Selbyana 5(3-4): 342-377, 1981

NOTES ON *CALADIUM* (ARACEAE) AND ITS ALLIES

*Michael Madison**

The subfamily Colocasioideae of the Araceae is a group of 15 genera and about 200 species, the majority of which are terrestrial herbs with thick or tuberous stems. Geographically, the genera and species are about equally divided between tropical Asia and the neotropics. The subfamily is defined by a suite of floral features, by the presence of anastomosing laticiferous elements in the vegetative parts of the plant, and by the very distinctive colocasioid venation of the leaves which permits ready recognition of the subfamily even in plants lacking flowers.

The Colocasioideae is economically the most important subfamily of the Araceae, with species of 'elephant ears' (*Colocasia*, *Alocasia* and *Xanthosoma*) widely cultivated in the tropics as food crops. Both leaves and starchy stems are utilized for food for humans as well as for domestic animals. As with many cultivated plants, the classification of these groups is difficult, even at the generic level.

Within the tribe Caladieae, which comprises the non-scandent new world species of Colocasioideae, a 'typical' *Xanthosoma* or *Caladium* is readily identified to genus by its general appearance, but there are a great many atypical species that defy easy identification. This has lead to a dual classification in which specimens are seemingly randomly assigned to a genus, e. g., specimens of a pubescent colocasioid from Peru are about equally likely to be referred to *Caladium pubescens* N.E. Brown or *Xanthosoma pubescens* Poeppig, with no clear basis for the generic assignment. The aim of this study is to clarify the relationships of the genera of Caladieae and to provide descriptive notes on the species, except for species of *Xanthosoma* for which a monograph is in preparation elsewhere (by Sue Thompson).

DESCRIPTION AND HABITAT

The tribe Caladieae is predominantly South American, with only the largest genus, *Xanthosoma*, extending into Central America and Mexico. The center of diversity of *Xanthosoma* is in the Andes, as it is also for *Chlorospatha*. *Caladium* is most diverse and abundant around the margins of the Amazon basin, with plants relatively rare in the central Amazon area. The other genera are of limited distribution.

The Caladieae are strictly tropical; evidently they are intolerant of cool climates, and even near the equator they are rarely found above 1800 m elevation. The local distributions of many Caladieae reflect the availability of permanently wet habitats. Many species of *Xanthosoma* are understory herbs of tropical wet or premontane forest, occurring in the most humid spots. A few species are adapted to higher levels of light, and may be found at forest margins, in roadside ditches, or in open pastures, but always in saturated ground or even in standing or running water. *Chlorospatha*, like *Xanthosoma*, is restricted to wet habitats and often occurs as an emergent aquatic in small streams of the forest understory. *Jasarum* is entirely aquatic, with floating leaves and emergent inflorescences.

In contrast to this first group of genera, *Caladium*, *Aphyllarum* and *Scaphispatha* mostly occur in seasonally dry habitats in savannas, at the margins of gallery forest, or in the understory of semi-deciduous forest. Frequently they are found in spots which are flooded during the rainy season, but dry

* The Marie Selby Botanical Gardens, 800 S. Palm Avenue, Sarasota, Florida 33577, U.S.A.

the rest of the year. In these situations the plants are often leafless during the driest periods, persisting as dormant tubers which will renew growth in the wet season.

VEGETATIVE STRUCTURES

All species of Caladieae are terrestrially rooted herbs with more or less thickened stems, which may be rich in starch. The stems may be erect and sub-arborescent (to 3 m tall and 20 cm thick in *Xanthosoma sagittifolium*) or may consist of a subterranean globose or flattened tuber. In many species stems are dimorphic, with the secondary axes comprising rhizomes which can give rise to new plants at a distance of 10-80 cm from the parent plant. Often a large colony may be derived from a single plant by this type of rhizomatous spread.

In a number of Caladieae, vegetative reproduction is accomplished by lateral buds which develop as small tubers or bulbils and detach from the parent plant. In *Xanthosoma tarapotoense* several axillary buds on the erect, aboveground stem may develop as spherical tubers 1-3 cm in diameter which are easily knocked off the parent trunk. In other Caladieae, bulbils develop from supernumerary axillary buds collateral to or opposite to the normal axillary bud. For example, in *Xanthosma riopalenquense* about 80 collateral buds on each node develop into small pointed bulbils 3-7 mm long. In *X. viviparum* the number of bulbils is 3-400 per node; these are borne on a crescent-shaped patch of tissue opposite to the normal axillary bud, and they are strictly of epidermal origin (personal communication from Jack Fisher). In *X. pubescens* the number of collateral axillary bulbils may reach 8-900 per node, each less than 1 mm in diameter. These readily abcise and are scattered about, soon giving rise to numerous small plantlets. Collateral buds are not uncommon in other Caladieae, but usually they do not form bulbils, instead remaining dormant unless the plant is injured.

