (MO). **Colombia. Chocó:** 5°55′N × 76°10′W, 2100 m., Nov. 1972, *Madison 823* (GH). **El Valle:** Timba, 1100 m., March 1937, *von Sneidern 1133* (S). **Putumayo:** 40 km. south of Mocoa, 480 m., Nov. 1972, *Madison 871* (GH). **Ecuador. Pichincha:** road Aloag-Santo Domingo, Tandapi, 1500 m., Jan. 1967, *Sparre 14011* (S). **Canar:** 40 km. east of El Triunfo on road to Cuenca, 610 m., Dec. 1972, *Madison 912* (GH). **Loja:** 49 km. from Loja on road to Zamora, 1550 m., Dec. 1972, *Madison 920* (GH). **Peru. San Martín:** Tocache Nuevo, Fundo Consuelo, 5 km. abajo Puerto Pizana, April 1971, *Schunke V. 4826* (F,US). **Huanuco:** Río Monzón, 10 km. above Tingo Maria, 960 m., Dec. 1972, *Madison 944* (GH); Tingo Maria, Aug. 1940, *Asplund 12937* (S). **Pasco:** Río Paucartambo, 30 km. SW of Oxapampa, 1800 m., Dec. 1972, *Madison 951* (GH). **Cuzco:** Río Marcapato, 20 km. above Quincemil, 780 m., Jan. 1973, *Madison 990* (GH). **Venezuela. Yaracuy:** Cerro La Chapa, N of Nirgua, 1200–1400 m., Nov. 1967, *Steyermark, Bunting & Wessels-Boer 100324* (US,VEN); El Amparo, 7–10 km. N of Salom, 1200–1300 m., Dec. 1972, *Steyermark, Espinoza & Diederichs 106752* (VEN). **Distrito Federál:** between Portachuelo and Peñita, 6–8 mi. below junction of Junquito-Col. Tov. Road, 1300–1500 m., Feb. 1966, *Steyermark 94777* (US,VEN); between Petaquire and the sea, 3500 ft., Feb. 1857, *Fendler 2122* (GH). **Aragua:** Rancho Grande, 1100 m., Aug. 1946, *Pittier 15230* (VEN). **Anzoátegui:** tributaries of Río Neveri, NE of Bergantin, 800–1200 m., March 1945, *Steyermark 61388* (F,NY,VEN). **Sucre:** Peninsula de Paria, Cerro de Humo, 800–1000 m., March 1966, *Steyermark 95099* (US,VEN). **Apuré:** Reserva Forestal San Camilo, Cerro Nulita, 250–280 m., April 1968, *Steyermark, Bunting & Blanco 101860* (VEN).

This species was first collected by Lechler in Peru in 1854. His specimen, consisting of a single leaf, was sent to Hooker and was subsequently seen by Schott who described it as a new species in 1860. A few years later Schott observed a live individual of *Monstera lechleriana* cultivated from a propagule of Mexican origin. He described this as a separate species, *M. egregia*, although he did not clarify its distinctness from *M. lechleriana.*

Engler (1879) treated *Monstera lechleriana* as a synonym of *M. pertusa,* but he was uncertain as to its varietal affinities. He maintained the leading synonym, *M. egregia,* noting its apparent similarity to *M. karwinskyi.* In 1908, Engler and Krause went a step further and reduced *M. egregia* to synonymy under *M. karwinskyi.* These two names have been applied primarily to Mexican material, and somewhat inconsistently so, although the two species in question are quite distinct and are referrable to different sections of the genus. Bunting (1965) finally clarified the situation and revived the name *M. egregia.*

Engler and Krause (1908), having subjugated the names *Monstera lechleriana* and *M. egregia* to synonymy under other species, described a new species, *M. maxima,* to accommodate specimens here considered to be *M. lechleriana.* Their new name was based on material from Ecuador and Peru, and the description is adequate except that the leaves are described as irregularly laciniate, which is presumed to be a result of rough treatment of the specimens.

In 1966 Bunting described *Monstera standleyana* from material cultivated under the names *Philodendron guttiferum* Hort. and *Monstera guttifera* Hort., said to be from Costa Rica. Bunting's type has leaves usually without perforations, as do some collections from the wild, e.g., *Madison 772.* The material called *M. standleyana* also has only 14–18 primary lateral veins, in contrast to the 20–40 typical of *M. lechleriana.* However, in all other respects it conforms to *M. lechleriana.* The evidence does not seem to warrant the recognition of a separate taxon, at least on the basis of the single adult specimen known.

Monstera lechleriana characteristically grows on the lower trunks of large trees below the branches. The internodes are short and the leaves are borne in a tight head of ten to fifteen leaves at the top of the stem, which in the foliated part is completely hidden by the overlapping petiole bases. It is this habit of growth, together with its larger size in every respect, that distinguishes *M. lechleriana* from *M. adansonii.* Ecologically the two species are separated by the fact that *M. lechleriana* generally occurs at higher elevations than *M. adansonii.* In the Mexican material of *M. lechleriana,* the spadix is cream and the pistils are truncate; but collections from Central and South America have a yellowish spadix, and the upper portion of the pistil is conical. In Venezuela some plants intermediate between this species and *M. adansonii* var. *klotzschiana* are found, and the shorter spadices with conical pistils of a yellow color in the Venezuelan specimens suggest introgression from *M. adansonii.*

In Mexico, *Monstera lechleriana* is close to *M. acacoyaguensis,* the latter species being distinguished by its numerous large leaf perforations in several series and by the much narrower spadix on which the ovaries are only half as long as those of *M. lechleriana.* In addition, *M. acacoyaguensis* has longer internodes and the leaves are not borne in a tight head. The specimens examined of *M. lechleriana* are somewhat heterogeneous, and it is possible that several sibling species are included. However, the available material is so inadequate that there is at present no basis for recognizing other taxa.

3. Monstera acacoyaguensis Matuda

FIG. 36, MAP 7

Monstera acacoyaguensis Matuda, Madroño **10**:48 (1949). *Monstera magnispatha* Matuda var. *acacoyaguensis* (Matuda) Matuda, Ann. Inst. Biol. Mex. **25**:172 (1954). TYPE: Mexico, Chiapas, shaded woods or forest along the Rio Grande, Acacoyagua, near Escuintla, 100 m., 25 May 1948, *Matuda 17853* (holotype Matuda Herbarium, *non vidi;* isotypes F no. 1330971, MEXU).

Monstera magnispatha Matuda, Rev. Soc. Mex. Hist. Nat. **11**:97 (1950). LECTOTYPE (here designated): Mexico, Chiapas, en orilla de arroyo, bosque alto, Esperanza, Escuintla, 160 m., 28 Sept. 1947, *Matuda 17015* (Matuda Herbarium, *non vidi;* isolectotypes F no. 1273057, 1273060, MEXU,NY). LECTOPARATYPES OF UNCERTAIN AFFINITY: same locality, 11 July 1947, *Matuda 17797* (Matuda Herbarium, *non vidi*); Chiapas, Esperanza, orilla de un arroyo, 5 August 1948, *Matuda 19503* (Matuda Herbarium, *non vidi*). EXCLUDED SYNTYPES: Mexico, Chiapas, bosque claro, Cruz de Piedra, July 1947, *Matuda 17795* (Matuda Herbarium, *non vidi,* MEXU) = *Monstera acuminata* C. Koch; Mexico, Chiapas, Esperanza, 160 m., 11 July 1947, *Matuda 17796* (Matuda Herbarium, *non vidi,* MEXU) = *M. acuminata* C. Koch.

Epiphytic on the lower trunks of large trees to 5 m. tall. *Juvenile:* terrestrial creeper, stem smooth, green, internodes 2–4 cm. long, leaves exserted and erect, petiole vaginate for ⅓ to ⅚ its length, the sheath wings persistent; the petiole about equal in length to the lamina, the lamina subcoriaceous, glossy adaxially, entire, ovate, cuneate at the base, acute at the tip, slightly unequal. *Adult stem:* subterete, smooth, green, 3–5 cm. thick, internodes 3–8 cm. long; leaf scars 1–2 cm. across at the widest point, the ends of each scar overlapping for 0.5–1.0 cm.; axillary buds flat, semicircular, 0.5–1.0 cm. wide, half as tall, in a slight depression on the stem. *Petiole:* smooth, 40–65 cm. long, about ⅔ the length of the lamina, vaginate to the base of the geniculum, the sheath wings persistent, the geniculum 5–6 cm. long. *Lamina:* subcoriaceous, glossy adaxially, paler below, ovate, about twice as long as wide, 60–85 cm. long, 35–45 cm. wide, the base truncate, where it joins the petiole contracted into a cuneate portion about 6 cm. wide and 6 cm. long, the tip acute; margin entire, perforations in one or usually two series on each side of the midrib, the perforations ovate to elliptic, 2–5 cm. wide, 4–12 cm. long, the margin of the perforations often curled adaxially; primary lateral veins parallel, 12–16 in number, 3–5 cm. distant, secondary lateral veins parallel to the primary. *Peduncle:* smooth, terete, about 2 cm. thick, 25–30 cm. long. *Spathe:* light yellow to cream, thickly coriaceous, 25–35 cm. tall, 18–25 cm. around, acuminate, at maturity widest about 5 cm. from the tip. *Flowering spadix:* yellowish, cylindric, not tapered, 18–22 cm. long, 1.5–2.0 cm. thick, the pistils prismatic, truncate at the apex, 4–6 mm. long, 2.5–4.0 mm. across. Fruit and seeds unknown.

ETYMOLOGY. After Acacoyagua, Chiapas, the type locality.

COMMON NAMES. Mimbre, Conte arpón, Bejuco arpón (Mexico, Chiapas).

DISTRIBUTION. Mexico (Western Chiapas), and Belize, at elevations of 0-200 meters.

REPRESENTATIVE SPECIMENS. **Mexico. Chiapas:** Esperanza, Escuintla, 150 m., Dec. 1949, *Matuda 18716* (MEXU,NY,US); El Triunfo, 100 m., Aug. 1974, *Madison 1783* (GH); Acacoyagua, 100 m., 25 May 1948, *Matuda 17853* (F, MEXU). **Guatemala.**

FIG. 36. *Monstera acacoyaguensis:* habit (*Madison 1783,* GH).

Izabal: Modesto Mendez, Río Sarstun, 10 m., June 1970, *Harmon 2562* (MO). **Belize.** Gracie Rock, Sibun River, May 1935, *Gentle 1649* (MICH,MO).

In his original description of this species, Matuda cited five collections. Two of these he later separated as paratypes of *Monstera viridispatha* Matuda, here considered referrable to *M. acuminata* C. Koch. Mixed collections may be involved, as *Matuda 17795* was collected on 25 July

FIG. 37. *Monstera siltepecana:* variation in adult leaf shape, from different individuals (to the same scale).

1947 and the next number, *17796,* on 11 July; *17015* is dated 28 Sept. on some sheets and 15 Sept. on others.

Monstera acacoyaguensis, although known only from a few collections, represents a distinct element in section Monstera. It is most closely allied to *M. lechleriana,* from which it differs in the following respects: the flowering spadix is 1.5–2.0 cm. thick *vs.* 2.5–4.5 cm. thick in *M. lechleriana;* the base of the lamina is contracted into a cuneate portion about 6 cm. long *vs.* the lamina base is abruptly truncate; the lamina having large perforations in several series *vs.* the lamina entire or with a single series of small perforations; and occurrence at elevations of 0–200 m. *vs.* occurrence at elevations mostly above 800 m. in *M. lechleriana. Monstera acacoyaguensis* also has longer internodes and the leaves are not borne in a tight head as in *M. lechleriana. Monstera acacoyaguensis* is readily distinguished from *M. adansonii* by its much longer peduncle, spathe, and spadix.

According to notes on Matuda's specimens, *Monstera acacoyaguensis* occurs in very open situations either along streams or in clearings; I encountered it in Chiapas growing in full sunlight. Matuda (1950) describes the spathes as persisting at maturity for 15–20 days. If this is so, it is distinguished by this feature from other monsteras for which the period of flowering is only two to three days.

4. **Monstera siltepecana** Matuda

FIGS. 37–38, MAP 12

Monstera siltepecana Matuda, Rev. Soc. Mex. Hist. Nat. **11**:97 (1950). TYPE: Mexico, Chiapas, Orillo de Río Naranjo, Cascada, Siltepec, 1200 m., 11 April 1949, *Matuda 18642* (holotype Matuda Herbarium, *non vidi;* isotype MEXU). PARATYPES: Mexico, Chiapas, Col. San Juan Panama, 1830 m., 23 July 1948, *Matuda 18168* (MEXU); Mexico, Chiapas, Río Naranjo, Cascada, Siltepec, 1600 m., 2 June 1949, *Matuda 18792* (photo BH,MEXU,UC); Mexico, Chiapas, Cascada, Siltepec, 1700 m., 21 April 1950, *Matuda 19657* (MEXU).

Juvenile: terrestrial creeper, internodes 1–3 cm. long, leaves exserted and erect, lamina ovate to widely ovate, cordate at the base, acuminate or acute, membranaceous, unequal with one side 1.1 to 2.0 times wider than the other. *Adult stem:* subterete, smooth, in climbing shoots 2.0–3.5 cm. thick, internodes 4–8 cm. long; in stolons 1–2 cm. thick with internodes 20–30 cm. long; leaf scars narrow, the ends of each scar joining in the back of the stem; axillary buds lanceolate to ovate, acuminate, in a depression in the stem not extended into a sulcus. *Petiole:* 30–45 cm. long, about equal in length to the lamina, vaginate to the geniculum, the wings neatly deciduous, the geniculum 3.0–4.5 cm. long. *Lamina:* subcoriaceous, ovate, unequal, sometimes falcate or the midrib curved, 30–60 cm. long, 20–35 cm. wide, broadly cordate at the base, the tip acuminate; margins entire, perforations mostly numerous in 2 to 4 series on each side of the midrib, round near the midrib, elongate near the margin (rarely perforations only one or two); the primary lateral veins parallel, 8 to 12 in number, secondary lateral veins reticulate. *Peduncle:* smooth, green, terete, 8–20 mm. thick, 5–12 cm. long. *Spathe:* thickly coriaceous, greenish-white outside, rose-colored within, 18–25 cm. long, 15–20 cm. around, cuspidate. *Flowering spadix:* white, cylindric, 10–13 cm. long, 3.0–3.5 cm. thick; flowers near the base sterile, the fertile pistils prismatic; stigma round, sessile. *Fruiting spadix:* deep green, cylindric, 12–17 cm. long, 4.5–6.0

cm. thick, the berries mostly one-seeded; seeds light brown, 6–7 mm. long, 3–5 mm. wide, 2–3 mm. thick.

ETYMOLOGY. After Siltepec, Chiapas, the type locality.

COMMON NAMES. Arpón, Hoja de calador (Guatemala); Conte (Mexico); Pico de Zope, Piña anona (El Salvador).

DISTRIBUTION. Mexico (Chiapas and Vera Cruz), Guatemala, El Salvador, and Honduras, in cloud forest at elevations of 1200–2500 meters.

REPRESENTATIVE SPECIMENS. **Mexico. Vera Cruz:** Km. 52 on Jalapa-Misantla road, 1350 m., Dec. 1971, *Madison 598* (GH,MEXU). **Chiapas:** Tenejapa, 8400 ft., Jan. 1966, *Ton 588* (MICH,NY); 52 km. from Huixtla on road to Siltepec, 1850 m., Aug. 1972, *Madison 647* (GH). **Guatemala. Alta Verapaz:** Camche, 6000 ft., April 1889, *J. D. Smith 1538* (US); swamp E of Tactic, 1450 m., April 1941, *Standley 92343* (F). **San Marcos:** between San Rafael Pie de la Cuesta and Palo Gordo, 1800–2400 m., Dec. 1963, *Williams, Molina & Williams 25655* (F,NY); 15 km. from San Marcos on road to Tapachula, 2200 m., Oct. 1974, *Madison 1780* (GH). **Quezaltenango:** between Quebrada Chicharro and Montaña Chicharro, SE facing slopes of Volcán Santa Maria, 1300–1400 m., Jan. 1940, *Steyermark 34358* (F); Los Positos, SW of San Martín Chile Verde, 1500 m., March 1939, *Standley 67904* (F). **Chimaltenango:** between Chimaltenango and San Martin Jilotepeque, 1500–1700 m., Dec. 1940, *Standley 80918* (F); 8 km. S of Acatenango, 2350 m., Sept. 1972, *Madison 673* (GH). **Sacatepequez:** barranco above Dueñas, 1590–1800 m., Jan. 1939, *Standley 63164* (F); Volcán Acatenango, 9000 ft., Feb. 1905, *Kellerman 5253* (US). **Guatemala:** Volcán de Pacaya, 1800–2300 m., Dec. 1940, *Standley 80460* (F). **Baja Verapaz:** region of Patal, 1600 m., March 1939, *Standley 69588* (F). **El Progresso:** slopes SE of Finca Piamonte, 2400–2500 m., Feb. 1942, *Steyermark 43398* (F,NY). **Jalapa:** Volcán Jumay, 1300–2200 m., Dec. 1939, *Steyermark 32362* (F). **Zacapa:** upper Rio Sitio Nuevo, 1500–1800 m., Jan. 1942, *Steyermark 43232* (F,MO,US). **Chiquimula:** Amatillo, 900–1510 m., Oct. 1939, *Steyermark 30527* (F,US). **Escuintla:** Santa Lucia Cotz., Feb. 1927, *Morales 669* (US). **Santa Rosa:** Volcán Jumaytepeque, 6000 ft., Dec. 1892, *Heyde & Lux 4279* (GH,M,NY,US). **El Salvador. Ahuachapan:** Sierra de Apaneca in the region of Finca Colima, Jan. 1922, *Standley 20209* (GH,NY,US). **La Libertad:** Comasagua, Dec. 1922, *Calderon 1358* (GH,US). **Morazan:** Montes de Cacaguatique, 13°46′N × 88°13′W, 1500 m., Dec. 1941, *Tucker 652* (BH,F,K,MICH,NY,PH,UC,US). **Honduras. La Paz:** km. 110 carratera Marcala, 1600 m., April 1956, *Molina 6505* (GH,US). **Distrito Central:** between Cofridia and Rancho Quemada, May 1970, *Barkley & Errazuriz 40313* (GH). **Morazan:** above San Juancito, 1800 m., March 1951, *Williams 17554* (F,GH); Cerro de Uyuca, 1530–1600 m., Feb. 1947, *Standley & Molina 4271* (F).

Monstera siltepecana was first collected in 1889 in Guatemala by John Donnell Smith. The specimen, consisting of a spathe, a flowering spadix, and a leaf, was determined by Engler as *Monstera pertusa* var. *jacquinii*. Apparently Engler considered this material as merely representing a range extension of a polymorphic species already known from southern Central America. In 1922 *M. siltepecana* was collected in El Salvador by Calderon, whose specimen was determined as *M. friedrichsthalii*. This identification was followed by later collectors, and the species became generally known as *M. friedrichsthalii*. In the 1930's and the 1940's Standley and Steyermark made extensive collections of plants in Guatemala, including numerous gatherings of this species. The results of their floristic studies were published in the *Flora of Guatemala* (1958), where they applied the name *M. friedrichsthalii* to this taxon and listed *M. siltepecana* in synonymy. In the meantime, other collections had extended the known range of the species to Mexico and Honduras.

FIGS. 38–39. 38. *Monstera siltepecana:* habit; 39. (right) *Monstera oreophila:* holotype (*Stern, Chambers, Dwyer & Ebinger 1104,* MO).

Apparently the name *Monstera friedrichsthalii* came to be applied to this species in part through a misunderstanding of the type locality. *Monstera friedrichsthalii* Schott is typified by Schott Aroideae No. 2245 based on Friedrichsthal No. 1206, a specimen which was in the herbarium at Vienna, but no longer exists. Schott gave the locality of this collection as Niquimono, Guatemala; however, this is probably not in Guatemala but it does correspond to the present day Niquinohomo in the Departamento of Masaya, Nicaragua. Although superficially resembling *M. siltepecana,* the type of *M. friedrichsthalii* clearly is referrable to *M. adansonii* var. *laniata,* which occurs in Nicaragua and not in Guatemala. Thus, the earliest name for the distinct species occurring in Guatemala is *M. siltepecana* Matuda. In his description of this species, Matuda compares it to *M. pertusa,* from which he distinguished it because of the smaller leaves with numerous perforations and by its occurrence at high elevations. He makes no mention of *M. friedrichsthalii,* of which he was apparently unaware, or else he did not consider it to be closely related.

Monstera siltepecana is a distinctive species. Its outstanding features are the numerous leaf perforations in several series, the reticulate secondary venation, the spathe which is rose-colored within, and the thick, dark green, fruiting spadices. It is most closely allied to *M. oreophila* and *M. adansonii* var. *laniata* of southern Central America.

Monstera siltepecana occurs in cloud forests at elevations of 1200–2500 meters. Characteristically it produces numerous droppers and stolons, and where it is abundant the forest is filled with its climbing and hanging shoots and the ground is criss-crossed with stolons. Because trees in cloud forests are mostly small, *M. siltepecana* often becomes established in trees too weak or too short to allow the individual to grow to maturity; the production of dropper shoots and stolons allows for recovery from this situation.