In the morphology of their stems, species of Caladieae show close correlations to the habitats in which they occur. Elongate arborescent stems are found predominantly in species inhabiting shady, permanently wet habitats. Growth of the stems is continuous throughout the year, and evidently the stem serves to elevate the crown of leaves above the surrounding terrestrial herb layer to a position of higher light intensity. The pachycaul stems of arborescent species are composed chiefly of parenchymatous tissue lacking in starch; starch is present only in narrow cylinders surrounding the fiber bundles and latex vessels.

The species of Caladieae which are of economic importance because of the high starch content of their stems typically inhabit more or less continuously wet habitats which have a high light intensity, such as wet spots at forest margins, ditches, or pastures. In these species the stems are usually cylindric or fusiform, and while they may protrude above the ground they do not usually become arborescent. More commonly growth of these stems takes the form of a well-developed system of branched rhizomes. This may be interpreted as a modification of the arborescent stem of forest understory species that enables the plants to keep all adventitious roots underground, protecting them from dessication by direct sunlight. Selection by humans for shorter, thicker rhizomes as foodstuffs has perhaps led to the origin of such forms from wild types which have more slender and elongate rhizomes.

Species inhabiting strongly seasonal environments for the most part have globose or flattened tubers 3-10 cm below the surface of the soil, and

they pass the dry season in a leafless, dormant condition. The tubers are high in starch content, which is largely exhausted in the elaboration of new leaves and inflorescences at the beginning of the rainy season. In a few cases, remains of old tubers may persist for 2-3 years, showing clearly the annual increments and the intermittent nature of the stem growth. Offset tubers frequently are produced, which morphologically are equivalent to the thickened rhizomes of the edible species.

INFLORESCENCES AND FLOWERS

Inflorescence morphology is fairly uniform in the Caladieae. The spathe is constricted centrally, dividing it into a lower tube and upper limb which unfurls at anthesis, allowing pollinators access to the spadix. The spadix consists of female flowers at the base, sterile male flowers in the middle part, and fertile male flowers apically. In all genera the male flowers consist of 3-6 stamens united in a synandrium with the thecae opening by terminal pores. The female flowers consist of an ovary lacking both perigon and staminodes. The inflorescences are protogynous, with anthesis of the male flowers occurring a day after anthesis of the female flowers. In *Caladium bicolor* if an inflorescence at anthesis is cut into parts and these are separated, it quickly becomes apparent that the sweet fragrance is produced by the sterile flowers. Whether this is true of other Caladieae is not known.

The shape and morphology of the inflorescence in aroids is intimately related to pollination biology. In the Caladieae the majority of species are pollinated by ruteline scarab beetles which fly to the inflorescence at dusk, presumably attracted by sweet or fruity odors and by the white color of the spathe limb. The beetles are trapped in the spathe tube for 24 hours, and are released the following evening after the sticky pollen is shed. Species of Caladieae pollinated by these beetles show remarkably similar inflorescences in terms of size, color, shape, and relative proportions of female, male and sterile flowers.

Some Caladieae, however, clearly have a different pollination syndrome. This is seen most radically in *Chlorospatha* in which the spathe is long and narrow, opening for only a short distance at the tip. The spathe tube is too small to accommodate the large ruteline scarabs, and flies and small beetles (Scarabidae, Staphylinidae) have been collected in the inflorescences.

Within the rather uniform inflorescence structure of the ruteline-pollinated Caladieae there is considerable variation in the structure of the female flowers. They may be 1-, 2-, 3-, or 4-locular with parietal, axile, or basal placentation, and the stigma may be sessile or elevated on a discoid style which is coherent to the styles of adjacent flowers. Ovules may be solitary or there may be a large number in one ovary.

Traditionally variations in these floral features have been the basis for the generic classification of the Caladieae. However, under close scrutiny they prove to be elusive, and many intermediates are found. For example, the occurrence of a discoid style is difficult to define. In *Xanthosoma robustum* it is clearly evident, and in *Caladium ternatum* it is clearly absent, but a number of intermediate situations occur in which the style is represented by a thickened band of cells different in color or texture from adjacent areas, and this may be so slight as to be barely evident.

There is a correlation of presence of a well-developed discoid style with 3-4 placentae and a large number of ovules in the ovary, and with large flower size (3-4 mm diameter) with the ovary sub-globose. Absence of a discoid

style correlates with slender (0.5-1.5 mm diameter) ovaries with 1-2 placentae, few ovules, and a regular prismatic shape. A possible interpretation of this is that the large number of ovules in a larger ovary in some way leads to a rounded shape to the ovary, thereby creating cracks between adjacent flowers. The function of the discoid style is to bridge these cracks with the result that at anthesis the stigmatic fluid has a smooth and even surface on which to flow freely from one flower to the next, creating in effect a single large stigma in which pollen deposited at one point may flow to other flowers. In those species with slender, prismatic female flowers which are tightly packed for their total height, this result is achieved without a discoid style.

There is a notable modification of the style in species of *Chlorospatha*, which evidently are derived from a *Xanthosoma*-like ancestor with a discoid style but which have a different pollination system. In these the discoid style has been modified from a rather tough, rubbery tissue to a delicate spreading structure only 1-2 cell layers thick which quickly deliquesces at anthesis. In some species in which the female flowers are widely spaced, the style may be three times the diameter of the ovary, thereby still maintaining contact with the styles of adjacent flowers. How these function in pollination is not known.

Placentation is another floral feature that is not always well defined. For example, in *Xanthosoma robustum* a cross section near the apex of the ovary shows 4 intrusive parietal placentae in a unilocular ovary, while in a cross section near the base of the ovary the intrusive placentae have coalesced, presenting a 4-locular ovary with axile placentation. Another source of difficulty is exemplified by *Xanthosoma striatipes*, in which 2-, 3-, and 4-locular ovaries may be found within a single inflorescence.

In terms of its adaptive importance, the aspect of placentation that is significant in the aroids probably is its correlation with seed size. When seeds are large, we find a unilocular ovary with basal placentation; intermediate size seeds frequently occur in a unilocular ovary with two or three parietal placentae, and numerous tiny seeds occur in multilocular ovaries with axile placentation. This pattern is repeated, with some variations, in the subfamilies Monsteroideae, Lasioideae, Philodendroideae and Colocasioideae. The functional basis for these correlations probably has to do with the mechanics of fitting various numbers and sizes of seeds into a limited ovarian space.

In the Caladieae species of *Xanthosoma* mostly have multilocular ovaries with numerous ovules, developing into berries with an abundance of tiny seeds. These plants inhabit continuously wet habitats in which seed dormancy is not a requirement, and many of them have pronounced weedy tendencies of which copious production of small seeds is one feature. At the other extreme we have *Scaphispatha*, *Aphyllarum* and *Caladium ternatum* with unilocular ovaries giving rise to a single large seed. These are plants inhabiting regions with an extended dry season for which large seeds capable of a period of dormancy and rapid growth at the onset of rains are evidently well adapted.

POLLEN

In *Xanthosoma* pollen grains are inaperturate, smooth to slightly scabrous, ca. 30 μ broad, and are shed and transported in tetragonal tetrads. *Chlorospatha* species have similar pollen, also borne in tetragonal tetrads, but the grains are smaller (ca. 15-20 μ). *Caladium*, *Aphyllarum*, *Scaphispatha* and *Jasarum* have smooth or verruculose inaperturate solitary pollen grains 34-40

μ long. There is thus a correlation of pollen in tetrads with multi-ovulate ovaries and solitary pollen grains with few-ovuled ovaries. Pollen grains of Caladieae are starch-filled, as in other Colocasioideae.

GENERIC CLASSIFICATION

Ideally a generic classification will reflect the natural relationships of the species while being based on characters that allow for ready generic identification of specimens. In order to construct such a classification it is helpful to have some hypotheses about evolutionary relationships within the group.

While other interpretations are possible for the Caladieae, I will assume that the ancestral form of the group was ruteline beetle-pollinated and inhabited the understory of wet forests where growth was nearly continuous throughout the year, leading to elongate stems that are parenchymatous but not especially rich in starch. From this putative ancestral form, three main evolutionary trends may be identified.

One involves colonization of continuously wet habitats with high light intensities, e.g. wet ditches, forest margins, and streams in savannas. Morphologically this habitat shift is associated with elaboration of underground rhizome systems high in starch content and with multiocular ovaries containing numerous seeds as one component of a syndrome of weediness. These species are the ancestors from which the cultivated edible Caladieae are derived.

A second evolutionary trend involves a change in pollination system away from ruteline scarabs, leading to a considerable modification of inflorescence morphology and in some cases a loss of floral fragrances. This group (*Chlorospatha* spp.) has retained the mesic forest understory habitat and subarborescent stems of the primitive form.

The third evolutionary trend involves species that have colonized seasonally dry habitats to the south and east of the Andes. These species have subterranean tuberous stems high in starch content reflecting their intermittent growth and protracted dry season dormancy. Increase in seed size has been selected for a shift from axile to parietal or basal placentation, leading to changes in ovary structure such as reduction in the numbers of placentae and ovules, and reduction or loss of the discoid style. From this group a further evolutionary line encompasses invasion of the aquatic habitat (*Jasarum*).

These evolutionary trends are not limited to single phyletic lines, but they may have occurred repeatedly. For example, colonization of intermittently dry habitats with associated reduction in seed number is seen independently in *Aphyllarum*, *Scaphispatha*, and *Caladium ternatum*. Evolution of deeply buried tuberous stems is not limited to this group but also occurs in some species of *Xanthosoma* sect. *Acontias*.

Consideration of the correlations and discontinuities in the occurrence of morphological characters in the Caladieae in relation to the proposed evolutionary scheme indicates that four small genera, *Aphyllarum*, *Scaphispatha*, *Jasarum*, and *Chlorospatha* are evolutionarily distinct entities which are easily recognized. The remaining fifty or so species form a field of more or less continuous variation.

There are several ways to deal with this remaining group of species. One is to unite them into a single diverse genus, as suggested by Crisci (1971), and compelling arguments can be made for such an action. However, this ap-

proach produces a result inconsistent with the generic classification of the rest of the family in that it unites in one genus elements with very diverse floral structures. Further, since both *Caladium* and *Xanthosoma* are economically important with a large corpus of published literature about them, it is particularly distasteful and impractical to alter their generic names.