5. **Monstera oreophila** Madison, *sp. nov.*

FIG. 39, MAP 12

Caudex epiphyticus scandens, 1.5–2.5 cm. crassus, internodiis 2–3 cm. longis. *Foliorum petiolus* lamina paulo longior, 35–55 cm. longus, vagina membranacea marcescens instructus; lamina ovata, 35–50 cm. longa, 17–30 cm. lata, basi late truncata, apice breviter mucronata, integra vel foraminata foraminibus utrinque unserialibus vel biserialibus; nervis lateralibus I. numerosis, patentibus, utrinque 25–50, parallelis, 5–10 mm. inter se remotis; nervis lateralibus II. subparallelis. *Pedunculus* 20–30 cm. longus. *Spatha* salmonea, 15–22 cm. longa. *Spadix fructifer* albus, 15–20 cm. longus, 3–4 cm. crassus, sessilis, cylindricus, obtusus.

TYPE. Panama: Chiriqui, vicinity of Boquete, Finca Collins, 5500 ft., oak-laurel cloud forest, 24 July 1959, *Stern, Chambers, Dwyer & Ebinger 1104* (holotype MO no. 1757942, 1758219; isotypes GH,LE,US no. 2396875).

ETYMOLOGY. From Greek, *oreophilus,* "mountain-loving," referring to the habitat of the species.

COMMON NAME. Comida de Culebras (Costa Rica).

DISTRIBUTION. Costa Rica and Panama, cloud forests, 1600–2500 m. elevation.

REPRESENTATIVE SPECIMENS. **Costa Rica. Alajuela:** road out of Sucre towards Laguna Pozo Verde, 2000 m., Dec. 1974, *Luteyn, Wilbur & Utley 4504* (DUKE).

Heredia: Cerro de Gallito, 1800 m., Nov. 1940, *Leon 326* (CR); vicinity of Vara Blanca, Río Sarapiqui, 1800 m., May 1972, *Luteyn 3026* (DUKE). **San José:** vicinity of Santa Maria de Dota, 1500–1800 m., Dec. 1925, *Standley 41688* (US); Forêts de Santa Rosa du Copey, 1800 m., Feb. 1898, *Tonduz 11932* (CR,US); Asseri, Feb. 1946, *Echeverria 237* (CR). **Cartago:** near Maria del Socorro Power Plant, 5 km. NW of Tres Ríos, 1700 m., May 1967, *Lent 1006* (CR,F). **Panama. Chiriqui:** SW slopes of Cerro Horqueta, 6 km. NW of Boquete, 1700–1800 m., Dec. 1971, *Wilbur, Almeda & Luteyn 15459* (DUKE); Casita Alta, Volcán de Chiriqui, 1500–2000 m., June-July 1938, *Woodson, Allen & Seibert 985* (GH,MO); Audubon Camp, Cerro Punta, 5400 ft., *Tyson 6601* (MO); between Bajo Grande and Paso de Respingo, 2100–2400 m., Dec. 1971, *Wilbur, Almeda & Utley 15172* (DUKE); Cerro Horqueta, 7000 ft., July 1966, *Blum & Dwyer 2673* (MO). **Coclé:** hills north of El Valle, Jan. 1942, *Allen 2950* (F); Cerro Pilon, April 1971, *Croat 14337* (MO).

Monstera oreophila is one of the three Central American species of section Monstera inhabiting cloud forests at elevations of 1600–2500 meters. Included are *M. siltepecana* and *M. epipremoides* to which it is closely related. Like *M. siltepecana*, it has a salmon- or rose-colored spathe and deciduous petiole sheath wings; it differs in having a peduncle twice as long, yellowish white instead of dark green fruit and leaves with numerous parallel veins rather than a few reticulated ones. *Monstera epipremnoides* is separated by its pale yellow spathe and leaves regularly pinnatifid rather than with entire margins. The most distinctive feature of *M. oreophila* is the large number (25–50) of parallel primary lateral veins only 5–10 mm. apart.

Monstera oreophila was recognized as new by H. H. Bartlett, who annotated specimens but did not publish a name.

6. **Monstera membranacea** Madison, *sp. nov.*

FIG. 40, MAP 15

Caudex epiphyticus scandens, internodiis teretibus, 1–2 cm. longis, 1–2 cm. crassis. *Foliorum stirpis juvenculae* lamina exserta, ovata, basi cordata, apice acuminata, foraminibus destituta. *Foliorum stirpis adultae petiolus* 40–50 cm. longus, lamina paulo longior, ad ⅔ vel ⅚ longitudinus usque vagina lata persistente instructus; *geniculum* 3–4 cm. logum; *lamina* membranacea, ovata, basi cordata, apice breviter, mucronata, 40–50 cm. longa, 25–32 cm. lata, integra vel irregulariter pinnatifida, foraminibus rotundis uniserialibus juxta costam instructa, nervis lateralibus I. utrinque 6–9, subparallelis, nervis lateralibus II. inter se reticulatis. *Pedunculus* 13–17 cm. longus, cicatricibus spathae 3–8 cm. decurrens notati. *Spadix fructifer* 10–18 cm. longus, 2.5–3.5 cm. crassus. *Baccae virides,* partibus supernis deciduis semina in pulpa aurantiaca praebentibus. *Semina* globosa, 6 mm. longa.

TYPE. Costa Rica: Prov. San José, western slope of Cerro Tufares, 800 m., 2 October 1972, deep woods, *Madison 738* (holotype GH; isotypes to be distributed CR,MO).

ETYMOLOGY. Latin *membranacea,* "membranaceous," referring to the very thin texture of the lamina, unique in the genus.

DISTRIBUTION. Costa Rica, wet forests, 50–800 meters.

REPRESENTATIVE SPECIMENS. **Costa Rica. Alajuela:** vicinity of Capulin, on the Río Grande de Tarcoles, 80 m., April 1924, *Standley 40148* (US). **Puntarenas:** 8°42′N × 83°31′W, 5 km. W of Rincon de Osa, 50–200 m., Jan. 1970, *Burger & Liesner 7212* (F); same locality, March 1973, *Burger & Gentry 8865* (F); Curridabat, April 1932, *Kupper 951* (M). **San José:** road from Santiago to Parrita, 600 m., Sept. 1967, *Lent 1319* (CR,NY,US).

This is a very distinctive, easily recognized species. It possesses at

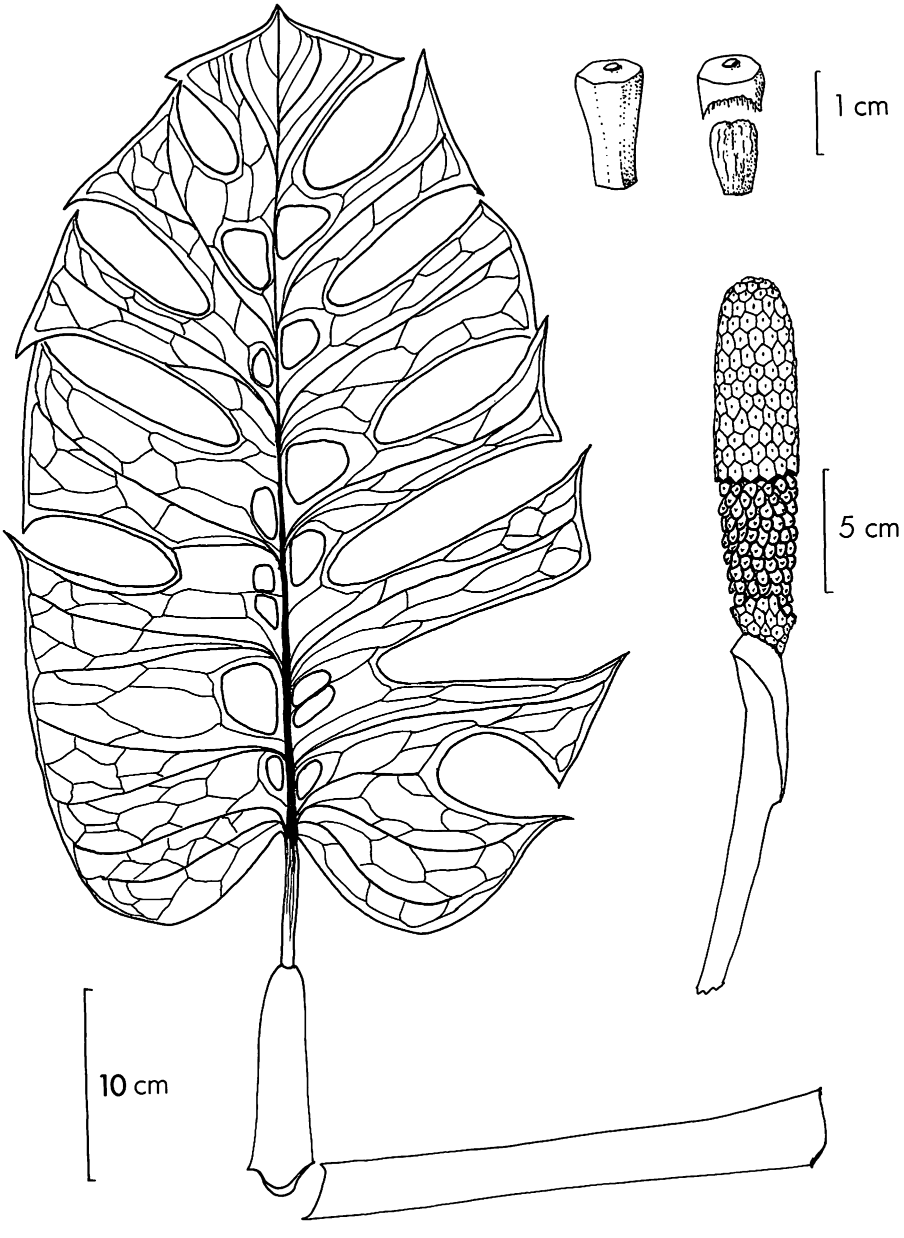


Fig. 40. *Monstera membranacea:* with a fruiting spadix, showing the abscission of the upper portion of berries to reveal the seeds in a colored pulp (based on *Madison 738,* GH).

least four characters unique in the genus: the lamina is very thin and membranaceous, somewhat bullate in live material; the spathe is decurrent on the peduncle for 3–8 cm.; the fruit is green with the stylar portion deciduous to expose the seeds in a bright orange pulp; and the seeds are spherical, with the S-shaped raphe forming a bump on the surface.

The juvenile of *Monstera membranacea* is similar to that of *M. siltepecana,* but many features of the adults separate the two species. Other than this, *M. membranacea* does not appear to be closely allied to any other species, although it clearly belongs in section Monstera.

7. Monstera dilacerata (Koch & Sello) Koch

FIGS. 41–42, MAP 2

Monstera dilacerata (Koch & Sello) Koch, Ind. Sem. Hort. Bot. Berol. App. 5 (1855). *Scindapsus dilaceratus* Koch & Sello, Ind. Sem. Hort. Bot. Berol. (1853). *Tornelia dilacerata* (Koch & Sello) Schott, Prodr. Syst. Aroid. p. 356 (1860). TYPE: cultivated, Berlin, *Carl Koch s.n.* (B, *non vidi,* photo NY,US).

Monstera pinnatipartita Schott, Oest. Bot. Woch. 7:197 (1857). TYPE: Venezuela, Caracas, *Reichenbach f. s.n.* (location unknown, *non vidi*).

Monstera peruviana Engler, Bot. Jahrb. 37:117 (1905). TYPE: Peru, Dept. Huanuco, Prov. Huamalies, in Ufergeholzen am Monzon, 1000 m., August 1903, *Weberbauer 3575* (B, *non vidi,* BH, photo GH,SEL,US).

Monstera longipedunculata Matuda, Soc. Bot. de Mexico, Bol. **14**:22 (1952). TYPE: Belize, Stann Creek District, Middlesex, epiphyte in high ridge on hilltop, 25 May 1939, *Percy H. Gentle 2796* (MICH).

Tornelia dissecta Schott, Oest. Bot. Zeit. 8:179 (1858). TYPE: Costa Rica, Volcán de Turrialba, *Herb. Wendland* (location unknown, drawing of holotype = Schott Aroideae No. 2237, W, *non vidi,* BR, photo C,GH,NY,S,US).

Epiphyte to 10 m. tall, the leaves borne in a cluster at the top of the stem. *Juvenile:* terrestrial creeper, internodes 1–6 cm. long, leaves exserted and erect, petiole vaginate for $\frac{1}{2}$ to $\frac{5}{6}$ its length, the sheath wings persistent; lamina ovate to lanceolate, 3–5 times longer than broad, falcate, coriaceous, the base acute, the tip acute, glossy adaxially, slightly unequal; earliest leaves entire, rarely followed by several leaves with 1–4 perforations before the elaboration of pinnatifid leaves, more commonly going from entire to pinnatifid leaves without bearing perforate leaves. *Adult stem:* elliptic in cross section, green or brown, smooth to slightly papillose, 1.5–3.0 cm. thick, 2.0–4.0 cm. across, the internodes 1.0–3.5 cm. long; the leaves borne in a cluster at the apex of the stem, leaf scars shallow, less than 2.0 cm. wide at the widest point, encircling the stem with the ends of each scar overlapping for 0.5–1.0 cm., the lower part terminating behind the axillary bud of the preceding leaf; axillary bud 6–8 mm. wide, about half as tall, in a depression on the stem. *Petiole:* smooth, 35–75 cm. long, about equal in length to or somewhat shorter than the lamina, vaginate nearly to the lamina base or on the largest leaves to within 7 cm. of the lamina base, the wings persistent; the geniculum 3–5 cm. long. *Lamina:* coriaceous, glossy adaxially, ovate, about twice as long as wide, 40–70 cm. long, 20–40 cm. wide, pinnatifid, the pinnae 4–12 in number on each side, with 1–4 primary lateral veins per pinna, the total number of primary lateral veins 10–20, arising at an angle of about 80° with the midrib near the leaf base, arising at an angle of 30–60° above the base (rarely 60–80°), the pinnae acuminate; the base of the lamina acute to truncate, unequal, the apex acuminate. *Peduncle:* smooth, green toward the apex, white at the base, elliptic in cross section, 1.0–1.6 cm. thick, 1.3–2.5 cm. across, 12–27 cm. long, at least 1 cm. longer than the spadix. *Spathe:* white, 15–25 cm. tall, constricted 5–8 cm. below the apex, acuminate, when fully open the margins 4–8 cm. distant. *Flowering spadix:* white, 1.8–2.0 cm. thick, 7–16 cm. long, cylindric or slightly tapering, the flowers near the base sterile, the fertile pistils prismatic, truncate at the apex. *Fruiting* *spadix:* green, becoming pale yellow at maturity, 10–18 cm. long, 3.5–4.5 cm. thick, berries about 1 cm. across. *Seeds:* brown, 8–10 mm. long, 4–5 mm. wide, 3–4 mm. thick.

ETYMOLOGY. Latin *dilacerata,* "cut" or "torn," referring to the cut or pinnatifid condition of the leaf lamina.

COMMON NAMES. Bejuco de murcielago (Panama); Campanillia (Honduras).

DISTRIBUTION. Guatemala and Belize to Peru, Venezuela, and Amazonian Brazil.

REPRESENTATIVE SPECIMENS. **Guatemala. Alta Verapaz:** 6–8 miles NW of Cubilguitz, 210–250 m., March 1942, *Steyermark 45022* (F,MO). **Belize:** Stann Creek District, Middlesex, May 1939, *Gentle 2796* (MICH). **Honduras. Cortes:** Nacimiento del Río Lindo, 600 m., April 1951, *Williams & Molina 18267* (F). **Atlantida:** Lancetilla Valley, near Tela, 20–600 m., Dec. 1927–March 1928, *Standley 54465* (F,US). **Nicaragua. Zelaya:** vicinity of Rama, 50–100 m., Sept. 1972, *Madison 718* (GH). **Costa Rica. Guanacaste:** near Tilaran, El Silencio, 750 m., Jan. 1926, *Standley & Valerio 44814* (US). **Alajuela:** 5 mi. from La Fortuna on road to Chachagua, 250 m., Sept. 1972, *Madison 726* (GH). **Puntarenas:** Forêts de Santo Domingo de Golfo Dulce, March 1890, *Tonduz 9896* (CR,US). **San José:** Candelarta, 800 m., Oct. 1972, *Madison 746* (CR, GH). **Cartago:** vicinity of Santiago, 1050 m., April 1906, *Maxon 97* (NY). **Limón:** Zent, 50–100 m., Oct. 1972, *Madison 753* (GH). **Panama. Chiriqui:** Burica Peninsula, San Bartolo Limite, 400–500 m., Feb. 1973, *Liesner 204a* (MO). **Coclé:** N rim of El Valle de Anton, near Cerro Turega, 650–700 m., June 1940, *Woodson & Schery 185* (MO). **Panama:** 1 mile below Cerro Azul, 900–1000 m., June 1972, *Luteyn 3212* (DUKE). **Canal Zone:** Barro Colorado Island, Feb. 1969, *Croat 7906* (MO,US). **San Blas:** 2–5 miles S of Mandinga Airport, Oct. 1967, *Duke 14820* (US). **Darien:** Río Balsa between Nanene and Guayabo, Nov. 1967, *Duke & Nickerson 14956* (US). **Colombia. Magdalena:** NW slope of Sierra Nevada de Santa Marta, near Las Nubes, 800 m., March 1973, *Madison 1246* (GH). **Bolivar:** Quimari, 500 m., March 1949, *von Sneidern 5721* (S); Torrecilla, near Turbaco, 150–300 m., Nov. 1926, *Killip & Smith 14417* (GH). **Meta:** 2°77′N × 73°35′W, 300 m., March 1973, *Madison 1213* (GH). **Huila:** La Jagua, Sept. 1924, *Allen 587* (MO). **Nariño:** S end of Gorgona Island, near sea level, Feb. 1939, *Killip & Garcia 33110* (US). **Caqueta:** 20 km. S of Montañita, 300 m., Feb. 1973, *Madison 1184* (GH). **Ecuador. Esmeraldas:** Río San Antonio, Finca El Horizonte, Aug. 1967, *Sparre 18298* (S). **Pichincha:** road from Santo Domingo de los Colorados to Quevedo, Km. 38, 500 m., Oct. 1971, *Dodson & Thien 1131* (MO). **Guayas:** vicinity of Guayaquil, Cerro Azul, Sept. 1955, *Asplund 17592* (S). **Los Ríos:** Hacienda Clementina, between Babahoyo & Montalve, 20 m., Feb. 1967, *Sparre 14555* (S). **Peru. Loreto:** Prov. Maynas, Dtto. Alto Nanay, NW of Santa Maria de Nanay, 130 m., March 1968, *Schunke 2464* (F,US). **Huanuco:** Río Monzón, 10 km. above Tingo Maria, Dec. 1972, *Madison 945* (GH). **Venezuela. Zulia:** Sierra de Perija, SW of Machiques, 550 m., Aug. 1967, *Steyermark & Fernandez 99823* (NY,VEN). **Miranda:** 5.5 km. W of Aricagua, 50 m., March 1973, *Steyermark & Espinoza 106897* (VEN). **Brazil. Amazonas:** Rio Purus—Rio Itaxi, Rio Curuquete, 30 km. above mouth of Rio Coti, July 1971, *Prance et al., 14458* (NY,US). **Acre:** 15 km. below Tarauaca, Sept. 1968, *Prance, Ramos & Farias 7437* (NY).

As with many species of *Monstera,* the type of *M. dilacerata* is an inferior specimen consisting of a few leaves from an immature cultivated plant of uncertain geographic origin. Engler and Krause (1908) applied the name to later unambiguous collections (e.g., *Tonduz 13320*) and it has thus come to be widely used as in its present interpretation.

The Peruvian material of this species generally has only 4–6 pinnae per side, whereas Central American *Monstera dilacerata* has 7–12 pinnae; this has been the basis for the separation of *M. peruviana.* However, material from the two areas agree in all other respects and as the extremes of pinna condition are connected by many intermediates there appears

FIGS. 41–42. *Monstera dilacerata:* 41. habit (*Madison 1184,* GH); 42. flowering shoot with overlapping leaf bases, a juvenile shoot to the right (*Madison 1246,* GH).

to be little or no basis for maintaining *M. peruviana* as a separate taxon.

The lengths of the peduncle and the spadix are quite variable in *Monstera dilacerata*, the former ranging from 12–27 cm. However, these characters are quite variable, even within an individual plant, and appear to have no taxonomic significance.

Monstera dilacerata is most easily recognized by its regularly pinnatifid leaves borne in a tight head at the apex of the stem. It occurs either in dark forests or exposed situations. It is readily distinguished from *M. tenuis* and *M. spruceana* by the exserted juvenile leaves, the peduncle exceeding the flowering spadix, the leaves borne in a tight head, and the petiole nearly equaling the lamina. In addition, these two other species have pinnae arising nearly at right angles to the costa, whereas in *M. dilacerata* the pinnae generally arise at an angle of 30–70°.

Monstera subpinnata is distinguished from *M. dilacerata* by the pinnae being constricted at the base and arising at a wide angle, and by the pistil that is prolonged into a conical, rather than truncate, style.

8. **Monstera subpinnata** (Schott) Engler

FIG. 43, MAP 5

Monstera subpinnata (Schott) Engler, D. C. Monog. Phan. **2**:267 (1879). *Tornelia subpinnata* Schott, Prodr. Syst. Aroid. p. 357 (1860). TYPE: Peru, Pompayacu, *Poeppig 1557* (W, destroyed; isotype P, photo BH,US).

Monstera uleana Engler, Bot. Jahrb. **37**:118 (1905). TYPE: Peru, Pampas de Ponasa, 1100 m., *E. Ule 3p* (B, *non vidi*, photo BH,GH,NY,US).

Monstera latiloba Krause, Notizbl. Bot. Gart. Berlin **11**:615 (1932). LECTOTYPE (here designated): Peru, Loreto, Balsapuerto (Lower Rio Huallaga Basin), 150–350 m., dense forest. Epiphyte, spike orange, 28–30 August 1929, *E. P. Killip & A. C. Smith 28421* (B, *non vidi*, photo BH; isolectotypes NY,US no. 1462005, 1462006). LECTOPARATYPE: same locality and date, *E. P. Killip & A. C. Smith 28620* (B, *non vidi*, NY,US no. 1462152).

Scandent epiphyte to 12 m. tall. *Juvenile:* unknown. *Adult stem:* 1.5–2.5 cm. thick, internodes 3–8 cm. long, covered by a thick, light brown cuticle which flakes off in dried material. *Petiole:* 25–38 cm. long, about equaling the lamina, vaginate to within 5 cm. of the blade base, the sheath wings deciduous. *Lamina:* 25–40 cm. long, 18–30 cm. wide, deeply pinnatifid, the pinnae 3–12 in number per side, usually contracted into a narrowly cuneate portion at the base, rarely the pinnae 4–7 cm. wide and then narrowed to 2–4 cm. wide at the base, acuminate at the tip, the terminal portion of the lamina about equaling in size and shape the lateral pinnae; primary lateral veins 8–14 in number, the secondary lateral veins parallel to the primary, arising at an angle of 70–90° with the costa. *Peduncle:* terete, 5–10 mm. thick, 8–12 cm. long, equaling or somewhat shorter than the flowering spadix. *Spathe:* white, cream, or yellowish-pink, 12–18 cm. tall. *Flowering spadix:* pale yellow to yellow, 8-12 cm. long, 1.5–2.0 cm. thick, cylindric or slightly tapering, the pistils prolonged into a pronounced conical or acute style 2–4 mm. long. *Fruiting spadix:* green, becoming yellow or orange at maturity, 12–17 cm. long, 2.0–3.5 cm. thick; seeds about 7 mm. long, 5.5 mm. wide, 3 mm. thick.

ETYMOLOGY. The epithet refers to the pinnatifid condition of the lamina.

COMMON NAMES. Costilla de Adan, katipas, magkamak (Peru).

DISTRIBUTION. Ecuador, Peru and Bolivia, 300–1100 m., elevation.

REPRESENTATIVE SPECIMENS. **Ecuador. Napo-Pastaza:** Mera, 1100 m. 21 Nov. 1955, *Asplund 18540* (S); Mera, March 1940, *Lugo 155* (S). **Morona-Santiago:** Gualaquiza, Mision Bomboiza, 700–800 m., Sept. 1967, *Sparre 19081* (S). **Zamora-Chinchipe:**

5 km. N of Cumbaraza, 900 m., April 1974, *Harling & Anderson 13788* (GB). **Peru. Amazonas:** Yuwientsa, 1700–2000 ft., March 1973, *Ancuash 97* (MO); Río Cenepa, 800–900 ft., December 1972, *Berlin 665* (MO). **Loreto:** Balsapuerto, 150–350 m., Aug. 1929, *Killip & Smith 28241* (B,NY,US); Yurimaguas, 155–210 m., June 1929, *Williams 4694* (F,NY,US). **San Martin:** Prov. Mariscal Caceres, Dtto. Tocache Nuevo, Jan. 1970, *Schunke V. 3724* (F); Alto Río Huallaga, 360–900 m., Dec. 1929, *Williams 6582* (F,US). **Junin:** Río Pinedo, N of La Merced, 700–900 m., May 1929, *Killip & Smith 23639* (NY,US). **Ayacucho:** Río Apurimac Valley, near Kimpitiriki, 400 m., May 1929, *Killip & Smith 22949* (NY,US). **Bolivia. La Paz:** San Buenaventura, 1500 ft., Nov. 1921, *Cardenas 1853* (NY,US).

Monstera subpinnata inhabits the forested western slopes of the Andes.

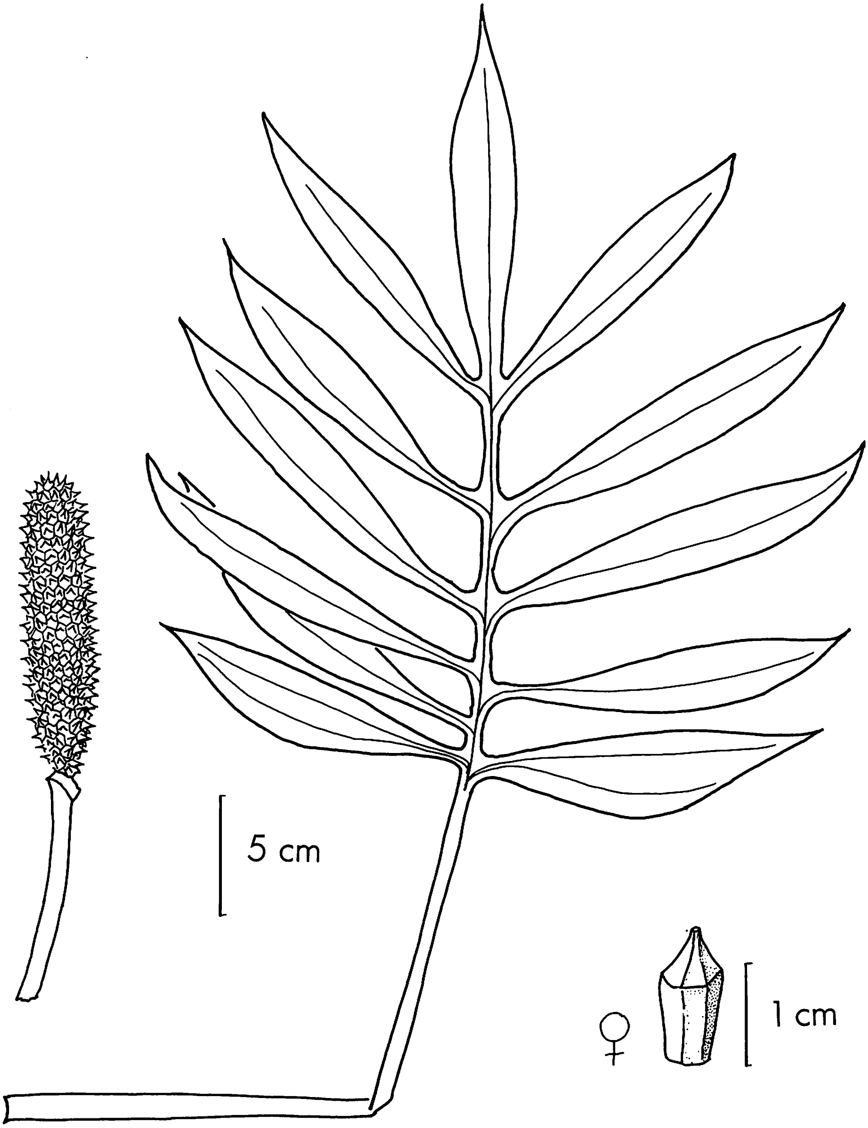


Fig. 43. *Monstera subpinnata:* with the spiny spadix characteristic of the species.

It is distinct among the pinnatifid monsteras by having the pinnae constricted into a narrowly cuneate portion at the base. In a few specimens the pinnae are 4–7 cm. wide rather than the usual 1–3 cm., and though narrowing to 2–4 cm. wide at the base, they are not narrowly cuneate. Plants with the wider pinnae have been separated previously as *M. latiloba,* but they seem to represent only a slight and unimportant variation within *M. subpinnata,* with which they agree in other respects. An additional diagnostic feature of *M. subpinnata* is the prolongation of the pistil into an attenuate conical style. This allows for ready identification of both living and dried material.

9. **Monstera gracilis** Engler

FIG. 44, MAP 5

Monstera gracilis Engler, D. C. Monog. Phan. II:258 (1879). TYPE: Colombia, Meta, Villavicentia, Llano de St. Martin, *Karsten* (W, destroyed, the description is now the type). REPRESENTATIVE COLLECTION: Colombia, Meta, 20 km. southeast of Villavicencio, 500 m., 17 March 1939, *E. P. Killip 34288* (F,US).

Slender root-climbing epiphyte, 2–3 m. tall. *Juvenile:* terrestrial creeper, the leaves exserted and erect, the lamina ovate, acute at the apex, membranaceous, perforate even among the earliest leaves. *Adult stem:* subterete, smooth, green, 0.5–1.0 cm. thick, the internodes 1–3 cm. long. *Petiole:* 18–35 cm. long, slightly shorter than the lamina, vaginate to the base of the geniculum, the sheath wings deciduous, the geniculum 1.0–2.5 cm. long. *Lamina:* ovate, 20–30 cm. wide, 25–38 cm. long, membranaceous, truncate to broadly acute at the base, the apex acute; perforate and pinnatifid or pinnatifid only, the perforations small and near the midrib, the pinnae irregularly shaped, 4–10 per side in number, mostly long acuminate at the apex; primary lateral veins 1–2 per pinna, 8–12 in number per side, arising at an angle of 70–90° with the midrib, secondary lateral veins parallel to the primary. *Peduncle:* slender, 5–8 mm. thick, 8–15 cm. long, to 18 cm. long in fruit. *Spathe:* cream to pale yellow, 5–8 cm. tall. *Flowering spadix:* pale yellow, 4–6 cm. long, 1.0–1.2 cm. thick, the pistils truncate, the upper portion of the pistil containing numerous trichosclereids. *Fruiting spadix:* green, becoming yellow at maturity, 6–8 cm. long, 1.5–2.0 cm. thick, the berries prismatic.

ETYMOLOGY. Latin *gracilis,* "thin" or "slender," in reference to the diminutive stature of the plant and its parts.

DISTRIBUTION. Colombia, Meta to Putumayo.

REPRESENTATIVE SPECIMENS. **Colombia. Meta:** 20 km. SE of Villavicencio, 500 m., March 1939, *Killip 34288* (F,US); Villavicencio, 450 m., Aug. 1917, *Pennell 1398* (NY); Sierra de la Macarena, North Ridge, 1400 m., Dec. 1949, *Philipson & Idrobo 1989* (BM,US); Río Guapaya, 500 m., Jan. 1950, *Philipson, Idrobo & Jaramillo 2198* (BM); Llanos de San Martín, 450 m., Nov. 1972, *Madison 843* (GH). **Vaupes:** Río Inirida, 70°50′W, near Santa Rosa, 220 m., Jan. 1953, *Fernandez 1966* (US). **Caqueta:** Montañita, July 1926, *Juzepczuk 6027* (LE). **Putumayo:** Puerto Porvenir, Río Putumayo, 230–250 m., Nov. 1940, *Cuatrecasas 10664* (US).

Monstera gracilis is a rare species confined to a limited geographic area in eastern Colombia, and is known from only a few collections. The population of this species which I observed consisted of half a dozen individuals growing in a riparian forest in the llanos. None climbed above 2 m. without the terminal shoot converting to a stolon and returning to the ground; apparently this is not a high-climbing species, but none of the other collections give any data on this point.

Monstera gracilia differs from *M. dilacerata* in having a membranaceous (*vs.* coriaceous) lamina, deciduous (*vs.* persistent) petiole sheath wings, and much smaller spadices and slenderer stems. It is distinguished from *M. adansonii* by the smaller spathe and spadix and the pinnatifid leaves.

Some of the larger, perforated forms of *Monstera obliqua* approach *M. gracilis* vegetatively, but the fruits of the two species are quite distinct. In *M. gracilis* the yellow berries are prismatic and armed with numerous trichosclereids in the upper portion, whereas *M. obliqua* has orange-colored globose berries lacking trichosclereids in the stylar portion.

As with many aroids, typification of this species is problematical. The holotype collection by Karsten was in the herbarium at Vienna and has been lost. In their 1908 treatment of *Monstera gracilis,* Engler and Krause cite two specimens—the Karsten collection and *Triana 690* (deposited in BM) from the type locality. They provide an illustration of the species based on one of these two specimens. However, the Triana collection was not included in a loan of *Monstera* from the British Museum, and its existence is thus uncertain. The Juzepczuk collection at Leningrad, cited above, was determined by Krause, and this at least provides some basis for my interpretation and a measure of continuity in the identification of the species.

10. **Monstera epipremnoides** Engler

FIG. 45

Monstera epipremnoides Engler, Bot. Jahrb. 37:118 (1905). LECTOTYPE (here designated): Costa Rica, Prov. San José, Santa Maria de Dota, 1300 m., 4 April 1890, *H. Pittier 2486* (B, *non vidi,* photo BH,SEL, as *Biolley 2846;* isolectotype CR as *Biolley 2846,* BR as *Pittier 2486*). EXCLUDED SYNTYPE: Costa Rica, Prov. San José, La Uruca, 1100 m., July 1890, *Biolley 2846* (CR in part; specimens at B and BR under this number are actually *Pittier 2486*).

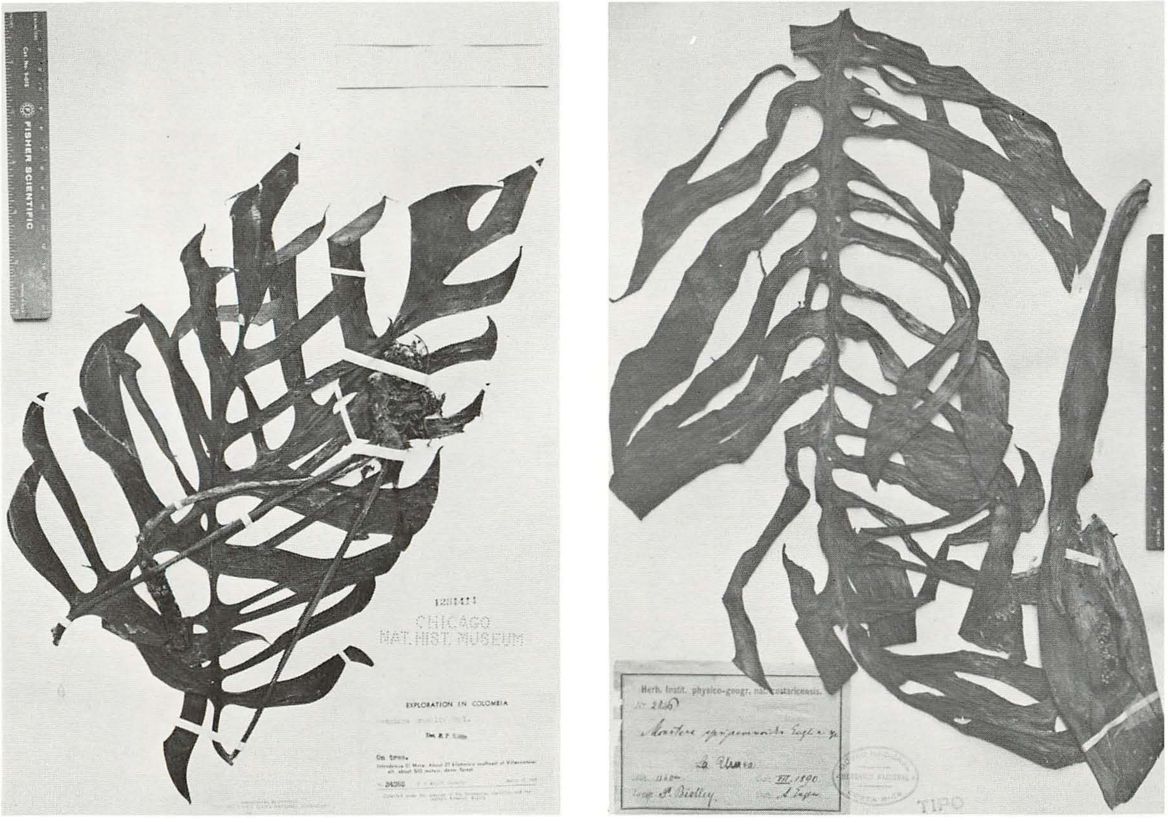
Epiphytic climber in cloud forest. *Juvenile:* unknown. *Adult stem:* 2–3 cm. thick. *Petiole:* 35–50 cm. long, vaginate to within 5 cm. of the lamina base, the sheath wings persistent. *Lamina:* ovate, subcoriaceous, 35–55 cm. long, 22–35 cm. wide, pinnatifid and perforate, the pinnae 12–20 in number on each side, 1.0–2.5 cm. wide, the sinuses extending to the midrib, primary lateral veins 1 or 2 per pinna, secondary lateral veins parallel to the primary; the perforations mostly small, 0.5–2.0 cm. across, round to elliptic, located along the midrib, other perforations very elongate and extending from the midrib nearly to the margin. *Peduncle:* about 1 cm. thick, 20–30 cm. long. *Spathe:* 15–22 cm. long. *Flowering spadix:* cylindric, 9–12 cm. long, about 2 cm. thick, the pistils truncate. *Fruit:* unknown.

ETYMOLOGY. *Epipremnoides* refers to the similarity in the appearance of the leaf to *Epipremnum pinnatum* (L.) Engler of Malesia.

DISTRIBUTION. Costa Rica, Prov. Cartago and San José.

REPRESENTATIVE SPECIMENS. **Costa Rica. Cartago:** without locality or date, *Orsted 15795* (C). **San José:** Santa Maria de Dota, 1300 m., April 1890, *Pittier 2486* (B, photo BH,BR,CR,SEL); 5 km. S of Santa Maria de Dota, 6000 ft., July 1972, *Primack & Stone 337* (DUKE).

CULTIVATED SPECIMENS. **Venezuela. Caracas:** cultivated in the garden of Mr. Wendlinger, plants originally from Costa Rica, 1960, *Steyermark s.n.* (VEN).



FIGS. 44–45. 44. (left) *Monstera gracilis (Killip 34288,* F); 45. (right) *M. epipremnoides:* isolectotype (labelled *Biolley 2846,* is probably *Pittier 2486,* CR).

In his description of this species Engler cites two specimens: *Pittier 2486* and *Biolley 2846,* both collected in Costa Rica in 1890. The Biolley specimen at CR is a mixed collection, consisting of one sheet of *Monstera epipremnoides* and one sheet of *M. adansonii* var. *laniata.* La Uruca, the locality of the Biolley collection, is known as a locality for *M. adansonii* var. *laniata* by other collections (e.g., *Pittier 2839*) of the same year. In my opinion, the only collection of *M. epipremnoides* involved here is *Pittier 2486,* and because of the similarity of the two numbers and because both men were working at the same institution at the same time, I think that some of Pittier's specimens accidentally came to be labeled with Biolley's collection data. Engler's description and illustration clearly fit the Pittier collection, which is here designated as the lectotype.

Monstera epipremnoides is very close to *M. dilacerata,* from which it differs morphologically principally in the appearance of the leaves, which have narrower pinnae, as well as perforations which are not found in the leaves of *M. dilacerata.* It is further separated by its habitat. *Monstera epipremnoides* occurs in cloud forests at 1300–1800 m., while *M. dilacerata* mostly occurs below 1000 meters.

Jonker-Verhoef and Jonker (1966) included *Monstera epipremnoides* in the flora of Surinam, based on the collection *Wessels-Boer 872,* housed at Utrecht. However, I consider this specimen to be *M. adansonii* var. *laniata. Monstera epipremnoides* should be excluded from consideration as a taxon in the flora of Surinam.

11. **Monstera xanthospatha** Madison, *sp. nov.*

FIG. 46, MAP 14

Planta epiphytica scandens. *Caulis* teres 5–10 mm. crassus, internodiis 3–6 cm. longis. *Foliorum petiolus* 12–18 cm. longus, ad geniculum usque vaginatus, vagina decidua; *lamina* oblique lanceolata, 16–25 cm. longa, 5–8 cm. lata, inequilatera, basi cuneato-angustata, apice acuminata, integra vel pauciforaminata foraminibus inter nervos primarios solitariis anguste ellipticis ad 5 cm. longis. *Pedunculus* 15–26 cm. longus, petiolo paulo longior. *Spatha* extus aurea, intus alba, circ. 9 cm. longa. *Spadix florifer* flavus, 6–8 cm. longus, 2 cm. crassus, inferne sterilis. *Spadix fructifer* nutans, aurantiacus vel ruber. *Baccae* subprismaticae.

TYPE. Colombia: Dept. El Valle, Cordillera Occidental, La Cumbre, 1600–1800 m. Climbing herb. 14–19 May 1922, *Killip 5668* (holotype GH; isotypes NY, US no. 1142004, PH no. 612990).

ETYMOLOGY. Greek *xanthospatha,* "yellow spathe," referring to the deep yellow color of the abaxial surface of the spathe.

DISTRIBUTION. Colombia, Cordillera Occidental and Cordillera Central.

REPRESENTATIVE SPECIMENS. **Colombia. Antioquia:** Angelópolis, 2000 m., Aug. 1910, *Mayor 169* (Z); Boqueron, between Medellín and Palmitas, 2300–2500 m., Jan. 1948, *Barkely & Klevens 52* (US); Salgar, near Medellín, July 1928, *Toro 1304* (NY). **Caldas:** Canaan, S of Salento, 1400–1700 m., July 1922, *Pennell 9055* (GH,US). **El Valle:** La Cumbre, 1600–1800 m., May 1922, *Killip 5668* (GH,NY,PH,US); 1 km. E of Bitaco, 4500 ft., Nov. 1963, *Hutchison & Idrobo 3038* (US); Hoya del Río Cali, 1580–1650 m., Nov. 1944, *Cuatrecasas 18765* (F); Baga de la Tulia, 1850–2000 m., Oct. 1944, *Cuatrecasas 18382* (F); Dagua, Buenaventura, 600 m., *Lehmann 5312* (K); La Cumbre, 1700–2200 m., Sept. 1922, *Killip 11408* (GH,NY,PH).