The alternative is to recognize two or more genera in this group. Schott (1858) divided the group into three genera of about equal size (*Caladium*, *Acontias*, and *Xanthosoma*), while Engler (1879) united *Xanthosoma* and *Acontias*, resulting in a small genus, *Caladium*, and a large one, *Xanthosoma*. In whatever manner the division is made, intermediates will remain that must be more or less arbitrarily assigned to one genus or the other. Nonetheless, division of these species into two genera, *Caladium* and *Xanthosoma*, seems to be both most practical and to reflect the evolutionary structure of the group. The single inflexible character separating them is the shedding of pollen in tetrads in *Xanthosoma* and in solitary grains in *Caladium*.

A more exact resolution of the generic difficulties in the group must depend on the discovery and evaluation of new characters, either anatomical, biochemical, or cytological. Cytological studies in progress by Mark Moffler indicate a diversity of chromosome numbers and numerous instances of polyploidy in the Caladieae, a situation not suprising in view of the taxonomic difficulty of the group.

Acknowledgments

This treatment is based on field studies in tropical America, herbarium studies, and examination of 22 species of Caladieae cultivated at the Marie Selby Botanical Gardens. Herbarium species were kindly lent from the following institutions: MO, F, NY, UC, US, K, U, VEN, P, and M. Living plants and photographs were supplied by J. Bogner, T. Plowman, L. Besse, H. Luther, E. Spear, C. H. Dodson, M. Birdsey, and T. Fennell.

TAXONOMIC TREATMENT

Tribe Caladieae Engler, Nova. Acta. Acad. Caes. Leop.-Carol. German. Nat. Cur. 39. 149. 1877.

Terrestrial herbs of the neotropics. Stem tuberous, creeping, or arborescent, often with a ramifying system of rhizomes, and frequently with supernumerary or adventitious axillary buds at the nodes. Leaves entire or pedatisect, lacking pulvini, with a collecting vein running between and parallel to each pair of primary lateral veins. Inflorescences terminal, solitary or in monochasia, the spathe constricted centrally to form a tube below and a free limb above. Spadix in three parts with naked female flowers basally, sterile synandrodia centrally, and male flowers comprising synandria of 3-6 stamens apically; the pollen starchy, shed in sticky threads through terminal pores of the thecae. Fruit a white or colored berry, the seeds ovoid, white, with endosperm surrounding an axile embryo.

Key to the genera:

1. Submerged aquatic plant ..... *Jasarum*
1. Emergent semi-aquatic, or terrestrial
   2. Spathe tube narrow and elongate, female part of the spadix mostly adnate to the spathe; female flowers with a thin, mantle-like style ... . *Chlorospatha*

2. Spathe tube sub-globose, female part of the spadix mostly free from the spathe; female flowers lacking a style or if style is present not thin and spreading
   3. Ovary with 3-4 placentae and 20-100 ovules; discoid style usually present: pollen in tetrads ..... *Xanthosoma*
   3. Ovary with 1-2 placentae and 1-20 ovules; discoid style lacking; pollen grains solitary
      4. Placentation parietal, placentae 2, seeds several .... *Caladium*
      4. Placentation basal or sub-basal, placenta one, seed solitary
         5. Sterile flowers lacking, ovary with a narrow style .... *Scaphispatha*
         5. Sterile flowers present between female and male flowers, ovary without a narrow style ..... *Aphyllarum*

Jasarum Bunting, Acta Bot. Venez. 10:264 (1975)

Type species: *Jasarum steyermarkii* Bunting

Submerged aquatic with creeping rhizomatous stems anchored by thick roots. Petioles fleshy, lamina elongate, translucent, thin, floating, with numerous lateral veins; bullate between the veins. Inflorescence emergent, the spathe slightly constricted, spadix with female flowers basally consisting of unilocular ovaries with two basal ovules, capped by a sessile stigma; synandrodia separating male and female flowers; male flowers comprising synandria of four stamens.

Etymology: *JAS*, the initials of Julian A. Steyermark, collector of the type, and *-arum*, an aroid.

Only one species is known:

1. **Jasarum steyermarkii** Bunting

Jasaurm steyermarkii Bunting, Acta Bot. Venez. 10:264, 1975.

Type: Venezuela: Bolivar: km 201.9 of Carretera El Dorado-Santo Elena, elev. 1200-1400 m, 19-22 Feb. 1971, *Steyermark et al. 105500* (VEN).

Submerged herb, each shoot with 6-12 leaves, connected to adjacent shoots by creeping rhizomes, the rhizomes ca. 1.7 cm thick, white in the cortex, yellow in the center, giving rise to numerous thick, white roots 0.6-0.8 cm in diameter. Petiole succulent, 25-35 cm long, vaginate in lower 2/3, subterete and about 0.5 mm thick in upper third. Lamina membranaceous and translucent but firm, dark green, linear, 28-32 cm long, 1.6-2.2 cm wide, bullate-undulate between the primary lateral veins which number 35-50 pairs per leaf, collecting veins along the margin two. Peduncle dark green, to 60 cm long, emergent. Spathe ca. 15.5 cm long, purplish-green at the base, yellowish white above, terminating in a tubular process ('vorleuferspitze') ca. 1.5 cm long. Spadix sessile, 7.5-9 cm long, female portion yellow, 2.5-3 cm long and 0.7-0.9 cm thick, sterile portion cream colored, 0.5-2.0 cm long and ca. 0.5 cm thick; fertile male portion cream or purplish colored, ca. 3.5-5 cm long and 0.6 cm thick, obtuse, fertile synandria 4-5-6-sided, prismatic, ca. 2-3 mm wide. Spathe limb and upper part of spadix deciduous after anthesis, the lower spathe tube persisting. Berries purplish green, irregularly sub-globose, ca. 1.5 cm in diameter with one or two ovoid seeds ca. 0.7 cm long and 0.5 cm thick.

Additional collections seen. Venezuela: Bolivar: km 204 Carretera El Dorado-Sta. Elena, Aug. 1972, *Blanco 1544* (VEN); km 189, Dec. 1974 *Steyermark 111311* (US); Guyana: Upper Mazaruni River Basin, Kako River, 10 hours above mouth, elev. 500 m, 1960, *Tillett & Tillett 45527* (NY, US).

With its thin, linear leaves and aquatic habit *Jasarum* is an unusual and easily recognized member of the Caladieae. In its morphology it shows similarities to *Xanthosoma striatipes* and to *Aphyllarum tuberosum*, two species adapted to tolerate drought. However, during their growing season these plants inhabit vernal pools and similar temporarily flooded localities, and thus the evolution of a completely aquatic form from an ancestor similar to these two is not unreasonable.

Jasarum steyermarkii has the largest seeds of the Caladieae, though their dispersal biology and even whether they float or sink is not known. However, the occurrence of the species in two independent river systems indicates that it is capable of overland dispersal.

Chlorospatha Engler, Gartenflora 27:97, 1878.

Type species: *Chlorospatha kolbii* Engler
Synonym: *Caladiopsis* Engler, Bot. Jahrb. Syst. 37:139, 1905.
Type species: *Caladiopsis lehmannii* Engler

Terrestrial herbs of the forest understory. Stem cylindric, elongate, erect or creeping. Leaves erect, sagittate, hastate, or pedatisect, usually with two collecting veins parallel to the margins. Inflorescences in monochasis of 4-8, the peduncles slender and weak, 1.5-3 mm thick. Spathe tube narrow and elongate, less than 1 cm in diameter. Female part of the spadix adnate to the spathe or not, female flowers loosely spaced, 3-4-locular with axile placentation (rarely one-locular with 2-3 intrusive parietal placentae), ovules few per loculus, the ovary with a thin, spreading style usually containing numerous red chromoplasts. Synandrodia irregular or fungiform, not prismatic. Synandria of 3-5 stamens, subprismatic with sinuate margins. Pollen borne in tetragonal tetrads.

Etymology: From Gr. *chloro-*, 'green,' and *spatha*, 'spathe,' referring to the spathe of *C. kolbii.*

Chlorospatha includes ten known species of terrestrial herbs native to wet middle elevation forest of the northern Andes. Most are of small size with arborescent or creeping cylindric stems 1-3 cm thick. The genus is most closely related to *Xanthosoma* from which it differs in its pollination biology and hence in its floral and inflorescence structure. The most notable features are the weak, elongate, slender peduncles less than 3 mm thick, the very narrow and elongate spathe tubes which often are longer than the spathe limb, and the widely spaced female flowers which have a thin, deliquescent spreading style that contains numerous red chromoplasts. The sterile flowers are widely spaced and irregular or fungiform in shape rather than prismatic as in other Caladieae.

Although *Caladiopsis* Engler is a more commonly used name for these species, *Chlorospatha* is an earlier legitimate name and so must be used. Several of the species are quite handsome, with deep purple velvety leaves, but they perform poorly in cultivation and are not likely to become useful ornamentals.

Key to species of *Chlorospatha* Engler:

1. Leaf compound, trifoliate or pedate, often with scattered pale spots
   2. Leaf pedate with 5-11 parts, margin undulate ..... *C. kolbii*
   2. Leaf ternate with regular margins ..... *C. mirabilis*
1. Leaf hastate or sagittate, not compound, lacking pale spots
   3. Male flowers bright orange
      4. Leaf hastate to nearly trifid with pointed lobes; spadix 6-10 cm long ..... *C. dodsonii*
      4. Leaf cordate with rounded posterior lobes; spadix 3-4 cm long ..... *C. besseae*
   3. Male flowers cream colored
      5. Female part of the spadix mostly free from the spathe
         6. Peduncle 3-7 cm long ..... *C. longipoda*
         6. Peduncle 10-55 cm long
            7. Female flowers orange with a narrow style; leaves deep purple below ..... *C. atropurpurea*
            7. Female flowers greenish or white, lacking a style; leaves chiefly green.
               8. Petiole 25-35 cm long, peduncle 10-16 cm long, leaf dull ..... *C. cutucuensis*
               8. Petiole 80-100 cm long, peduncle 30-50 cm long, leaf shiny ..... *C. ilensis*
      5. Female part of the spadix adnate to the spathe
         9. Spathe tube purple; stigma sessile ..... *C. castula*
         9. Spathe tube green; stigma elevated on a narrow style ..... *C. lehmannii*

2. **Chlorospatha kolbii** Engler

Chlorospatha kolbii Engler, Gartenflora 27:98, 1878.