FIGS. 46–47. 46. (left) *Monstera xanthospatha:* holotype (*Killip 5668,* GH); 47. (right) *Monstera minima:* holotype (*Duke 14758 (3),* MO).

CULTIVATED SPECIMENS. **Colombia.** July 1959, *Kyburz 11* (US); Medellín Jardin Botanico, *Plowman s.n.* (photograph only, to be deposited GH).

Monstera xanthospatha shows close affinities to *M. obliqua* from which it differs by its larger size in every respect and by the subprismatic berries which contain trichosclereids in the stylar portion. The berries of *M. obliqua* are globose and lack trichosclereids in the stylar portion. In addition, the two species are ecologically quite distinct. *Monstera obliqua* occurs mostly near sea level, while *M. xanthospatha* ranges from elevations of 1400 to 2500 meters. *Monstera xanthospatha* is distinguished from the remaining species of the section in various ways, and always by the deep yellow abaxial surface of the spathe.

The three Central American species of *Monstera* with a similar elevational range do not show a close alliance to *M. xanthospatha,* which apparently has not arisen from a high-altitude species complex, but has evolved from some lowland ancestor.

In all but one of the fruiting specimens examined the spadix is nodding from the erect peduncle, a character not known in other *Monstera* species.

12. Monstera obliqua Miquel

FIG. 48, MAP 3

Monstera obliqua Miq., Linnaea **18**:79 (1844). TYPE: Surinam, Vredenburger-Zandrits, October 1842, *Focke 719* (U, photo BH,SEL).

Monstera microstachya Schott, Oest. Bot. Woch. **5**:274 (1855). TYPE: Brazil, *Hoffmannsegg s.n.* (Willdenow Herb. No. 7140, B, *non vidi,* photo BH, microfiche IDC 7440. 493:III. 2).

Monstera expilata Schott, Prodr. Syst. Aroid. p. 367 (1860). *Monstera obliqua* Miq. var. *expilata* (Schott) Engler, in Martius, Flora Brasiliensis **III** (2):113 (1878). TYPE: Brazil, Amazonas, Rio Negro, Japura et Rio Solimões, in aboribus sylvarum, *Martius 1196* (M, photo BH; drawing of holotype = Schott Aroideae No. 2243, W, *non vidi,* photo BR,C,GH,S,US).

Monstera falcifolia Engler, Bot. Jahrb. **37**:117 (1905). TYPE: Brazil, Amazonas, Jurua Miry, July 1901, *Ule 5622* (holotype B, *non vidi,* photo BH,GH,US; isotypes K,L,MG, photo BH).

Monstera fendleri Engler, Bot. Jahrb. **37**:117 (1905). TYPE: Trinidad, 1877–1880, *Fendler 736* (holotype K; isotypes NY,P).

Monstera sagotiana Engler, Bot. Jahrb. **37**:117 (1905). TYPE: French Guiana, Karouany, *Sagot 609* (BM, photo BH).

Monstera unilatera Rusby, Bull. New York Bot. Gard. **6**:494 (1910). TYPE: Bolivia, Dept. La Paz, San Buena Ventura, 1400 ft., 25 November 1901, *Williams 526* (NY).

Monstera boliviana Rusby, Bull. New York Bot. Gard. **6**:494 (1910). TYPE: Bolivia, Isapuri, common on trees, 1500 ft., 10 October 1901, *Williams 676* (holotype NY; isotypes US no. 1312955, BM,K, photo BH,SEL). Type is a mixed collection with *M. adansonii* var. *klotzschiana*).

Monstera snethlagei Krause, Notizbl. Bot. Gart. Ber. **9**:272 (1925). TYPE: Brazil, Maranhão, Jury-assu, Mta. de Allegria, Ketterpflanze im Igapowald, gelb, Hullblatt ebenfalls gelb, 14 November 1923, *Snethlage 327* (B, *non vidi,* photo BH,GH,US).

Monstera killipii Krause, Notizbl. Bot. Gart. Berlin **11**:614 (1932). TYPE: Peru, Dept. Loreto, Iquitos, 100 m., epiphyte, spathe and spadix light yellow, woods, 2–8 August 1929, *Killip & Smith 27372* (holotype B, *non vidi,* photo BH,SEL; isotypes F no. 616009, NY, US no. 1461136).

Monstera falcifolia Engler var. *latifolia* Krause, Notizbl. Bot. Gart. Berlin **11**:614 (1932). TYPE: Peru, Dept. Loreto, Puerto Arturo, Lower Río Huallaga below Yurimaguas, 135 m., 24–25 August 1929, *Killip & Smith 27795* (holotype B, *non vidi,* photo BH,SEL; isotypes NY, US no. 1461494).

Slender climbing epiphyte on trees, saplings, or shrubs. *Juvenile:* terrestrial creeper, the leaves entire, exserted and erect, the lamina membranaceous, ovate to lanceolate. *Adult stem:* green, smooth, terete, 2–7 mm. thick, the internodes 1–6 cm. long, occasionally producing hanging and creeping stolons with internodes 10–30 cm. long. *Petiole:* 5–15 cm. long, vaginate for most of its length, the sheath wings deciduous; geniculum 5–15 mm. long. *Lamina:* membranaceous, quite variable in shape, ranging from lanceolate 35 cm. long and 4 cm. wide with an acute base to broadly ovate, 14 cm. long and 12 cm. wide with a truncate to subcordate base; mostly ovate, somewhat falcate, 8–15 cm. long and 4–6 cm. wide, the base oblique, unequal, with one side about twice as wide as the other; usually entire but sometimes perforated, the holes one to many in a single series on each side of the midrib; primary lateral veins not prominent. *Inflorescences:* produced sympodially in groups of six to eight, rarely fewer. *Peduncle:* terete, 1–2 mm. thick, 7–15 cm. long, elongating throughout the development of the fruit. *Spathe:* green to white when immature, becoming a bright yellow at maturity, 4–7 cm. long, 3–5 cm. across when fully open, acuminate or mucronate for 3–8 mm. at the tip. *Flowering spadix:* deep yellow, 5–10 mm. thick, 2.5–6.0 cm. long. *Fruiting spadix:* green to olive-green tinged with orange when immature, becoming lighter and finally deep orange at maturity, 10–15 mm. thick, 4–8 cm. long; the berries globose, 5–8 mm. in diameter, capped by the persistent stylar region, lacking trichosclereids, or if trichosclereides present confined to the walls, very rarely present in the stylar region; the berries free from one another.

ETYMOLOGY. Latin *obliqua,* "oblique," referring to the oblique leaf bases.

COMMON NAMES. Timbo titica (Brazil, Para); mamurillo (Venezuela).

DISTRIBUTION. Panama, Colombia, Peru, Bolivia, Venezuela, Trinidad, Tobago and the Guianas, and Amazonian Brazil.

REPRESENTATIVE SPECIMENS. **Panama. Bocas del Toro:** forest above RR stop at mile 7.5, July 1971, *Croat & Porter 16277* (MO); vicinity of Chiriqui Lagoon, Oct. 1940, *von Wedel 1091* (MO). **Veraguas:** 5 miles NW of Santa Fé, 700–1200 m., March 1973, *Liesner 801* (MO). **Coclé:** mountains beyond La Pintada, 400–600 m., Feb. 1935, *Hunter & Allen 544* (MO,NY,US); Cerro Pilon near El Valle, 700–900 m., June 1967, *Duke 12155* (MO). **Panama:** foot of Loma Larga, E of Cerro Azul, April 1973, *Dressler 4319* (MO). **San Blas:** Río Mulatupo, Aug. 1967, *Kirkbride 229* (MO). **Darien:** Cativo Swamp, Río Chucunaque, ½ hr. below Morti, May 1967, *Duke 11749* (MO,US). **Colombia. Chocó:** Río Nercua, near Camp Curiche, 10–294 m., May 1967, *Duke 11486* (US); Bahia Solano, near Ciudad Mutis, 75 m., Feb. 1939, *Killip & Garcia 33580* (COL,US). **Meta:** 22 km. W of Villavicencio, Aug. 1944, *Grant 9963* (US). **Vaupes:** 1°50′N × 67°W, Oct. 1952, *Schultes, Baker & Cabrera 18051* (BM, GH,NY,U,US); Río Apaporis, Soratama, 900 ft., Feb. 1952, *Schultes & Cabrera 15159* (US). **Putumayo:** Río Gineo, 8 km. W of Villagarzon, Nov. 1968, *Plowman 2047* (GH); Puerto Ospina and vicinity, March 1953, *Schultes & Cabrera 18978* (US). **Amazonas:** Río Loretoyacu, 100 m., March 1946, *Schultes 7177* (US); Puerto Narino, Jan.–Feb. 1969, *Plowman et al. 2344* (GH). **Peru. Loreto:** Río Ucayali near Iparia, 250 m., Sept. 1968, *Schunke 2803* (F,US); between Yurimaguas and Balsapuerto, 135–150 m., Aug. 1929, *Killip & Smith 28258* (NY,US). **San Martín:** Tocache Nuevo, Río Huallaga, Feb. 1970, *Schunke 3815* (F,GH,US). **Huanuco:** Río Pachitea, 20 km. above confluence with Río Ucayali, 300–400 m., July 1967, *Schunke 2126* (F). **Junin:** Río Richis, between Puerto Bermudez and Cahuapanas, 340–375 m., July 1929, *Killip & Smith 26706* (NY,US). **Cuzco:** Atalaya, 700 m., Oct. 1960, *Vargas 13431* (US). **Bolivia. La Paz:** basin of Río Bopi, Asunta, near Evenay, 690–750 m., July 1939, *Krukoff 10662* (F,GH,MICH,MO,NY,S,U,US); Rurrenabaque, 1000 ft., Oct. 1921, *Rusby 771* (NY). **Pando:** Río Madiera, 12 km. above Abuña, July 1968, *Prance et al. 6211* (NY,US). **Venezuela. Tachira:** 15 km. W of Santo Domingo, 420 m., March 1974, *Gentry, Morillo & Morillo 11094* (MO). **Yaracuy:** lower Yaracuy, Feb. 1926, *Pittier*

FIG. 48. *Monstera obliqua:* variation in adult leaf shape from different individuals (to the same scale).

12098 (US). **Carabobo:** between Urama and San Felipe, sea level, Jan. 1939, *Alston 6077* (VEN). **Anzoátegui:** near Carmelita, NE of Bergantin, 800–1100 m., Feb. 1945, *Steyermark 60987* (F,VEN). **Monagas:** Montaña de Aguacate, 600–900 m., April 1945, *Steyermark 62172* (F). **Delta Amacuro:** Río Acure, between La Margarita and Puerto Miranda, 80–100 m., Nov. 1960, *Steyermark 87766* (NY,US,VEN). **Bolivar:** 4°18′N × 63°06′W, 510–525 m., Jan. 1962, *Steyermark 90541* (BH,US,VEN). **Amazonas:** Brazo Casiquiare, Feb. 1931, *Holt & Blake 671* (US). **Trinidad.** Mts. of Aripo, Naranje Valley, L'Orange Est., 800 ft., Feb. 1947, *Simmonds 64* (K,TRIN); vicinity of Tabaquite, March 1921, *Britton, Freeman & Nowell 2603* (GH,NY,TRIN,US). **Tobago.** Black Hill, above Charlotteville, Oct. 1937, *Sandwith 1797* (K). **Guyana.** Demerara River, Oct. 1890, *Jenman 6243* (K,NY); Northwest District, Wanama River, 7°45′N × 60°15′W, May 1923, *De La Cruz 3946* (F,GH,MO,NY,PH,US); Pakaraima Mountains, Paruima Falls, Nov. 1951, *Maguire & Fanshawe 32455* (NY). **Surinam.** Pauluskreek, Oct. 1954, *Mennega 239*(NY,U); Marowijne District, Moengo, bank of Cottica River, Nov. 1961, *Hekking 1046* (A,U); Zuid River, 3°20′N × 56°49′W, 270 m., Sept. 1963, *Irwin et al. 55993* (NY). **French Guiana.** Maroni, 1856, *Sagot 614* (P); Rivière petite Ouaqui, July 1973, *Granville 1846* (US). **Brazil. Amazonas:** near mouth of Rio Embira, 7°30′S × 70°15′W, June 1933, *Krukoff 5890* (GH,NY); Rio Purus, 5 km. above Labrea, Oct. 1968, *Prance, Ramos & Farias 8119* (INPA,NY,US). **Pará:** banks of Rio Piria, S of Curapati, Nov. 1965, *Prance & Pennington 2056* (F,GH,NY,S,U,US); Planalto de Santarem, Estrada Mojui, June 1954, *Froes 30837* (RB). **Amapá:** Serro do Navio, Rio Amapari, above Igarape Sentinela, 70–300 m., Nov. 1954, *Cowan 38194* (NY). **Acre:** mouth of Rio Macauhan, 9°20′S × 69°W, Sept. 1933, *Krukoff 5774* (F,GH,M,MICH,MO,NY,S,U,US); Rio Moa, 15 km. NW of Cruzeiro do Sul, Oct. 1966, *Prance, Pena & Ramos 2772* (MG,NY,US). **Rondonia:** island in Rio Madeira at mouth of Rio Jaciparana, June 1968, *Prance et al. 5339* (INPA,NY,US); Santa Barbara, 15 km. E of km. 117, Aug. 1968, *Prance & Ramos 7010* (INPA,NY). **Mato Grosso:** 14°38′S × 52°14′W, Nov. 1968, *Harley et al. 11018* (K).

Various authors, including Engler and Krause (1908), cite this species as *Monstera obliqua* (Miq.) Walp., based on *Heteropsis obliqua* Miquel. In the publication describing this species, Miquel divided *Monstera* into two sections, section Monstera and section Heteropsis Miq., and indicated this species as "*Monstera* (Heteropsis) *obliqua.*" It is clear from examination of other examples in the same work that Miquel used this procedure to indicate the section of a genus to which a species belongs, and that he was undoubtedly describing *M. obliqua* in section Heteropsis, and not *H. obliqua.* Thus, the species is correctly called *M. obliqua* Miq. and not *M. obliqua* (Miq.) Walp.

Monstera obliqua has been divided into a number of putative species, principally on the basis of differences in leaf shape, but these variations are of little taxonomic significance. For example, about 80% of the specimens of this species that I have examined have entire leaves; the rest have leaves which are slightly to profusely perforated. The material with perforated leaves has been separated as *M. expilata,* but this variation shows no ecological or geographic pattern except that the perforated forms are absent from Panama. Furthermore, some individuals have mostly entire but occasionally perforated leaves.

There is also great variation in the relative width of the leaves, which is correlated with the shape of the leaf base. The shape ranges from narrow, lanceolate leaves with acute bases to broadly ovate leaves with truncate or subcordate bases. The narrowest have been separated as

Monstera falcifolia and the widest as *M. sagotiana*, but again this variation shows no ecological or geographic correlation, and it is impossible to draw a line separating the plants into two or more meaningful groups on this basis.

Jonker-Verhoef and Jonker, in the *Flora of Surinam* (1952), separated *Monstera sagotiana* and *M. expilata* from *M. obliqua* on the basis of leaf shape. They also described differences in the fruits, *M. sagotiana* supposedly having a white to yellowish-green spadix and *M. obliqua* white berries with orange styles. These apparently represent differences in maturity rather than taxonomic differences. In *M. obliqua* the spathe and spadix are green initially, becoming greenish-white and finally bright yellow. After anthesis the color of the spadix changes from yellow to green, in some cases to olive-green, later becoming pale and finally turning a deep orange at maturity.

In terms of its growth habit and floral and fruit morphology the species is a very coherent one, despite the variability in leaf shape. The deep yellow spathes, the flowering spadices and the orange fruits are equalled in the genus only by *Monstera xanthospatha* of the Colombian Andes. The fruits of *M. obliqua* are unique in several respects. The berries are globose and free from one another rather than prismatic and closely pressed together as in the other species. This is probably, in part, a consequence of the small size of the spadix and in particular its very narrow axis. With the exception of a few Panamanian specimens, trichosclereids are absent from the stylar region, though they may be present in the ovary walls. This is clearly related to the failure of the fruits of *M. obliqua* to break in two at maturity and the consequent loss of the ability to get rid of stylar trichosclereids which protect the developing seeds but would deter a dispersing agent when the seeds are mature. In this respect *M. obliqua* seems to have lost an adaptation shared by other *Monstera* species.

Another feature unique to *Monstera obliqua* is that the inflorescences are usually produced sympodially in groups of six to eight, rather than in groups of one to four.

The small size of *Monstera obliqua* enables it to exploit substrates unavailable to other monsteras. It can grow to maturity on saplings, in shrubs and on small twigs of trees; it may even be epiphytic on other aroids. These habitats are more ephemeral than the trunks of large trees, and it seems likely that *M. obliqua* may grow faster and mature more rapidly than other species. Plants of *M. obliqua* tagged in the wild showed an annual growth rate of 30–70 new leaves *vs.* 5–12 new leaves in large-leaved species.

Some of the larger, perforated individuals of *Monstera obliqua* approach *M. gracilis* vegetatively, but the latter species is separated by its lighter colored spathes and spadices and its prismatic berries with trichosclereids in the stylar region.

The distribution of *Monstera obliqua* is disjunct between Panama-Chocó and Amazonia-northern South America, with a gap of 700 km. between the closest collections. This gap may reflect the present-day aridity of the region of northern Colombia which could provide a low-elevation pathway between these two centers. However, the region is not well-known, and it is also possible that further collecting may reveal intervening populations. The Panamanian material of this species is much less variable than that from Amazonia, suggesting that the Panamanian populations may be descended from a limited immigrant line from South America, with a consequent decrease in genetic variability.

13. **Monstera minima** Madison, *sp. nov.*

FIG. 47, MAP 15

Planta exigua epiphytica scandens. *Caulis* teres, 3–4 mm. crassus, internodiis 1–2 cm. longis. *Foliorum petiolus* 2.0–3.5 cm. longus, ad laminam usque vaginatus, vagina decidua; *lamina* integra, lanceolata, 9–12 cm. longa, 2.0–2.8 cm. lata, basi angustate, apice acuta. *Pedunculus* 18 cm. longus, 2 mm. crassus, folium superans. *Spatha* ignota. *Spadix fructifer immaturus* viridis, 5 cm. longus, 1.8 cm. crassus. *Baccae* subprismaticae, 4–5 mm. longae, 6–7 mm. latae, apices truncati.

TYPE. Panama: Comarca de San Blas, trail east of Cangandi-Mandinga airport road, 2–5 miles south of Mandinga airport. Scandant epiphyte, spadix green, 27 October 1967, *J. A. Duke 14758*(3) (MO, sheet no. 2051569).

ETYMOLOGY. Latin *minima,* "very small," this being the smallest known species of *Monstera.*

This species, known only from the type collection, has a peduncle which is 1½ times longer than the leaves; this readily distinguishes it from all other monsteras, since they have peduncles shorter than the leaves. *Monstera minima* is closely related to *M. obliqua,* from which it differs by the much shorter petioles and by the subprismatic and truncate rather than globose berries.

MONSTERA section MARCGRAVIOPSIS Madison, *sect. nov.*

Plantula stoloniformis, 1–2 mm. crassa, 30–200 cm. longa. Folia stirpium juvenilium breviter petiolata, ad truncis arborum adpressae. Pistillum maturum 5–8 mm. latum. Spadix erectus; pendunculi spadices aequantes vel eis breviores.

TYPE SPECIES. *Monstera acuminata* C. Koch.

The species of this section show a heteroblastic development with three distinct phases. The seedling is stolon-like, 1–2 mm. in diameter and 30–200 cm. long. The earliest climbing plant has asymmetric ovate leaves that are cordate at the base, and are tightly appressed to the substrate and overlap one another on the stem. These leaves have a short petiole less than ½ the lamina length, with the sheath extended into a ligule about equal in length to the petiole. The adults have exserted leaves lacking a ligular extension of the sheath. In this section the peduncle is shorter than or equal to the spadix.

The species of section Marcgraviopsis are quite distinct from each other and are without intermediates, though *Monstera dubia*, *M. pittieri*, and *M. luteynii* are closely related.

14. Monstera acuminata C. Koch

FIGS. 49–51, MAP 11

Monstera acuminata C. Koch, Ind. Sem. Hort. Bot. Berol. App.:5 (1855). TYPE: Central America, live plant collected by Warszewicz cultivated at Berlin, *C. Koch s.n.* (B, *non vidi*). *Engler 45* (C,BM,GH,L,M,P,US) cultivated at Berlin, may represent later specimens of the type collection.

Monstera karwinskyi Schott, Oest. Bot. Woch. 9:99 (1859). TYPE: Mexico, Vera Cruz, Colipa, April 1841, *Karwinsky s.n.* (C, photo BH). PARATYPE: Mexico, Vera Cruz, Papantla to Colipa, 1841–42, *Karwinsky 838* (LE).

Monstera belizensis Lundell, Lloydia 2:76 (1939). TYPE: Belize, El Cayo District, 23 June 1936, *Lundell 6198* (MICH).