Type: Colombia, no specific locality, collected by Wallis and cultivated at Munich botanical garden but lost some time after 1879. The illustration in Gartenflora 27: t. 933, serves as the type.

Terrestrial herb. Cataphylls 5-10 cm long, 1-1.5 cm wide, rose colored. Leaf erect, the petiole ca. 30 cm long, 4-5 mm in diameter at the base, vaginate in the lower third, brownish- or purplish-variegated; lamina pedatisect, 7-9 parted, velvety deep green above, pale below, with crispate-undulate margins, the central segment 8-10 cm long and ca. 3 cm broad, the lateral segments somewhat smaller. Inflorescences several produced together, borne on very slender weak peduncles ca. 16 cm long which are enclosed by the sheath. Spathe green, 7-8 cm long, the tube 4 mm in diameter, the tube and the limb hardly distinguished by a constriction. Spadix stipitate by 1.5 cm, ca. 0.5 cm thick, the female part 2 cm long, adnate to the spathe, the female flowers scattered, sub-hemispherical with 2-3 deeply intrusive parietal placentae, the style disc-like, adherent to the ovary and narrower than the ovary, the stigma yellowish, 3-lobed. Sterile part of the spadix ca. 1 cm long, the synandrodia of 3-4 stamens obturbinate or lobed; male part of the spadix ca. 3 cm long; synandria truncate, comprising 3-5 stamens, the pollen shed in threads through pores.

Etymology: Named for Herr Kolb, Inspector of Munich Botanical Gardens in the 1870's.

Additional material examined: South America, cult. at Hort. Bull, Sept. 1878 (K).

The only feature separating the genus *Chlorospatha*, of which this is the type, from *Caladiopsis* is its pedate rather than trifoliate, hastate, or sagittate leaf. This is hardly adequate grounds for maintenance of a separate genus, and so the two have been combined.

Chlorospatha kolbii remains poorly known. The Kew specimen consists of a leaf only, and while it quite possibly is part of Wallis's collection, there is no way to be certain of this. So far as I know, the species has not been collected in the last hundred years, unless material of it lies somewhere misdetermined as *Xanthosoma flavomaculata*, a more common species which it somewhat resembles vegetatively.

3. Chlorospatha mirabilis (M. T. Mast.) Madison

Chlorospatha mirabilis (M. T. Mast.) Madison, comb. nov.
Synonym: *Xanthosoma mirable* M. T. Mast., Gard. Chron. 1874:258.

Type: Tropical South America: Roezl s.n., cultivated by nurserymen Carter and Bull, and at Kew. The illustration in *Gardener's Chronicle* (1874, p. 259, Fig. 54) serves as the type.

Stem initially subterranean, possibly becoming arborescent. Leaves several, erect, the petioles to 80 cm long and purplish at the base with a glaucous bloom, vaginate for 1/3 to 1/2 their length; lamina trifoliate, the lobes 20-30 cm long, the central lobe ovate, ca. 12 cm broad with 6 primary lateral veins per side, the lateral lobes asymmetric, about 8 cm broad with the inner side of the lamina narrowly attenuate at the base and the outer side broadly curved-truncate, the lamina decorated with scattered cream-colored spots. Inflorescences several at a node, the peduncle slender, 1-2 mm thick and ca. 30 cm long. Spathe narrow, the tube purplish, ca. 4.5 cm long and 9 mm in diameter, the limb cream, ca. 2 cm long. Female flowers purple with a pink thin style, female part of the spadix 2 cm long and 3 mm thick; sterile flowers greenish, the sterile part of the spadix 1.5 cm long and 2.5 mm thick; fertile male flowers cream, the male part of the spadix ca. 1.8 cm long and 4 mm thick.

Additional material examined: Colombia: sent by Kalbreyer to Hort. Veitch, Specimen prepared anonymously April, 1882, (K); Peru: sent by Forget to Sander & Sons, specimen prepared Dec. 1913 (K).

At the time this species was discovered the genus *Chlorospatha* had not yet been described, and in his comments on the species the author noted that it did not readily fit into *Xanthosoma*, *Caladium*, and *Acontias*. However, rather than describe a new genus, he placed it in *Xanthosoma* with a question mark. The species is clearly a *Chlorospatha* as evident by the long and very slender peduncles, the narrow spathe tube that is longer than the spathe limb, the thin style containing red chromoplasts, and the non-prismatic, scattered, sterile flowers.