Monstera grandifolia Standl. & Steyerm., Pub. Field Mus. Nat. Hist., Botany 23:212 (1947). TYPE: Guatemala, Petén, low forest between Finca Yalpemech and Chinaja, 28 March 1942, *Steyermark 45423* (holotype F no. 1129317–9; isotype US no. 1864956).

Monstera chiapensis Matuda, Madroño 10:48 (1949). SYNTYPES: Mexico, Chiapas, Finca California, Col. Turquia, Escuintla, 150 m., 29 August 1947, *Matuda 17789* (Matuda Herbarium, *non vidi*); Finca Esperanza, 10 km. NE of Escuintla, 200 m., *Matuda 17786* (Matuda Herbarium, *non vidi*).

Monstera viridispatha Matuda, Rev. Soc. Mex. Hist. Nat. 11:98 (1950). TYPE: Mexico, Chiapas, Esperanza, Escuintla, 150–250 m., 7 Dec. 1949, *Matuda 18717* (holotype Matuda Herbarium, *non vidi;* isotypes NY, UC no. 903869, photo BH). PARATYPES: holotype locality, 14 Oct. 1949, *Matuda 17796* (Matuda Herbarium, *non vidi*); 5 Aug. 1948, *Matuda 18318* (Matuda Herbarium, *non vidi*); 23 April 1948, *Matuda 17774* (Matuda Herbarium, *non vidi,* MEXU,NY); Cruz de Piedra, 4 km. N of Acacoyagua, 25 July 1947, *Matuda 17795* (MEXU).

Robust scandent epiphyte to 30 m. tall. *Seedling:* stem terete, 0.5–2.0 m. long, 1–2 mm. thick, internodes 3–10 cm. long, bearing cataphylls but not foliage leaves. *Juvenile:* a shingle plant, stem elliptic in cross section, internodes 1–5 cm. long, leaves highly asymmetric, tightly appressed to the substrate, the petiole 0.5–1.5 cm. long, the sheath extended into a ligule about equal in length to the petiole; the lamina subcoriaceous, slightly longer than wide, midrib curved, the base unequal, rarely peltate, the apex short acuminate. *Adult stem:* smooth or papillose, 2.0–3.5 cm. thick, internodes 6–11 cm. long, axillary buds located in a depression extending as a sulcus for most of the length of the internode. *Petiole:* shorter than the lamina, 25–45 cm. long, vaginate to the base of the blade, the sheath wings persistent, the geniculum 3.5–5.0 cm. long. *Lamina:* usually pendent from the erect petiole, coriaceous, dull green adaxially, paler abaxially, ovate, 15–35 cm. wide, 35–65 cm. long, the base unequal, truncate to acute, the midrib curved; primary lateral veins 10–22 in number, prominent and white abaxially, secondary lateral veins parallel to the primary. *Peduncle:* stout, terete, 1.5–2.5 cm. thick, 7–11(–13) cm. long, smooth or papillose. *Spathe:* greenish-white externally, cream within, 14–22 cm. long, exceeding the spadix by 3–5 cm., terminating in a 0.5–1.0 cm. long acumen. *Flowering spadix:* cream to yellow, cylindric, 2.5–4.0 cm. thick, (12–)15–20 cm. long, the lower 3–4 rows of flowers sterile. *Fruiting spadix:* 4.0–6.5 cm. thick, 15–23 cm. long, yellow at maturity, the stylar portion of the pistils deciduous to reveal the seeds in a gray pulp. *Seeds:* oblong, 16–20 mm. long, 5–8 mm. thick.

ETYMOLOGY. The epithet refers to the acuminate leaves.

COMMON NAMES. Bejuca de Tuza, Conte tuza, Conte arpón, Conte de mimbre (Mexico); Hoka de sereno (Honduras); Madre de harpón, se wan en, kolkuk (Guatemala).

DISTRIBUTION. Mexico, Guatemala, Belize, and Honduras, mostly at elevations of 0–600 meters.

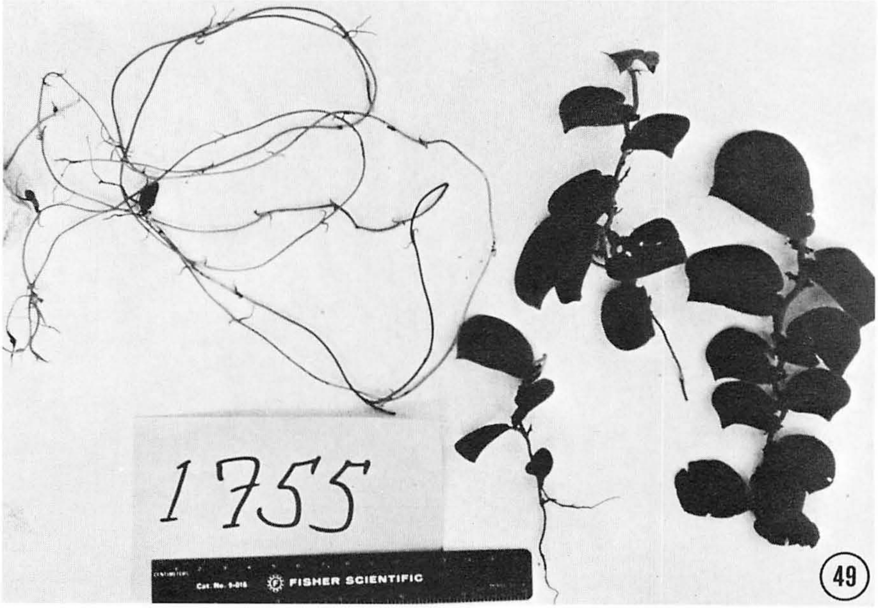
REPRESENTATIVE SPECIMENS. **Mexico. San Luis Potosí:** road to Xilitla 2 km. from junction with Road 85, 300 m., Aug. 1972, *Madison 601* (GH); N of Tamazunchale, July 1935, *Clark 7407* (MO). **Puebla:** Bosque Ajenjibre, March 1951, *Bravo 151* (MEXU). **Vera Cruz:** Coatzacoalcos, April 1895, *Smith 1069* (US); Barranca de Santa Maria at Hda. El Mirador, Sept. 1961, *Moore & Bunting 8859* (BH); Papantla, 100 m., Feb. 1968, *Gutierrez 75* (US). **Oaxaca:** cerro W of Sebastopol, Tuxtepec, March 1968, 200 m., *Rzedowski 25484* (MICH,US). **Chiapas:** Cascada Mizolá, 250 m., Oct. 1974, *Madison 1755* (GH); El Triunfo, 200 m., Oct. 1974, *Madison 1782* (GH); Turquia, Escuintla, August 1957, *Matuda 17785* (NY). **Tabasco:** Comalcalco, Aug. 1962, *Barlow s.n.* (US). **Guatemala. Petén:** Monte Polol, June 1933, *Lundell 3609* (MICH,NY); Uaxactun, April 1931, *Bartlett 12745* (MICH). **Huehuetenango:** Sierra de los Chuchumatanes, 150–200 m., Ixcan, July 1942, *Steyermark 49312* (F,US). **Alta Verapaz:** Teleman, 6000 ft., April 1889, *Smith 1531* (K,US); Pancajche, 360 m., April 1939, *Standley 70803* (F). **Izabal:** between Bananera and La Presa in Montaña del Mico, 40–300 m., March 1940, *Steyermark 38142* (F). **Retalhuleu:** Río Talculan, 5 km. W of Retalhuleu, 300 m., Feb. 1941, *Standley 87368* (F). **Suchiteqequez:** vicinity of Tiquisate, 100 m., June 1942, *Steyermark 47651* (F,MO). **Escuintla:** Escuintla, 1100 ft., March 1890, *Smith 2242* (US). **Santa Rosa:** Guazacaoan, 220 m., Dec. 1940, *Standley 78610* (F). **Belize:** Swasey Branch, Monkey River, March 1942, *Gentle 3956* (GH,MICH,MO,NY); Mile 28.5 on Hummingbird Highway, S of Belmopan, 200–300 ft., June 1973, *Croat 24558* (MO). **Honduras. Cortes:** Lake Yojoa, 600 m., *Williams & Molina 18268* (F). **Comayagua:** El Achote, 1350 m., June-Aug. 1936, *Yuncker, Dawson & Youse 6300* (A,F,GH). **Atlantida:** 35 km. S of La Ceiba, 980 m., Sept. 1972, *Madison 710* (GH); Tela, 20–600 m., Mar. 1928, *Standley 53214* (F,US). **Olancho:** between Catacamas and La Presa, 500–600 m., Mar. 1949, *Standley 18697* (F).

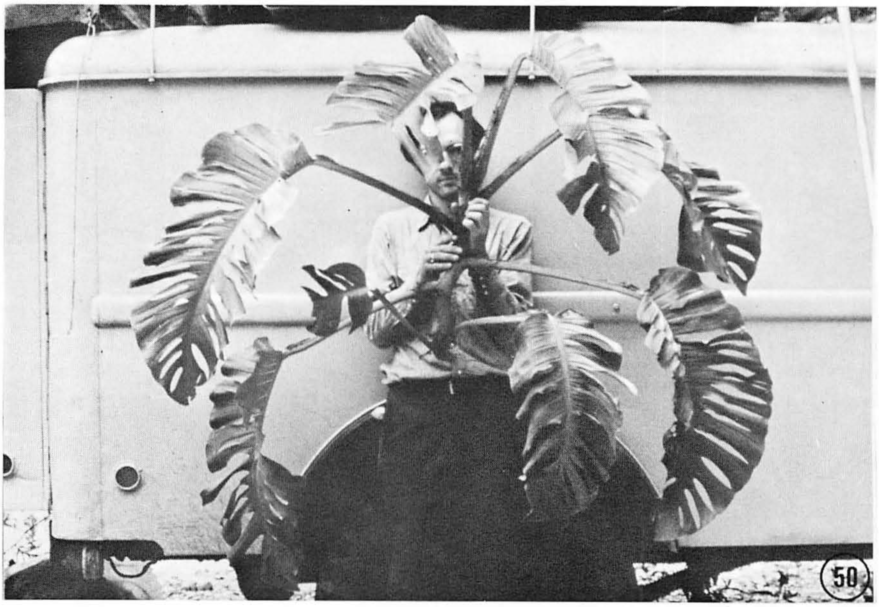
Monstera acuminata was first collected in Central America by Warszewicz who brought it to Europe as a live plant. It was cultivated at the Berlin Botanic Garden where Carl Koch recognized it as a new species. Too impatient to await its maturity, he described *M. acuminata* on the basis of the juvenile form and made a specimen of two leaves for the type.

Engler and Krause (1908) redescribed *Monstera acuminata,* basing their expanded description in part on a further collection from Guatemala *(J. D. Smith 1533).* Unfortunately, this is a specimen of *M. tuberculata,* and Engler and Krause's description combines characters of both species. Apparently they did not understand Koch's concept, for mature material of *M. acuminata* examined by Engler was determined as *M. pertusa* var. *jacquinii* (e.g., *J. D. Smith 1531, 2234*). To further confuse the issue, Engler made a number of specimens of a plant cultivated in Berlin which he distributed as Engler Exsiccatae No. 45 under the name *M. pertusa.* These specimens are actually of *M. acuminata* and are quite probably from the original plant brought from Guatemala by Warszewicz!

The name *Monstera acuminata* emerged from this confusion with a peculiar status—it came to be used for any sterile specimen of a *Monstera* juvenile shingle plant. Thus, *M. acuminata* is cited in the *Flora of Peru* (1936), referring to juveniles of *M. dubia.*

In the meantime, the actual *Monstera acuminata* of Guatemala and Mexico came to be known as *M. karwinskyi.* Various species were segregated from this on the basis of differences in leaf size and presence or absence of perforations, but these are unimportant variations occurring





FIGS. 49–50. *Monstera acuminata:* 49. seedling and shingle plant; 50. mature shoot (both *Madison 1755,* GH).

FIG. 51. *Monstera acuminata:* habit (*Madison 1782*, GH).

sporadically throughout the range of the species, and I do not consider them taxonomically significant.

Monstera acuminata is readily distinguished from other species of section Marcgraviopsis by its large leaves with entire margins. The habit is also distinctive, with the somewhat falcate laminae pendent from the erect petioles.

The majority of collections of this species are sterile, probably because it flowers more than 15 meters above the ground. Individuals may grow to 30 m. tall, thoroughly covering the trunk of the host tree but without spreading into the branches.

Monstera acuminata is abundant in the central Petén, and may be found growing on the Mayan ruins at Tikal and Uaxactun. Its range extends north to San Luis Potosí, making it the northernmost of the species of *Monstera.*

15. Monstera dubia (HBK.) Engler & Krause

FIGS. 52–53, MAP 6

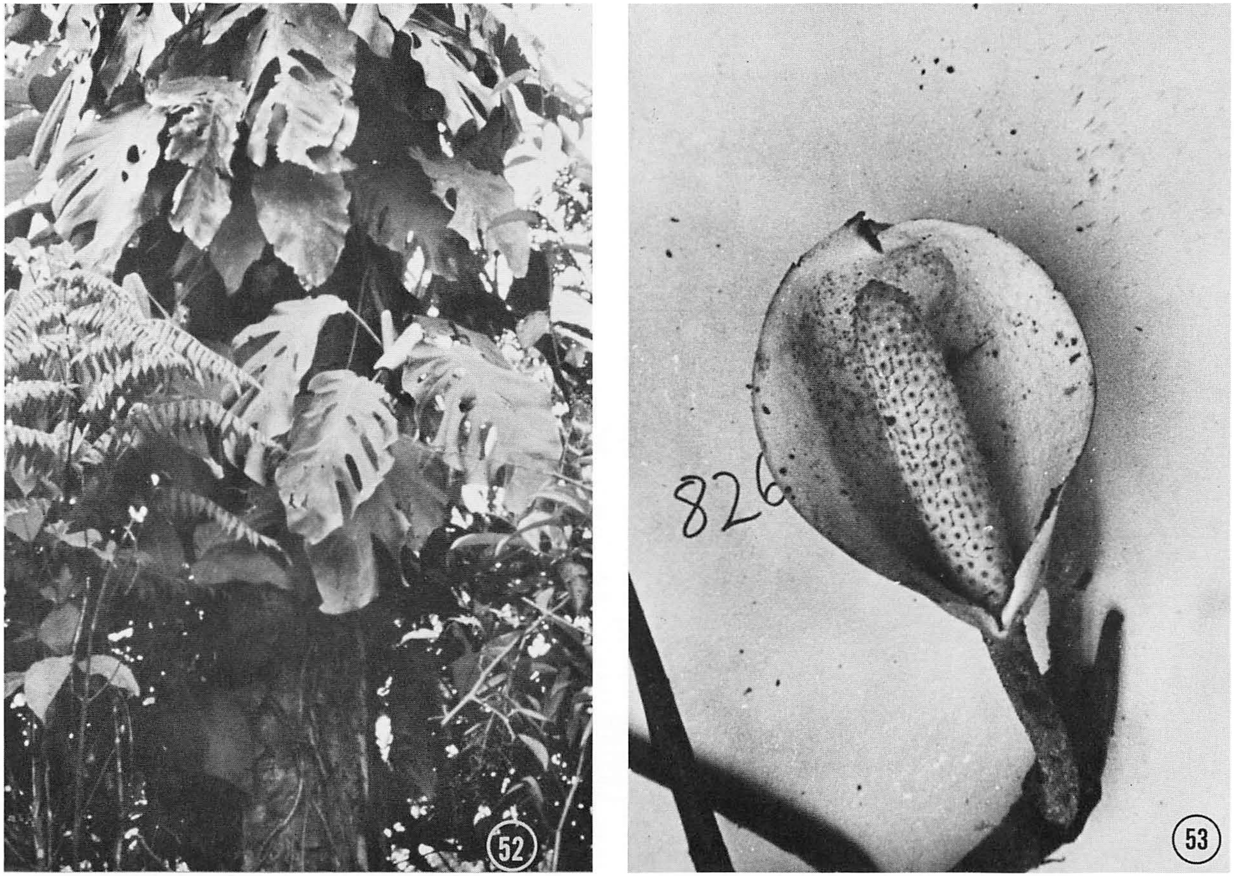
Monstera dubia (HBK.) Engler & Krause, Das Pflanzenreich IV 23B:112 (1908). *Marcgravia dubia* HBK., Nov. Gen. et Spec. Plant. 7:169 (1825). TYPE: Venezuela, Crescit ad arbores Novae Andalusiae, prope Cocollar et Caripense, alt. 400 hex. *Humboldt and Bonpland* (B, *non vidi*).

Monstera acreana Krause, Notizbl. Bot. Gart. Berlin 6:114 (1914). TYPE: Brazil, Acre, São Francisco am Alto Acre, August 1911, *Ule 9212* (B, *non vidi,* photo GH,BH,US).

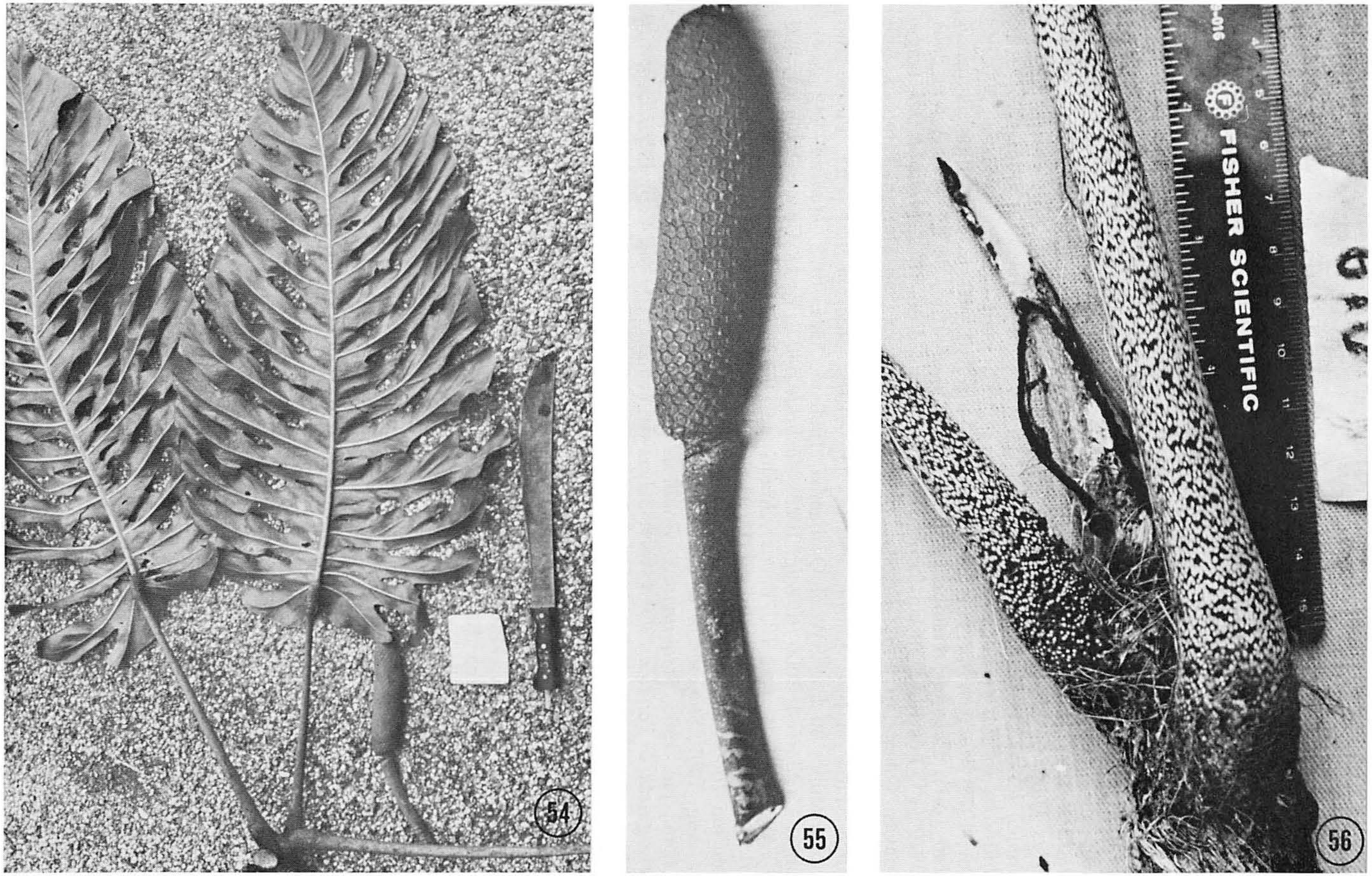
Monstera irritans Simmonds, Kew Bull.:398 (1950). TYPE: Trinidad, Cap de Ville, Feb. 1948, *Simmonds 296* (TRIN, *non vidi;* isotype K).