Chlorospatha mirabilis is readily distinguished from other species of the genus by its fully trifoliate leaves marked by scattered yellowish or cream spots. What may be this species has recently been reintroduced into cultivation in the Miami area from Colombia by E. Spear, but it has not yet flowered. The specimen at Kew indicating collection of the plant by Forget in Peru is probably in error, and the species should tentatively be regarded as a Colombian endemic.

4. Chlorospatha dodsonii (Bunting) Madison

Chlorospatha dodsonii (Bunting) Madison, comb. nov.
Caladiopsis dodsonii Bunting, Ann. Missouri Bot. Gard. 50:28. 1963.

Type: Ecuador: Pichincha: along Rio Baba 28 km S of Santo Domingo, elev. 350 m, Nov. 1961, Dodson & Thien 1190 (MO).

Terrestrial herb, the stem cylindric, erect, 2-4 cm thick, to 25 cm tall. Cataphylls green, thin, 10-15 cm long. Leaf erect, the petiole green or purplish, 30-50 cm long, vaginate for 1/2-2/3 its length. Lamina hastate to nearly trifoliate, dull medium green with a slightly wrinkled texture, the central lobe 18-25 cm long, 12-15 cm broad, acuminate at the apex, the lateral lobe 10-18 cm long, 5-8 cm wide, the two lateral costae denudate for ca. 1 cm at the base on the outside. Inflorescence held in the leaf sheath, peduncle 2-3 mm thick, 35-45 cm long. Spathe tube greenish, limb yellow-cream, spathe 11-15 cm long, tube 4-6 mm in diameter. Spadix slightly shorter than the spathe, the female part mostly or entirely adnate to the spathe 3-5 cm long, the female flowers cream with a narrow style 1-2 mm long. Sterile flowers in one or two whorls only, cream. Staminate part of the spadix 4-5 cm long, 3-4 mm in diameter, bright orange, the male flowers 3-4-5-androus with sinuate margins. Spadix in fruit nutant, with the spathe tube persistent.

Additional collections seen: Ecuador: Pichincha: near Alluriquin, elev. 900 m, March 1978, *Madison 4015* (SEL); La Centinela, elev. 600 m, Aug. 1977, *Dodson & Dodson 6755* (SEL); km 3 W of bypass around Santo Domingo, July 1979, *Dodson et al. 8530* (SEL); Esmeraldas: environs of Lita, elev. 550-560 m, June 1978, *Madison et al. 5065* (SEL).

Etymology: Named for C. H. Dodson, one of the collectors of the type.

Chlorospatha dodsonii is readily distinguished by the bright orange male flowers, the narrow styles of the female flowers, and the hastate to nearly trilobed leaves. The sterile flowers are few in number, or in some collections are lacking. The species is not uncommon in the remaining forest in the general region of Santo Domingo de los Colorados, Prov. Pichincha, Ecuador.

5. Chlorospatha besseae Madison

Chlorospatha besseae Madison, sp. nov.

Type: Ecuador: Esmeraldas: environs of Lita, wet submontane forest, elev. 550-650 m, June 1978, *Madison, Plowman, Kennedy & Besse 5144* (Holotype: SEL; Isotypes: QCA, F, K).

Terrestrial herb. Stem green or brown, carnose, cylindric, erect, 1-1.5 cm thick, to 30 cm tall, the internodes 2-3 cm long. Leaves several, erect, the petiole 20-28 cm long, vaginate for about one-half its length, lamina dark velvety green to medium green above, pale green below, sagittate, the central lobe 12-28 cm long, 12-16 cm broad, the posterior lobes short, blunt, 2-3 cm long. Peduncle 1-1.5 mm thick, 12-16 cm long, held by the sheath. Spathe tube green, limb cream, total length ca. 6 cm. Spadix 3.5-5 cm long, 2-3 mm thick, the female part ca. 2 cm long, completely adnate to the spathe, the female flowers white with a rose-colored discoid style, the sterile flowers resembling the male flowers but lacking pollen. Male part of the spadix ca. 2.5 cm long, bright orange, the synandria of 3-5 stamens, turning deep red if cut.

Additional collection: Ecuador: Carchi: El Pailon, ca. 45 km below Maldonado, wet montane forest, elev. 800 m, Dec. 1979, *Madison & Besse 7279* (SEL, QCA).

Etymology: *Chlorospatha besseae* is named for Elizabeth Besse, one of the collectors of the type and paratype.

Chlorospatha besseae is native to wet montane or premontane forests of western Ecuador where it forms small colonies in dark creekbeds or other muddy or boggy spots in the forest understory. Vegetatively it resembles the sympatric species *Xanthosoma daguense*, differing considerably, however, in floral structure. It is one of the smallest species of the genus, and is readily distinguished by the short, blunt posterior lobes of the leaf and by the tiny inflorescences with bright orange staminate flowers.

6. Chlorospatha longipoda (K. Krause) Madison

Chlorospatha longipoda (K. Krause) Madison, comb. nov.

Caladium longipidum K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 15:43. 1940.