Stout climber to 25 m., often with fertile hanging shoots; the adult leaves drooping. *Seedling:* a stolon-like creeper, 1–2 mm. in diameter, to 2 m. long. *Juvenile:* shingle plant, the lamina cordate, the sinus 5–10 mm. deep, the apex mucronate; often variegated with silver flecks. *Adult stem:* elliptic in cross section, roughly warty or tuberculate, rarely smooth, dark green to tan, with a thick cuticle; internodes 3–10 cm. long, 1–2 cm. thick and 1.5–3.0 cm. wide; axillary bud in a depression which is extended into a sulcus the length of the internode. *Petiole:* warty or tuberculate at the base or along its length, 20–55 cm. long, vaginate to the geniculum, the sheath wings neatly deciduous, the geniculum 4–7 cm. long. *Lamina:* oblong-ovate, falcate and oblique, coriaceous, dull dark green above, paler below, 20–100 cm. long, 13–50 cm. wide, 1½–2 times longer than wide; the earliest adult leaves entire and some individuals mature in this state, later leaves pinnatifid, the larger pinnatifid and with 1–3 rows of elliptic perforations per side, the perforations 2–8 cm. long, the pinnae truncate; the leaf base rounded to subcordate with a sinus 1–2 cm. deep, never broadly cordate, the apex acute; primary lateral veins 9–18 in number, cream-colored and prominent abaxially, furrowed adaxially, the secondary lateral veins reticulate. *Peduncle:* tuberculate, 0.8–1.4 cm. thick, terete, 5–9 cm. long. *Spathe:* thickly coriaceous, pink abaxially, white adaxially, obovate, 6–12 cm. tall, 4–6 cm. across, shortly mucronate or blunt at the apex, sometimes becoming curled-reflexed and splitting longitudinally before abscission. *Flowering spadix:* white, 5–10 cm. long, 1.5–2.5 cm. thick, the pistils bluntly truncate. *Fruiting spadix:* 7–14 cm. long, 3.5–5.5 cm. thick, pale yellow, the stylar portion of the pistils peeling off individually or in loosely fused groups to reveal the seeds in a gray pulp. *Seeds:* brown, oblong, 6–8 mm. long, 4–5 mm. wide, 2.0–3.5 mm. thick, the embryo turquoise blue in color.

ETYMOLOGY. Latin *dubia,* "dubious," because the authors were not certain that the sterile type specimen was really a *Marcgravia.*



FIGS. 52–53. *Monstera dubia:* 52. habit, with pendent flowering shoot; 53. inflorescence (both *Madison 826*, GH).



FIGS. 54–56. *Monstera punctulata:* 54. leaf; machete in the photo is 64 cm. long (*Madison 633*, GH); 55. fruiting spadix, 18 cm. long (*Madison 633*, GH); 56. petiole showing punctulate markings characteristic of the species (*Madison 610*, GH).

COMMON NAMES. Chalde (Ecuador); Malanga, Mamurillo, Pantano, Oreja de Tigre (Venezuela).

DISTRIBUTION. Costa Rica to Bolivia, Venezuela, Trinidad, and western Brazil, mostly below 1000 m., but reaching 1800 meters.

REPRESENTATIVE SPECIMENS. **Costa Rica. San José:** Candelarita, 800 m., Oct. 1972, *Madison 745* (GH); Río Paquita, 1–3 m., Aug. 1936, *Dodge & Goerger 9764* (CR,F, MO). **Puntarenas:** 12 km. E of Palmar Sur, Oct. 1973, *Madison 760* (GH); 1 mile S of Río Claro, Aug. 1972, *Vaughan et al. 621* (MO). **Panama. Chirqui:** 1.6 mi. W of Puerto Armuelles, 50 m., Feb. 1973, *Croat 21918* (MO). **Canal Zone:** Barro Colorado Island, May 1968, *Croat 5338* (MO). **Panama:** 34 km. E of Chepo, 100 m., Oct. 1972, *Madison 767* (GH). **Colombia. Magdalena:** Piojo, 400 m., Jan. 1929, *Elias 743* (US). **Norte de Santander:** 45 km. from Cucuta on road to Ocaña, 300 m., March 1973, *Madison 1243* (GH). **Chocó:** 30 km. from Quibdó on Medellín road, 140 m., Nov. 1972, *Madison 826* (GH). **Antioquia:** Villa Arteaga, 100 m., April 1948, *Soto & Barkley 18C543* (US). **Meta:** Sierra de la Macarena, Río Guapaya, 450 m., Dec. 1949, *Philipson, Idrobo & Fernandez 1661* (BM,UC,US); Llanos de San Martín, 500 m., Nov. 1972, *Madison 857* (GH). **Putumayo:** Puerto Asís, 300 m., Dec. 1968, *Plowman 2140* (GH). **Ecuador. Pichincha:** Santo Domingo, 300 m., Sept. 1949, *Acosta Solis 13940* (F). **Los Rios:** 30 km. N of Quevedo, 160 m., Dec. 1972, *Madison 905* (GH). **Guayas:** Balao, Jan. 1892, *Eggers 14229* (LE,US). **Peru. San Martin:** Tarapoto, Alto Río Huallaga, 300–900 m., Dec. 1929, *Williams 5673* (F). **Huanuco:** 10 km. above Tingo Maria on Río Monzón, 960 m., Dec. 1972, *Madison 946* (GH). **Pasco:** Río Paucartambo, 30 km. SW of Oxabamba, 1600 m., Dec. 1972, *Madison 952* (GH). **Junin:** La Merced, 2000 ft., Aug. 1923, *Macbride 5403* (F,US). **Cuzco:** Piliopata, 800 m., Aug. 1960, *Vargas 13377* (US). **Madre de Dios:** Río Tahuamanu, 180 m., Nov. 1973, *Alfaro 1723* (MO). **Bolivia. La Paz:** 10 km. N of Caranavi, 800 m., Jan. 1973, *Madison 1069* (GH). **Venezuela. Zulia:** Sierra de Parija, SE of Machiques, 350–500 m., Aug. 1967, *Steyermark & Fernandez 94972* (VEN). **Falcon:** Tocuyo de la Costa, 100 m., Jan. 1966, *Steyermark & Braun 94494* (US,VEN). **Yaracuy:** Aroa, July 1953, *Aristiguieta & Pannier 1900* (VEN); Selvas de Yumare, 100 m., Feb. 1959, *Bernardi 6971* (VEN). **Distrito Federal:** Cerro Naiguata, 1390–1500 m., Nov. 1963, *Steyermark 91917* (K,US,VEN). **Miranda:** El Guapo, 100 m., July 1957, *Aristiguieta 2876* (VEN). **Anzoátegui:** Río Maravilla, Fila Grande, 900–1400 m., March 1945, *Steyermark 61739* (F,NY,VEN). **Barinas:** Reserva Forestal Caparo, E of El Canton, 100 m., April 1968, *Steyermark, Bunting & Blanco 102010.* **Apure:** Reserva San Camilo, 2 km. SE of San Camilo, 250 m., March 1968, *Steyermark, Bunting & Blanco 101450* (VEN). **Trinidad.** Brazil-Arena Road, March 1959, *Cowan & Simmonds 1406* (US,NY); Tabaquite, Dec. 1955, *Simmonds, Herb Trin No. 15367* (TRIN). **Brazil. Acre:** Rio Moa at Serra da Moa village, April 1971, *Prance et al. 12502* (NY,US). São Francisco, Alto Acre, Aug. 1911, *Ule 9212* (B). **Rondonia:** 4 km. S of Nova Vida, Aug. 1968, *Forero & Wrigley 7077* (INPA,NY,US).

Though a common and abundant species, *Monstera dubia* is represented in the world's herbaria by fewer than 80 collections, more than one quarter of them from Barro Colorado Island. This reflects in part the lack of field botanists working in the Andean countries, as well as the nature of the species, which flowers well out of reach.

Only two collections of *Monstera dubia* are known before the twentieth century. A juvenile shingle plant was collected by Humboldt and Bonpland and described as *Marcgravia dubia* in 1825. While their type specimen itself does not admit to identification beyond inclusion in section Marcgraviopsis, the type locality in the state of Sucre in Venezuela dictates the specific identity. Only a single species of *Monstera* with a shingle plant juvenile is known to occur within 500 km. of this area, and this is the basis on which the name is applied in its present sense.

The first collection of flowering material of *Monstera dubia* was that of Eggers from Ecuador in 1892, which was identified as a *Philodendron.* Later collections were determined to be various different species of *Monstera,* but the name *M. dubia* was not used for any of them.

Hemsley (1885) was the first to recognize that several species described in *Marcgravia* really belong in *Monstera.* Engler and Krause (1908) implemented this and made the new combination *Monstera dubia* (HBK.) Engler & Krause. They provided a description and illustrations based on two specimens: the Humboldt and Bonpland type, and a flowering Seeman collection from Nicaragua. The latter, unfortunately, represents *M. tenuis* C. Koch, and thus the name *M. dubia* came to be generally applied to this Central American species. Further confusion was engendered at this time by Engler and Krause misrepresenting Humboldt and Bonpland's locality as Mexico rather than Venezuela.

Because the name *Monstera dubia* was used for what is in reality *M. tenuis,* the species *M. dubia* was considered to be without a name. Thus Krause gave it the new name, *M. acreana,* but he also inconsistently determined specimens of it as *M. pertusa* and *M. maxima.* This is typical of the history of this section, in which the widespread misapplication of names has led to considerable confusion of what are biologically very distinct and easily recognizable species.

Monstera dubia is a handsome plant which grows at low elevations and it characteristically climbs and hangs on large trees. The vegetative adult stage is variable, relating in part to the type of tree in which it grows. The earliest adult leaves are entire, and if the individual is growing on an inadequate support it may flower at this stage. However, with a large tree to grow on it will produce first entire leaves, then pinnatifid ones, and finally pinnatifid-perforate leaves. These may have a drooping, falcate lamina to 1 meter in length and about half as wide. The species may flower as a climbing plant attached to the trunk; this is most common in Costa Rica and Panama. However, it often flowers at the ends of hanging shoots which may be several times branched, and this is the way it usually grows in South America.

The inflorescences of *Monstera dubia* are very distinctive. The spathe is obovate and blunt, rose to salmon-colored outside and white within. The common name, *oreja de tigre* (tiger's ear), refers to the shape of the intact spathe. It often splits longitudinally and curls up around the abaxial side before abscising. The spadices are white in flower, becoming green in early fruit and pale yellow at maturity. There is a geographic cline in spadix size, the largest ones being found in Costa Rica and smaller ones to the south and east.

The only other species with which *Monstera dubia* might be confused is *M. punctulata,* which is distinguished in flower by its large white spathes, and in fruit by its dark green or golden-green spadices. The petiole of *M. punctulata* is densely marked with white flecks, in contrast to the solid green petioles of *M. dubia*. A further distinction is in the lamina, which in *M. punctulata* is bright green and of a soft texture, and in *M. dubia* is dull dark green and thickly coriaceous.

16. Monstera punctulata (Schott) Engler

FIGS. 54–56, MAP 9

Monstera punctulata (Schott) Engler, D. C. Monog. Phan. II:259 (1879). *Anadendrum punctulatum* Schott, Prodr. Syst. Aroid. 393 (1860). TYPE: Mexico, locality and collector unknown, plant cultivated at Vienna and illustrated by Schott Aroideae No. 2281, 3276, and 3279 (W, *non vidi*, photo SEL).

A robust climber on large trees, to 15 m. tall. *Juvenile:* a shingle plant, the stem strongly flattened. *Adult stem:* brown, roughly tuberculate, subterete, 3–4 cm. thick, internodes 3–6 cm. long, the stem often covered with the fibrous remains of petiole sheath wings; axillary bud in a depression extended into a sulcus; adventitious anchor roots numerous, feeder roots rare or absent. *Petiole:* smooth or tuberculate, densely flecked with white spots, 30–55 cm. long, vaginate to the geniculum, the sheath wings deciduous, sometimes persisting as fibrous remains at the base of the petiole, geniculum 3–4 cm. long, often of a rough texture and dark brown. *Lamina:* bright green, often remaining so in dried specimens, of a soft texture, not glossy, trichosclereids absent; 60–120 cm. long, 35–60 cm. wide, ovate to oblong-ovate, cordate at the base, the tip acute, pinnatifid and perforate, the perforations elliptic, 3–6 cm. long, in 1–3 series per side; primary lateral veins 12–18 in number, prominent below and above, milky white, secondary lateral veins reticulate. *Peduncle:* terete, 1.5–2.5 cm. thick, 14–18 cm. long, tuberculate. *Spathe:* white, obovate, 15–18 cm. tall, blunt or shortly mucronate. *Flowering spadix:* deep green to greenish gold, 14–19 cm. long, 3.5–5.5 cm. thick, in dried specimens a golden color, the apical surface of the pistils underlain by a layer of sclereids which form a sharp-edged papery cap in dried specimens.

ETYMOLOGY. Latin *punctulata,* "spotted," in reference to the numerous white spots on the petiole.

DISTRIBUTION. Mexico, Guatemala, Costa Rica, and Panama.

REPRESENTATIVE SPECIMENS. **Mexico. Vera Cruz:** Barranca de Santa Maria, km. 45 on road from Conejo to Jautusco, Sept. 1961, *Moore & Bunting 8861* (BH); 6 miles from Catemaco on road to Sontecomapan, 380 m., Sept. 1961, *Moore & Bunting 8939* (BH). **Oaxaca:** between Chipiltepec and Valle Nacional, 110 m., Aug. 1972, *Madison 633* (GH); 6 km. from Acatlan along road to La Capilla, 100 m., Aug. 1972, *Madison 610* (MEXU). **Guatemala. Petén:** 16°37′N × 89°31′W, 100 m., June 1973, *Madison 1537* (GH). **Costa Rica. Alajuela:** Quebrada La Calera, San Ramón, Feb. 1938, *Brenes 22643* (F). **Cartago:** Rio Virilla, San Juan, Nov. 1913, *Jiminez 922* (US). **Puntarenas:** 1 m. SW of Cañas Gordas, 1170 m., Feb. 1973, *Croat 22280* (MO); Río Coton, 1400–1500 m., 8°55′N × 82°55′W, Jan. 1967, *Burger & Matta 4559* (CR,F,GH,US). **Limón:** Hamburg Finca, Río Reventazon below Cairo, 55 m., Feb. 1925, *Standley & Valerio 48874* (US). **Panama. Chiriqui:** Palo Santo, 3 mi. N of Volcan, Feb. 1971, *Croat 13574* (MO); El Boquete, 1000–1300 m., March 1911, *Pittier 3151* (US). **Darien:** headwaters of Rio Tuquesa, Aug. 1974, *Croat 27179* (MO).

Monstera punctulata is easily recognized by a number of features, among them its brilliant green leaves of a soft texture. These leaves lack trichosclereids, and this is the only species in which I have observed damage to the leaves by leaf-cutter ants, suggesting that the abundant trichosclereids in the leaves of other *Monstera* species may be a defense against such predation. Other features of note are the densely white-spotted petiole with a brown tuberculate geniculum, the prominent white lateral veins of the lamina, and the dark green fruits which dry a golden color.

Monstera punctulata is a rare species in most of its range and is known from a relatively few collections. It is not uncommon in the limestone areas of the central Petén; I collected only a single specimen there as it was not in flower. Later I discovered that this was the first collection of the species from Guatemala.

17. Monstera spruceana (Schott) Engler

FIG. 57, MAP 4

Monstera spruceana (Schott) Engler, Flora Brasiliensis III (2):115 (1878). *Tornelia spruceana* Schott, Oest. Bot. Zeit. 9:40 (1859). TYPE: Brazil, Amazonas, São Gabriel, March 1852, *Spruce 2293* (K, photo BH,SEL; drawing of holotype = Schott Aroideae No. 2323, W, *non vidi*, photo BH,BR,GH,NY,S).

Climber to 5 m. tall. *Juvenile:* a shingle plant. *Adult stem:* smooth or slightly tuberculate near the nodes, subterete, 2–3 cm. thick, 3–4 cm. wide, internodes 4–10 cm. long, the stem slightly sulcate above the axillary bud. *Petiole:* 25–40 cm. long, the sheath wings disintegrating into fibers, geniculum 5–8 cm. long. *Lamina:* dull dark green, coriaceous, oblong-ovate, somewhat falcate, 50–70 cm. long, 25–40 cm. wide; pinnatifid, the pinnae 5–12 cm. wide with 2–4 primary lateral veins per pinna, pinnae 4–10 per side in number, some leaves pinnatifid on one side only, the lamina base acute to subtruncate, the apex acute; primary lateral veins 12–20 in number, arising at an angle of 70–90° with the costa, the secondary lateral veins subparallel to the primary. *Peduncle:* stout, terete, smooth, shorter than the spadix, 8–13 cm. long, 1.5–2.5 cm. thick. *Spathe:* white, blunt at the apex, 3–4 cm. longer than the flowering spadix. *Flowering spadix:* white, cylindric, tapering gradually toward the apex, 12–25 cm. long, 2.5–3.0 cm. thick, the pistils truncate. *Fruiting spadix:* white, 16–36 cm. long, 4–6 cm. thick.

ETYMOLOGY. After Richard Spruce (1817–1893), British botanist and botanical explorer, collector of the type specimen.

DISTRIBUTION. Costa Rica, Panama, Colombia, Ecuador, Peru, Venezuela, Guyana, and Brazil.

REPRESENTATIVE SPECIMENS. **Costa Rica. Puntarenas:** Golfo Dulce and Río Terraba, 30 m., Dec. 1947, *Skutch 5320* (US). **Panama. Panama:** Cerro Campana, below the summit, 900 m., Oct. 1972, *Madison 763* (GH). **Colombia. Magdalena** (?): Boca de Laino, am Río Magdalena, 100 m., July 1898, *von Bayern 46* (M). **Ecuador. Pichincha:** Road Aloag-Santo Domingo, Toachi, 850 m., Sept. 1967, *Sparre 18446* (S); Alluriquin, 600 m., March 1967, *Sparre 14796* (S). **Los Rios:** Río Palenque Biological Station, 220 m., Sept. 1973, *Dodson & Tan 5303* (US); 20 km. E of Santo Domingo, 680 m., Dec. 1972, *Madison 902* (GH). **Azuay:** Sanaguin, 850 m., May 1943, *Steyermark 52722* (NY). **Peru. Loreto:** Alto Río Itaya, 145 m., Oct. 1929, *Williams 3316* (F,US); Soledad, Río Itaya, 110 m., Sept. 1929, *Killip & Smith 29604* (NY,US). **Venezuela. Yaracuy:** El Guayabito Playon, 15 km. N of Marin, 150–250 m., Nov. 1971, *Steyermark & Bunting 105290* (VEN). **Bolivar:** Sierra Imataca, Río Toro, 200–250 m., Dec. 1960, *Steyermark 88145* (NY,VEN); Cerro Pichacho, 45 km. N of Tumerero, 100–300 m., Feb. 1961, *Steyermark 89207* (VEN). **Guyana.** Pakaraima Mountains, Parima Falls, 600 m., Nov. 1951, *Maguire & Fanshaw 32582* (NY,US, VEN); Minatta, Rupununi River, Oct. 1889, *Jenman 5765* (K). **Brazil. Amapá:** Rio Iaue, 2°53′N × 52°22′W, Aug. 1960, *Irwin, Pires & Westra 47776* (NY). **Amazonas:** São Gabriel, March 1852, *Spruce 2293* (K).

This is one of the few species in section Marcgraviopsis with an

Fig. 57. *Monstera spruceana:* holotype (*Spruce 2293*, K).

adequate, available type specimen, yet its characters remain obscure. Its known wide distribution in eight countries of Central and South America is based on a total of only 18 collections, which are all fairly different from one another. I am of the opinion that at least two species are included in the species as here described, but the paucity of specimens presently available does not permit a meaningful interpretation of the variation among them.

The major morphological features of the species are a pinnatifid leaf with broad pinnae arising at a wide angle from the costa, the petioles one-third to two-thirds the length of the lamina, and the peduncle terete and shorter than the spadix, which is tapered and 16–36 cm. long in fruit. In some specimens, however, the leaf is pinnatifid on only one side, and in *Skutch 5320* it is entire.

That the juvenile of this species is a shingle plant is verified by at least two collections, *Madison 763* and *Killip & Smith 29604*. However, in specimens from western Ecuador, the shingle plant stage is confined to less than a dozen leaves with the transition to the adult form occurring close to the ground.

A further complication for herbarium studies derives from the resemblance of the adult stage of this species to *Monstera dilacerata* and *M. subpinnata* in section Monstera. Though adequate specimens should be easily identifiable, the typical herbarium sheet consisting of a leaf lamina and spadix minus the peduncle makes determination difficult or impossible.

18. Monstera tenuis C. Koch

FIGS. 58–60, MAP 11

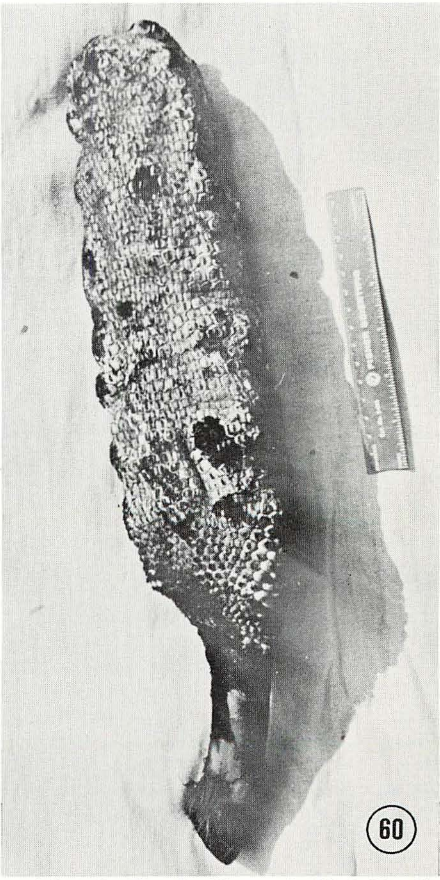
Monstera tenuis C. Koch, Ind. Sem. Hort. Bot. Berol. App. 5 (1855). TYPE: Central America, cultivated at Berlin, *Warszewicz* (B?, *non vidi*).

Monstera gigantea Engler, Bot. Jahrb. 37:118 (1905) not *M. gigantea* (Roxb.) Schott. TYPE: Costa Rica, Cartago, Tucurrique, 635 m., Jan. 1899, *Tonduz 13311* (B, *non vidi*, photo BH,GH,US; isotypes P,US).

A robust climber on large trees, to 30 m. tall, with an open habit of growth and exserted arching leaves. *Juvenile:* a shingle plant, the laminae nearly round, mucronate at the apex. *Adult stem:* smooth, 6–8 cm. wide, 4–6 cm. thick, the internodes 8–12 cm. long; leaf scars shallow, less than 2 cm. wide at the widest point, axillary bud in a depression not extended into a sulcus. *Petiole:* ⅓ to ½ the length of the lamina, 30–60 cm. long, vaginate to the lamina base, the sheath wings persistent, to 6 cm. broad near the base, geniculum 3–5 cm. long, 2–3 cm. thick. *Lamina:* bright green, not glossy, oblong ovate, truncate at the base, the apex acute, 60–125 cm. long, 45–70 cm. wide, deeply and regularly pinnatifid, the sinuses extending to the midrib, 12–30 pinnae per side, the pinnae nearly perpendicular to the midrib, 2–5 cm. wide, constricted near the base; primary lateral veins one per pinna, prominent and white abaxially, the secondary lateral veins parallel to the primary. *Peduncle:* subterete, 10–15 cm. long, 3–4 cm. thick. *Spathe:* white, 20–25 cm. tall. *Flowering spadix:* white, cylindric, tapering to the apex, 18–24 cm. long, 3.5–5.0 cm. thick, the pistils truncate. *Fruiting spadix:* green, becoming yellow at maturity, 22–35 cm. long, 5.5–9.5 cm. thick, the seeds oblong, 10–12 mm. long, pistachio green within.

(58)

(59)



(60)

FIGS. 58–60. *Monstera tenuis:* 58. flowering shoot (photo by Timothy Plowman); 59. habit; 60. fruiting spadix, 32 cm. in length.

ETYMOLOGY. Latin *tenuis*, "thin," referring to the membranaceous texture of the juvenile leaf lamina.

DISTRIBUTION. Nicaragua, Costa Rica, Panama, below 1600 meters.

REPRESENTATIVE SPECIMENS. **Nicaragua. Zelaya:** vicinity of Rama, 50 m., Sept. 1972, *Madison 717* (GH). **Costa Rica. Guanacaste:** between Santa Rosa and H. Tenorio, 300–600 m., Sept. 1972, *Madison 722* (GH). **Alajuela:** Forêts de San Ramón, 1500–1600 m., May 1913, *Tonduz 17722* (P). **Heredia:** Río El Angel, between Vara Blanca and Cariblanco, 900–1000 m., March 1953, *Moore 6623* (BH); 10°27'N × 84°07'W, 110 m., May 1973, *Madison 1527* (CR). **Puntarenas:** Finca las Cruces, 4.5 mi. from San Vito de Java, 5000 ft., March 1969, *Stevens 233* (US). **Cartago:** Río Naranjo, 3 km. E of Cachi, 1300 m., April 1969, *Lent 1589* (CR,F,US); Río Sombrero, El Muñeco, 1300 m., June 1972, *Luteyn 3240* (DUKE,MO). **Limón:** 10°5'N × 83°29'W, 50–100 m., Dec. 1969, *Burger & Liesner 6955* (CR,F,MO); 10 km. S of Limón, 0–10 m., Oct. 1972, *Madison 751* (GH); Siquierres, Feb. 1932, *Kupper 582* (M). **Panama. Chiriqui:** 12 km. from Escuela San Benito in Volcán on road to Río Serano, 1200 m., Aug. 1974, *Croat 26495* (MO).

Carl Koch originally described *Monstera tenuis* based on the juvenile stage of a cultivated plant at Berlin, obtained somewhere in Central America by Warszewicz. Koch's specimen was studied by N. E. Brown, who subsequently determined a plant growing at Kew as *M. tenuis.* Whether or not the propagule of the Kew plant was obtained from Berlin is not known. At any rate, the Kew specimen includes both the juvenile and adult leaves, and I am taking it as the basis for interpreting the name *M. tenuis.*

The only other name available for this species, *Monstera gigantea* Engler, is a later homonym of *M. gigantea* (Roxb.) Schott, and is thus illegitimate. Engler and Krause mistakenly applied the name *M. dubia* to this species, and it is illustrated in *Das Pflanzenreich* under that name.

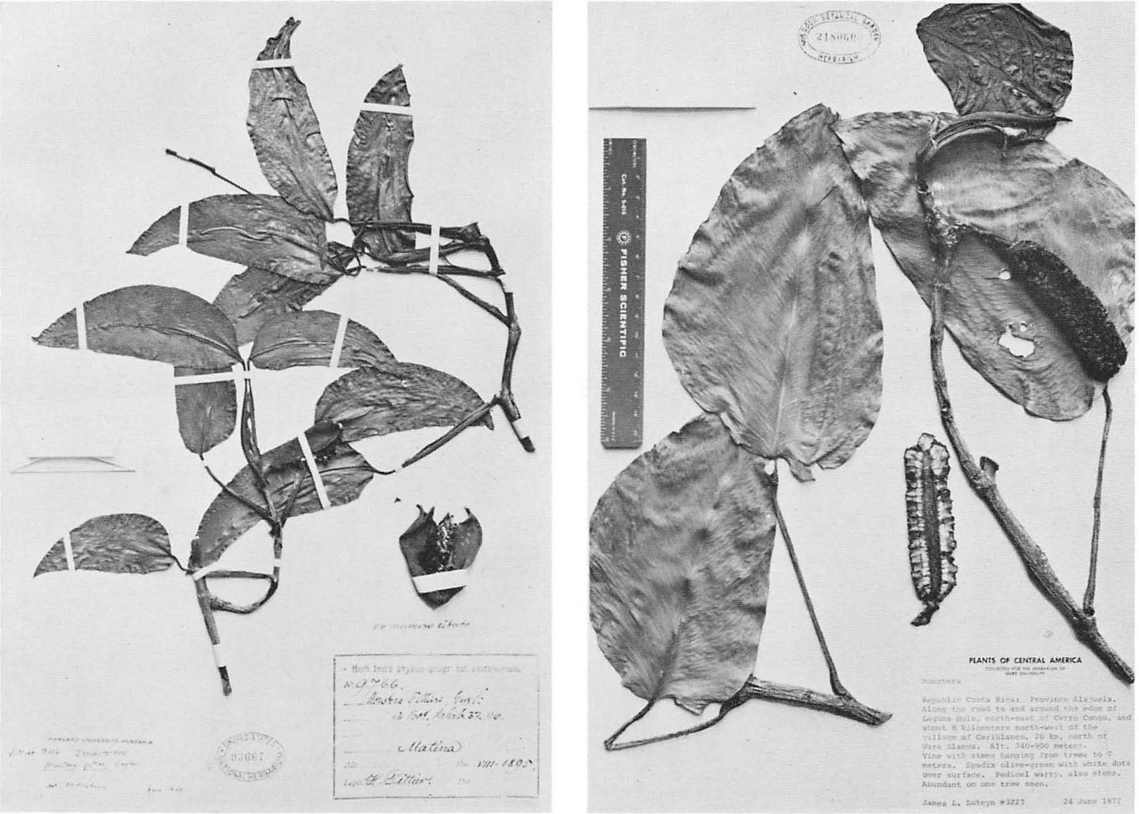
Monstera tenuis is one of the most elegant species of *Monstera,* and is worthy of cultivation. It abounds on the Atlantic coastal plain of Nicaragua and Costa Rica, and ascends the mountains to 1500 meters. It is easily recognized by the regularly pinnatifid leaves with 15–30 pinnae per side, the internodes 8–12 cm. long, and the massive fruiting spadices the dimensions of a man's forearm. At maturity the fruits are often pendent; apparently they are so heavy that the peduncle cannot support them in an erect position.

19. Monstera pittieri Engler

FIG. 61, MAP 16

Monstera pittieri Engler, Bot. Jahrb. 37:116 (1905). LECTOTYPE (here designated): Costa Rica, Limón, Matina, Aug. 1895, *Pittier 9766* (B, *non vidi,* photo BH, SEL; isolectotypes CR, BR, US no. 936670). LECTOPARATYPE: Costa Rica, Limón, La Concepción, Llanuras de Santa Clara, 250 m., Feb. 1896, *J. D. Smith 6809* (K, US no. 936671).

Slender climber with pendent shoots from tree branches, the fruit held erect. *Juvenile:* a shingle plant. *Adult stem:* subterete or flattened, 5–10 mm. thick, the internodes 4–9 cm. long, with a thick, tan-colored cuticle which may flake off in dried specimens; adventitious roots lacking in the pendent portions of the stem. *Petiole:* 8–20 cm. long, vaginate nearly to the blade base, the sheath wings ultimately deciduous, sometimes disintegrating into fibres. *Lamina:* coriaceous, dull green, entire,



FIGS. 61–62. 61. (left) *Monstera pittieri:* isolectotype (*Pittier 9766,* US); 62. (right) *Monstera luteynii:* holotype (*Luteyn 3227,* MO).

ovate to lanceolate, 2–5 times longer than wide, strongly falcate and unequal, the base obliquely acute, the apex acute; the veins obscure and not prominent on either surface. *Peduncle:* terete, 2.5–4.0 mm. thick, 2–6 cm. long. *Flowering spadix:* 1.2–1.6 cm. thick, 3–6 cm. long, the pistils truncate at the apex. *Fruiting spadix:* 5–9 cm. long, 2.0–3.5 cm. thick, tapered to either end, the stylar portions of the pistils well separated from one another, giving the fruiting spadix a spiny aspect.

ETYMOLOGY. After Henry Pittier (1857–1950), collector of the type specimen.

DISTRIBUTION. Atlantic Costa Rica, and Panama, below 400 meters.

REPRESENTATIVE SPECIMENS. **Costa Rica. Limón:** Matina, Aug. 1895, *Pittier 9766* (BR,CR,US); La Concepción, 250 m., Feb. 1896, *Smith 6809* (K,US); Río Destierro, Santa Clara, 200 m., June 1899, *Pittier 13398* (US); Guapiles, 250 m., Aug. 1951, *Carpenter 421* (US); Jamburg Finca, Río Reventazon below Cairo, 55 m., Feb. 1926, *Standley & Valerio 48899* (US). **Panama. Colon:** East Ridge, Feb. 1968, *Duke 15280* (US). **Panama:** El Llano-Carti Road, 7–12 km. from Interamerican Highway, 360–400 m., July 1974, *Croat 25175* (MO).

Monstera pittieri is a diminutive climbing and hanging species of Costa Rica and Panama. The Panamanian material is more robust, with larger and more strongly falcate leaves than the Costa Rican plants, but they are clearly the same species.

Monstera pittieri is in appearance like a small version of one of the entire-leaved manifestations of *M. dubia,* and illustrates a possible line of reduction which I hypothesize led to the origin of *M. tuberculata.*

Engler's illustrations of this species in *Das Pflanzenreich* (IV 23B p. 100), are misleading in two respects. He illustrates a flower (fig. H) with six stamens, when the normal number in this species, as in all species of *Monstera,* is four. His drawing of a fruiting spadix (fig. G) shows the pistils tightly crowded together and the spadix with a continuous surface, whereas in the fruiting material I have seen, the stylar portions of the pistils are separate and the surface of the spadix thus irregular and with a spiny aspect. It is this spiny fruit, together with the much narrower leaves, that distinguish *M. pittieri* from *M. luteynii.*

Some specimens of *Monstera pittieri* have been misidentified as *M. falcifolia* (= *M. obliqua*), but the much shorter peduncles and stouter spadices of the former readily distinguish these two species.

20. **Monstera luteynii** Madison, *sp. nov.*

FIG. 62, MAP 16

Planta epiphytica scandens et dependens; rami pendentes floriferi. *Caulis* teres, 5–10 mm. crassus, internodiis 5–9 mm. longis. *Foliorum petiolus* 8–12 cm. longus, ad geniculum usque vaginatus, vagina decidua; *lamina* integra, coriacea, oblique ovata, 12–18 cm. longa, 9–13 cm. lata, basi truncata vel subcordata, apice acuta. *Pedunculus* teres, 5–8 mm. crassus, 1–6 cm. longus. Spatha ignota. *Spadix fructifer* circ. 8 cm. longus, 2 cm. crassus. *Baccae* subprismaticae et truncatae.

TYPE: Costa Rica: Alajuela, along road to and around the edge of Laguna Hule, NE of Cerro Congo, and about 8 km. NW of the village of Cariblanco, 20 km. N of Vara Blanca. Alt. 740–900 m. Vine with stems hanging from trees to 7 m. Spadix olive-green with white dots over surface. Pedicel warty, also stems. Abundant on one tree seen. June 1972. *Luteyn 3227* (holotype MO no. 2180600; isotypes US no. 2684199, DUKE no. 230028).

ETYMOLOGY. Named for James L. Luteyn, ardent collector of Costa Rican Araceae.
DISTRIBUTION. Costa Rica, Provinces of Cartago and Alajuela.
REPRESENTATIVE SPECIMENS. **Costa Rica. Cartago:** Forêts des Tuis, 650 m., Nov. 1897, *Pittier 11370* (BR,US); Forêts de La Vueltas, Tuqurrique, 635–700 m., Jan. 1899, *Tonduz 13312* (US); Las Vueltas, Tuqurrique, 635 m., Dec. 1898, *Tonduz 12841* (GH,K,US).

Monstera luteynii is one of several species of *Monstera* which characteristically flower on pendent shoots. It is perhaps closest to *M. dubia,* from which it differs by its much smaller and entire leaves, narrower stems, and very short peduncles.

Monstera luteynii resembles two other pendent species with entire leaves, *M. pittieri* and *M. tuberculata.* However, both of these have the stylar portions of the pistils separate in the fruiting spadix, giving the spadix a spiny aspect. This is in contrast to the smooth fruiting spadix of *M. luteynii. Monstera pittieri* may be distinguished vegetatively by its lanceolate leaves, 2–5 times longer than wide, whereas in *M. luteynii* the leaves are ovate and less than two times longer than wide. *Monstera tuberculata* has petioles less than 4 cm. long with the sheath extended into a ligule equalling the petiole, in contrast to the petioles of *M. luteynii* which are 8–12 cm. long with a very short ligule.

MONSTERA section ECHINOSPADIX Madison, *sect. nov.*

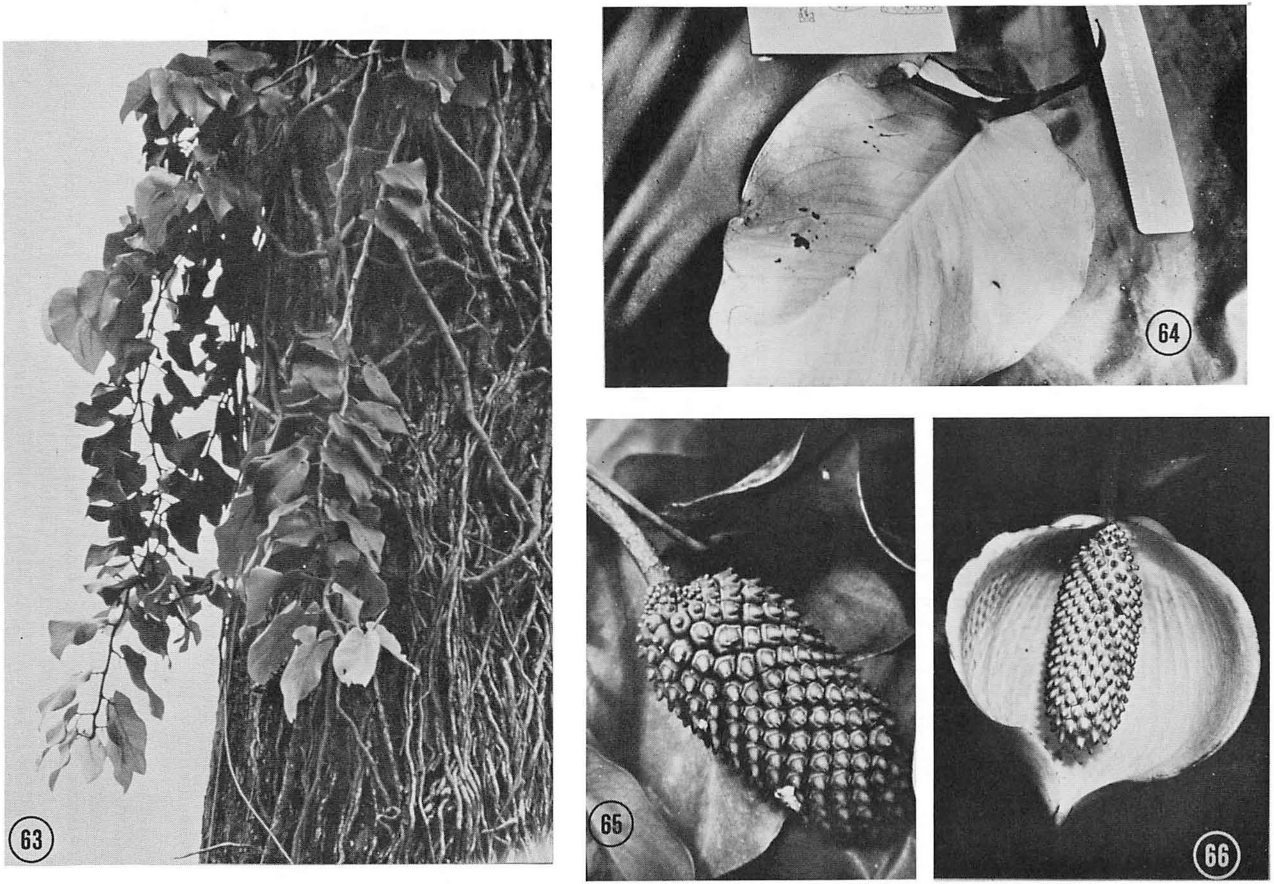
Plantula stoloniformis. Folia stirpium juvenilium ad truncis arborum adpressae. Vagina petioli foliorum omnium ligulata, ligula petiolum aequans. Pistillum maturum 6–7 mm. latum. Spadix pendens.
TYPE SPECIES: *Monstera tuberculata* Lundell.

Monstera tuberculata, while showing close affinity to section Marcgraviopsis, is placed in a separate section because of two specializations. The third (adult) phase of heteroblastic development as seen in section Marcgraviopsis is not represented here; *Monstera tuberculata* flowers on what is morphologically a juvenile (second phase) shoot in section Marcgraviopsis. *Monstera tuberculata* is the only species with pendent spadices; in all others the spadices are held erect, even if produced on hanging shoots.

21. **Monstera tuberculata** Lundell

FIGS. 63–66, MAP 13

Climbing and hanging epiphyte, flowering in the pendent portions, the juvenile and adult not distinct. *Adult stem:* terete, verruculose, with a thick tan cuticle which flakes off if the stem is twisted, 1.0–1.5 cm. thick, the internodes 6–12 cm. long, a tuft of adventitious roots borne near each node. *Petiole:* 1–4 cm. long, canaliculate to within 6 mm. of the blade base, the sheath wings extended into a ligular outgrowth as long as or exceeding the petiole, 2–6 cm. long, this and the sheath wings deciduous. *Lamina:* entire, coriaceous, smooth or papillose, obliquely ovate, cordate at the base, mucronate or acute at the apex, 8–18 cm. long, 5–11 cm. wide, the lateral veins subparallel, not separable into primary and secondary laterals. *Peduncle:* smooth, terete, 2–6 mm. thick, 4–8 cm. long, the inflorescence pendent. *Spathe:* white, when open



FIGS. 63–66. 63. *Monstera tuberculata* var. *tuberculata:* habit (*Madison 631,* SEL); 64–66. *Monstera tuberculata* var. *brevinodum: 64.* leaf, showing ligule; 65. fruit; 66. inflorescence (all *Madison 752,* GH).

about as wide as tall, 5–9 cm. tall, 5–10 cm. across when open, acuminate, the acumen 1.0–1.5 cm. long. *Flowering spadix:* white, 2–3 cm. thick, 6–9 cm. long, the pistils extended into a conical acuminate style 4–8 mm. long, curved toward the apex of the spadix. *Fruiting spadix:* green, 7–11 cm. long, 4.5–5.5 cm. thick, the berries 7–9 mm. across, the curved stylar region ultimately deciduous to reveal the seeds in a slimy gray pulp. *Seeds:* brown, oblong, 9–12 mm. long, 4–5 mm. across.

KEY TO VARIETIES

Outer surface of the pistil smooth, with no clear demarcation of the style and ovary. .... var. *tuberculata.*

Style arising from a depression on the apex of the ovary, resulting in a pronounced ridge around the pistil at the junction of the style and ovary. .... var. *brevinodum.*

21a. **Monstera tuberculata** Lundell var. **tuberculata**

Monstera tuberculata Lundell, Lloydia 2:78 (1939). TYPE: Belize, El Cayo District, Valentin, on trees in high advanced forest, June 1936, *C. L. Lundell 6238* (MICH, *non vidi;* isotype GH).

As described in the key, the distinctive feature of this variety is the smooth surface of the pistils with the ovary not demarcated from the style.

ETYMOLOGY. Latin *tuberculata,* "tuberculate," in reference to the spiny aspect of the spadix.

COMMON NAMES. Chile montaña, trepepoyo (Mexico).

DISTRIBUTION. Mexico, Guatemala, Belize, at low elevations.

REPRESENTATIVE SPECIMENS. **Mexico. Oaxaca:** Mogoñe, March 1953, *MacDougall* MEXU *no. 76682* (MEXU); Ubero, 30–90 m., June 1937, *L. Williams 9454* (F). **Vera Cruz:** Playa Escondida, 28 km. NE of Catemaco, 50 m., Aug. 1972, *Madison 631* (SEL); 4 km. NE of Minatitlan, 50 m., Aug. 1958, *King 1114* (MICH,US). **Tabasco:** Estapilla, Tenosique, June 1939, *Matuda 3495* (MEXU,MICH). **Guatemala. Alta Verapaz:** Río Sebol, downstream from Carrizal, 150–200 m., April 1942, *Steyermark 45788* (F,US). **Petén:** 5 mi. S of entrance to Tikal National Park, June 1973, *Croat 24747* (MO). **Izabal:** Bay of Santo Tomas, 2 m., April 1940, *Steyermark 39246* (F). **Livingston:** Río Dulce, 0 m., March 1889, *J. D. Smith 1533* (GH,US). **Belize. El Cayo District:** Valentin, June 1936, *Lundell 6238* (GH,MICH).

21b. **Monstera tuberculata** Lundell var. **brevinodum**
(Standl. & L. O. Wms.) Madison, *stat. et comb. nov.*

Philodendron brevinodum Standl. & L. O. Wms., Ceiba 1:231 (1951). TYPE: Costa Rica, Cartago, Turrialba, Moravia, 1100 m., June 1950, *Jorge Leon 2548* (photo NY, US no. 2215909).

In this variety there is a sharp ridge around the pistil demarcating the junction of the style and ovary.

ETYMOLOGY. Latin *brevinodum,* "short nodes," as the species was considered to have short internodes (?) for a *Philodendron.*

DISTRIBUTION. Costa Rica.

REPRESENTATIVE SPECIMENS. **Costa Rica. Alajuela:** W slope of Volcán Arenal, 300 m., Sept. 1972, *Madison 725* (CR). **Cartago:** Turrialba, Moravia, 1100 m., June 1950, *Leon 2548* (US). **Limón:** Zent, 50 m., Oct. 1972, *Madison 752* (CR,GH,MO); Río Santa Clara, 1.6 km. E of Guapiles, 200 m., July 1949, *Holm & Iltis 409* (A,F,P,U).

Monstera tuberculata was first collected in 1889 in Guatemala by J. Donnell-Smith. Engler erroneously identified this specimen as *M. acuminata* Koch, and redefined the species to include Donnell-Smith's specimen. Subsequent collections of *M. tuberculata* have mostly been determined as *M. acuminata.* In his original description of *M. tuberculata,* Lundell remarked that it seemed close to *M. acuminata* Koch, but since the application of the latter name has been quite chaotic to the present, it is not clear what relationship he intended to indicate by that statement.

Monstera tuberculata shows a disjunction between Guatemala-Mexico and Costa Rica, although in the intervening area there is continuous wet lowland forest which appears to be a suitable habitat for the species. The northern and southern populations have diverged strikingly in the morphology of the gynoecium, though they are indistinguishable in other respects. I have separated these two gynoecial types as varieties. It is possible that botanical exploration in Nicaragua and Honduras will turn up intermediate forms.

Monstera tuberculata seems most closely related to the pendent species of section Marcgraviopsis—*M. pittier, M. luteynii,* and *M. dubia*—all of which are distinguished from it by their erect fruits and long-petiolate leaves. The adult leaves of *M. tuberculata* have the asymmetric lamina with a short petiole and long ligule typical of the juvenile (shingle plant) stage of these species, and in my opinion *M. tuberculata* is vegetatively a neotonous derivative of section Marcgraviopsis. In its floral morphology, however, the species is highly specialized. It is the only species with pendent spadices, and the curvature and attenuation of the styles are probably related to the pendent orientation of the spadix, although the mechanism of the relationship is not known. In other species of *Monstera* the sterile flowers at the base of the spadix often have long curved styles, suggesting that the genetic capability for producing this kind of flower is present throughout the genus.

A specimen of *Monstera tuberculata* from Tabasco *(Matuda 3380)* is annotated "comestibile;" presumably it is the ripe spadix which is edible. A peasant living near the locality of *Madison 752* (Zent, Prov. Limón, Costa Rica) showed me rough baskets used for storing maize made from the pendent stems of this species.

MONSTERA section TORNELIA Madison, *stat. nov.*

Tornelia Guttierez, Linnaea 26:382 (1853).

Folia plantulae et stirpis juvenilis exserti. Pistillum maturum 10–18 mm. latum; semina 16–22 mm. longa. Spadix erectus.

TYPE SPECIES: *Monstera deliciosa* Liebm.

Monstera deliciosa does not show the heteroblastic development of section Marcgraviopsis, but neither is it similar to the species of section Monstera. A number of features distinguish it: (1) in large-leaved individuals the petiole is vaginate for only $\frac{1}{6}$ its length, as opposed to at least $\frac{5}{6}$ the length in other species; (2) the juvenile leaf has a petiole 2–4 times the lamina length, as opposed to less than or equalling the lamina length in other species; (3) axillary buds are represented only by a swollen region on the stem rather than being distinct and prominent; (4) anatomically, of 16 species I have investigated it is the only one to have asterosclereids in the leaf lamina, and the only one to have trichosclereids in the roots; (5) the berries are about twice the width and the seeds twice the weight of those of other species; and (6) *M. deliciosa* often grows to maturity as a terrestrial or rupestral plant, whereas other *Monstera* species flower only as epiphytes, or very rarely on rocky cliffs.

22. **Monstera deliciosa** Liebmann

FIG. 67, MAP 10

Monstera deliciosa Liebmann, Kjoeb. Vidensk. Meddel. **19**:9 (1849). *Tornelia fragarans* Guttierez, Linnaea **26**:382 (1853). TYPE: Mexico, Oaxaca, Western Cordillera, 5000–7000 ft., Dec. 1842, *Liebmann s.n.* (C).

Monstera borsigiana Engler, D. C. Monog. Phan. **II**:266 (1879). *Monstera deliciosa* Liebm. var. *borsigiana* (Engler) Engler and Krause, Das Pflanzenreich IV **23B**:111 (1908). TYPE: Mexico, Valle de Cordoba, Jan. 1866, *Bourgeau 1904* (holotype B, *non vidi;* isotypes BR,C,GH,L,LEP,S,US).

Monstera tacanaensis Matuda, Ann. Inst. Biol. Univ. Nat. Aut. Mex. **43**: Ser. Bot. (1)55 (1972, published 1974). TYPE: Mexico, Chiapas, Unión Juarez, W slope of Volcán Tacana, 850 m., Feb. 1969, *Matuda 37584* (MEXU).

Monstera deliciosa Liebm. var. *sierrana* Bunting, Gentes Herbarum **9**:320 (1965). TYPE: Mexico, Oaxaca, Sierra de Juarez, 15 mi. S of Valle Nacional on road to Oaxaca, 1220 m., Sept. 1961, *Moore & Bunting 8918* (holotype BH no. 100023; isotypes UC no. 1327227, K, US no. 2578977).

Philodendron pertusum Kunth & Bouché, Ind. Sem. Hort. Berol.:11 (1848). *Monstera lennea* C. Koch, Bot. Zeit. **10**:277 (1852) based on the same type as *P. pertusum.* TYPE: cultivated at Berlin, propagule collected in Guatemala by Warscewicz, C. Koch (B, destroyed? *non vidi*).

Stout sprawling plant, rupestral or epiphytic. *Juvenile:* a terrestrial creeper, the leaves with erect petioles about twice the length of the lamina, the lamina thickly coriaceous, glossy deep green adaxially, pale abaxially, ovate, cordate at the base, acuminate at the tip. *Adult stem:* smooth, green, 2–8 cm. thick, the internodes 4–10 cm. long, the axillary buds not distinct but represented by a swollen region of the stem above the node. *Petiole:* 30–100 cm. long, tuberculate or smooth, vaginate for $\frac{1}{6}$ to $\frac{9}{10}$ its length, the sheath wings marcescent or deciduous, geniculum 2.0–3.5 cm. long, sometimes with a crispate margin. *Lamina:* coriaceous, glossy adaxially, pale green abaxially, ovate, 25–90 cm. long, 25–75 cm. wide, shorter than the petiole, cordate at the base, acute or mucronate at the apex; regularly pinnatifid, perforate or not, the perforations in 1–5 series per side, elliptic, 0.5–8.0 cm. long; primary lateral veins prominent abaxially, 6–14 in number per side, the secondary lateral veins reticulate. *Peduncle:* tuberculate or smooth, terete, 1.0–1.8 cm. thick, 10–18 cm. long. *Spathe:* white or cream to yellow, thickly coriaceous, 16–25 cm. long. *Flowering spadix:* white or green, 10–18 cm. long, 2.5–3.0 cm. thick, the pistils truncate, 6–11 mm. across. *Fruiting spadix:* green or bluish-green, 15–22 cm. long, 4.5–6.0 cm. thick, the berries 10–18 mm. across. *Seeds:* spheroidal, 16–22 mm. long, 10–13 mm. across, green within.

ETYMOLOGY. Latin *deliciosa,* "delicious," in reference to the sweet edible fruits.
COMMON NAMES. Harpón (Guatemala); Piñanona (Mexico).
DISTRIBUTION. Mexico, Guatemala, Costa Rica, Panama.
REPRESENTATIVE SPECIMENS. **Mexico. Oaxaca:** western Cordilliera, 5000–7000 ft., Dec. 1842, *Liebmann, s.n.* (C); 15 mi. S of Valle Nacional, 1200 m., Sept. 1961, *Moore & Bunting 8918* (BH,K,UC,US); 40 km. above Pochutla on road to Oaxaca, 950 m., Oct. 1974, *Madison 1803* (MEXU). **Vera Cruz:** Laguna Encantada near San Andrés

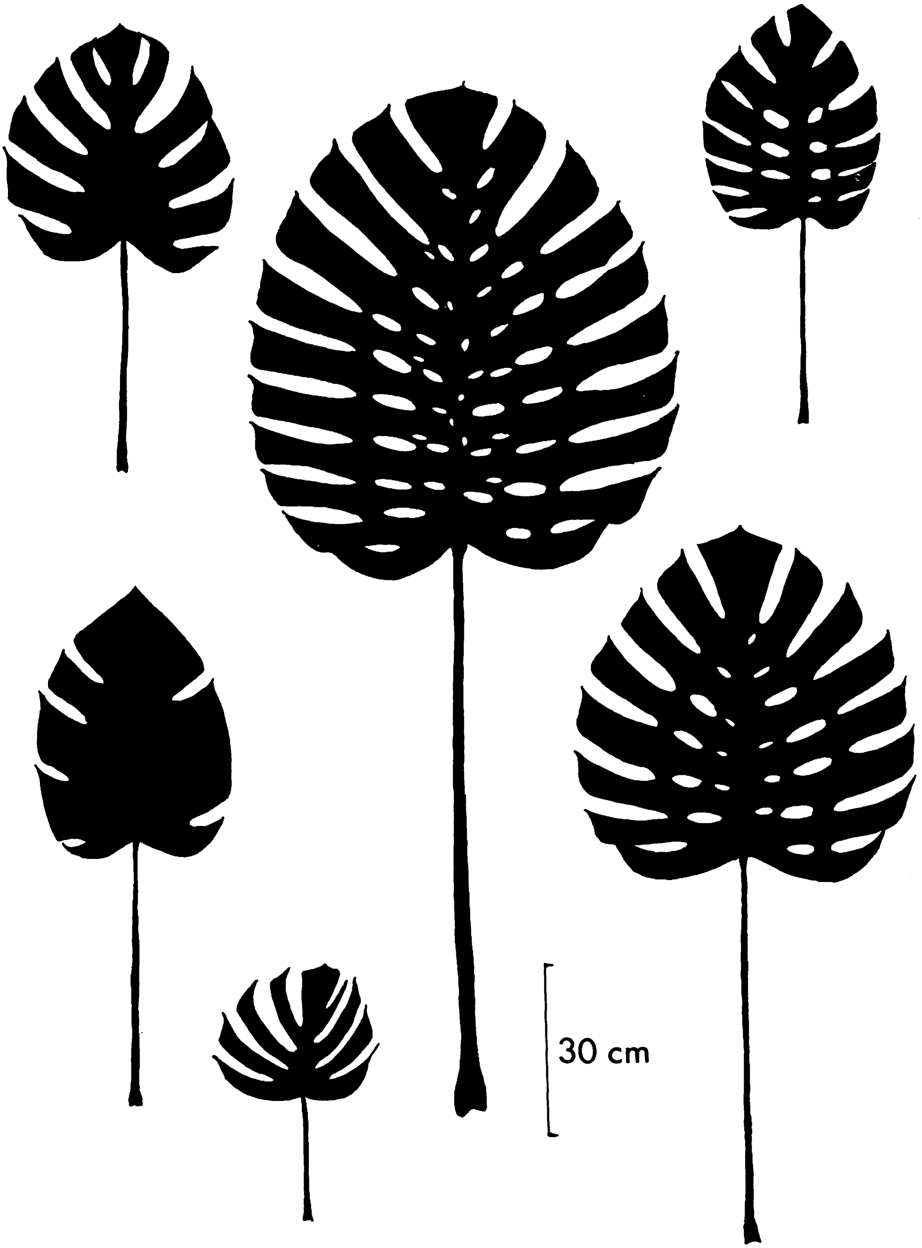


Fig. 67. *Monstera deliciosa:* variation in adult leaf shape, from different individuals (to the same scale).

Tuxtla, April 1952, *Moore & Cetto 6231* (BH,MEXU); Barranca de Santa Maria, km. 45 on Conejo-Huatusco road, Sept. 1961, *Moore & Bunting 8860* (BH). **Chiapas:** canyon N of Chacona NW of Tuxtla G., Dec. 1949, *Miranda 5842* (MEXU); Unión Juarez, W slope of Volcán Tacana, 850 m., Feb. 1969, *Matuda 37584* (MEXU). **Guatemala. Huehuetenango:** Paso del Boqueron, below La Libertad, 1200–1300 m., Aug. 1942, *Steyermark 51186* (F,US); above Democracia on trail towards Jutal, 1000 m., Aug. 1952, *Steyermark 51060* (F,MO). **Quezaltenango:** 10 miles from Colomba on road to San Juan, 1850 m., Aug. 1972, *Madison 657* (GH). **San Marcos:** S facing slopes of Volcán Tajumulco, 1300–1500 m., March 1940, *Steyermark 37200* (F); Finca Vergel, near Rodeo, 900 m., March 1939, *Standley 68917* (F). **Costa Rica. Alajuela:** 8 km. from La Fortuna on road to Chachagua, 250 m., Sept. 1972, *Madison 727* (CR). **Puntarenas:** 6 km. S of San Vito de Java, 5000 ft., Aug. 1967, *Raven 21860* (CR,GH). **San José:** 9°29′N × 83°37′W, 1600 m., Dec. 1969, *Burger & Liesner 7103* (CR,F). **Panama. Chiriqui:** Bajo Chorro, 1900 m., July 1940, *Woodson & Schery 634* (F,GH,MO); roadside S of Cerro Punta, May 1970, *Croat 10434* (MO, UC). **Veraguas:** 5 mi. W of Santa Fé on Pacific side of divide, 800–1200 m., March 1973, *Liesner 909* (MO).

Monstera deliciosa is one of the most widely cultivated of ornamental plants. Its handsome dark leaves, slow rate of growth, and tolerance of shade and low humidity make it an excellent house plant for temperate regions. In the tropics it is widely grown both indoors and as a garden and patio plant.

Monstera deliciosa was first collected in Mexico by Karwinsky in 1832, but his specimen attracted no attention at Munich where it was sent. The species was next collected by Liebmann in 1842, who introduced it into cultivation by bringing cuttings from Mexico to Copenhagen. A second introduction was made in 1846 by Warscewicz, who sent cuttings to Berlin from Guatemala. The subsequent cloning of these two introductions is probably responsible for much of the *M. deliciosa* in cultivation today, as the species is rare in the wild and not often collected.

The species was first given a name by Kunth and Bouché who, in 1848, described the cultivated plant at Berlin as *Philodendron pertusum.* The following year Liebmann described his collection as *Monstera deliciosa.* Kunth and Bouché's name is older and has priority, but the epithet *pertusum* in *Monstera* is preoccupied by *Monstera pertusa* (Roxb.) Schott (1830). Thus, the earliest available legitimate name is *M. deliciosa* Liebm. In his description of the species, Liebmann makes no reference to Warscewicz's collection or to the name *Philodendron pertusum* Kunth and Bouché; clearly he is describing a new species rather than giving a *nomen novum* to *Philodendron pertusum* Kunth and Bouché, and *Monstera deliciosa* is thus typified by Liebmann's specimen and not by the type of *Philodendron pertusum.*

Guttierez (1853) proposed the new name *Tornelia fragrans* for *Monstera deliciosa;* the epithet is superfluous. The genus *Tornelia* was accepted by Schott but by no other authors. Carl Koch (1852) redescribed the Warscewicz plant at Berlin as *Monstera lennea,* considering it to be a different species from *M. deliciosa* (Koch, 1857).

Several species and varieties have been segregated from *Monstera* *deliciosa* on the basis of characters which are primarily related to differences in size. The largest clones at maturity have leaves four times the size of the smallest mature clones. The smallest ones have smooth petioles vaginate most of their length whereas the largest ones have tuberculate petioles vaginate for only $\frac{1}{6}$ their length. Although these differences are considerable, they represent extremes of a continuum in which numerous intermediate conditions are to be found. Under these circumstances I consider it most useful to recognize *M. deliciosa* as a polymorphic species without separating its different forms as varieties.

Monstera deliciosa is either rupestral or epiphytic, and the data accompanying about half of the specimens I have seen describe it as terrestrial. The large population at the type locality of var. *sierrana* grows almost entirely sprawling on the ground, rarely climbing the lower 1–2 m. of tree trunks. On the other hand, I have several times observed the species as an epiphyte climbing to 20 meters *(Madison 727, 1803).*

A chromosome count of $2n=60$ was made for this species by Pfitzer (1957). This was interpreted by Marchant (1970) as a hexaploid based on $x=10$.

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M. standleyana Bunting (2) 45
M. subpinnata (Schott) Engler (8) 60
M. surinamensis Miq. (1) 42
M. tacanaensis Matuda (22) 94
M. tenuis C. Koch (18) 85
M. tuberculata Lundell (21) 90
M. uleana Engler (8) 60
M. unilatera Rusby (12) 67
M. velloziana Schott (1c) 40
M. viridispatha Matuda (14) 73
M. xanthospatha Madison (11) 64
Philodendron brevinodum Standl. & L. O. Wms. (21b) 92
P. pertusum Kunth & Bouche (22) 94
Scindapsus dilaceratus Koch & Sello (7) 57
Tornelia dilacerata (Koch & Sello) Schott (7) 57
T. dissecta Schott (7) 57
T. fragrans Guttierez ex Linnaea (22) 94
T. laniata Schott (1b) 38
T. spruceana Schott (17) 83
T. subpinnata Schott (8) 60

EXCLUDED NAMES AND NOMINA NUDA

Monstera amomifolia Poepp. & Endl. = Stenospermation amomifolium (Poepp. & Endl.) Schott
M. cannaefolia (Rudge) Schott = Philodendron cannifolium (Rudge) Engler
M. cannaefolia Kunth = Spathiphyllum cannaefolium (Dryand) Schott
M. cuspidata Gard. = Philodendron propinquum Schott
M. decursiva (Roxb.) Schott = Rhaphidophora decursiva (Roxb.) Schott
M. gigantea (Roxb.) Schott = Epipremnum giganteum (Roxb.) Schott
M. latevaginata Engler & Krause = Scindapsus sp. ?
M. lingulata (L.) Schott = Philodendron lingulatum (L.) C. Koch
M. moritziana (Schott) Steyerm. = Rhodospatha sp.
M. occidentalis (Poepp.) Koch ex Ender = Scindapsus occidentalis Poepp.
M. officinalis (Roxb.) Schott = Scindapsus officinalis (Roxb.) Schott
M. peepla (Roxb.) Schott = Rhaphidophora peepla (Roxb.) Schott
M. pinnata (L.) Schott = Epipremnum pinnatum (L.) Engler
M. roseospadix Matuda = Rhodospatha roseospadix (Matuda) Matuda

NOMINA NUDA:

Monstera calloides Mortiz ex Ender, Index Aroidiarum 53 (1804).
M. glauca C. Koch ex Ender, Index Aroid. 54 (1804).
M. guatemalensis Bartlett, Carnegie Inst. Wash. Pub. 461:17 (1935).
M. haenkei Presl ex Ender, Index Aroid. 54 (1804).
M. inaequilatera Pr. ex Ender, Index Aroid. 54 (1804).
M. multijuga C. Koch ex Ender, Index Aroid. 54 (1804).
M. protensa Schott ex Engler, Flora Brasiliensis III (2):114 (1878).
M. trijuga C. Koch ex Ender, Index Aroid. 55 (1804).