Type: Ecuador: Pastaza: Rio Topo, elev. 1200 m, July 1938, *Schultze-Rhonhof 2591* (B, non vidi, photo SEL).

Caladium plowmanii Madison, Phytologia 35:104. 1976.

Type: Ecuador; Napo: 31 mi W of Lago Agrio on the road to Baeza, elev. 700 m, *Plowman et al. 3979* (GH, P. MO).

Terrestrial herb, the stem elongate, green ca. 1 cm thick, the internodes ca. 1 cm long, the stem repent, erect at the apex. Leaves erect or spreading the petiole 10-26 cm long, sheathing in the lower one-quarter. Lamina sagittate or hastate, the base only slightly lobed and nearly truncate to strongly hastate with the posterior lobes as long as the anterior lobe but narrower, the lamina 12-20 cm long, 6-12 cm broad, velvety dark green above, pale below, the marginal veins 3, the innermost ca. 6 mm from the margin. Inflorescences several at a node, the peduncle 3-7 cm long, ca. 1 mm in diameter; spathe tube green, 1-2 cm long and 3 mm in diameter, the limb yellowish or purplish green, 3-6 cm long and 8-12 mm broad. Female part of the spadix ca. 1 cm long, partly adnate to the spathe, the female flowers flattened, unilocular with a basal placenta; sterile flowers in 2-3 whorls, irregularly prismatic; staminate flowers 3-, rarely 4-androus, cream colored, the male part of the spadix 2-4 cm long.

Additional collections seen: Ecuador: Morona-Santiago: Cord. de Cutucú, about 25 km SE of Logroño, elev. 800 m, Jan. 1976, *Madison & Coleman 2567* (SEL, QCA): same locality, Nov. 1976, *Madison et al. 3357* (SEL, QCA, US).

Etymology: From Latin *longus*, 'long,' and Gr. *podus*, 'foot,' referring to the elongate stem.

In its phylogeny the Caladieae includes various parallel evolutionary lines encompassing a greater complexity than is evident in the generic classification proposed here. *Chlorospatha longipoda* is a case in point; in the structure of the ovary it technically belongs with *Caladium*, yet in the totality of its features it shows greatest affinity to *Chlorospatha*.

In *Chlorospatha longipoda* the discoid style is fused to the ovary rather

than free as in most other species of the genus. The ovary is unilocular with a basal placental ring derived from two carpels, at odds with the trilocular ovaries and axile placentation of other species of the genus. However, *Chlorospatha castula*, with a tricarpellate, semi-unilocular ovary and basal placentation that clearly derives from an axile condition constitutes an intermediate link.

In terms of its other features *Chlorospatha longipoda* fits much better with *Chlorospatha* than with *Caladium*. The wet montane forest habitat, the elongate stem and velvety deep green sagittate leaves are typical *Chlorospatha* characters, as are the minute, odorless inflorescences borne on extremely slender and weak peduncles. The shedding of pollen in tetragonal tetrads further confirms this generic assignment.

7. Chlorospatha atropurpurea (Madison) Madison

Chlorospatha atropurpurea (Madison) Madison, comb. nov.

Caladiopsis atropurpurea Madison, Contr. Gray Herb. 208:97. 1978.

Type: Ecuador: Los Rios: Rio Palenque Science Center, elev. 150-220 m, Aug. 1975, *Dodson 5911* (SEL, MO, RPSC).

Terrestrial herb, the stem erect, fleshy, 3-4 cm thick, to 50 cm tall, producing pointed bulbils 0.5-2 cm long here and there along its length. Cataphylls 10-15 cm long, purple, marcescent. Petiole deep purple, 50-80 cm long, 1-3 cm thick at the base, vaginate for 1/3-2/3 its length. Lamina glabrous, deep velvety green above, deep purple over all or most of the lower surface, sagittate, 35-40 cm long, 18-22 cm broad, the central lobe 25-30 cm long, the lateral lobes 15-18 cm long, their costae denudate for ca. 3 cm on the outer side at the base. Peduncle weak, terete, 1-2 mm thick, 25-55 cm long, cream colored, held within the sheath. Spathe cucullate, 10-12 cm long, the tube greenish to cream, the limb cream, opening at anthesis only by a narrow slit 2-3 cm long at the apex. Female part of the spadix ca. 2.5 cm long, the ovaries orange; sterile part of the spadix ca. 2 cm long with purple fungiform flowers; staminate part cream, 1.8 cm long.

Additional collection: Ecuador: Esmeraldas: environs of Lita, elev. 550-650 m, June 1978, *Madison et al. 5054* (SEL, QCA).

Etymology: Latin *atropurpurea*, 'dark purple,' referring to the abaxial surface of the leaf.

Chlorospatha atropurpurea is readily distinguished by its deep purple leaves and orange female flowers. It is a strikingly attractive plant, but performs poorly in cultivation.

8. Chlorospatha cutucuensis Madison

Chlorospatha cutucuensis Madison, sp. nov.

Type: Ecuador: Morona-Santiago: Cordillera de Cutucú, ca. 25 km SE of Logroño, elev. ca. 700 m, coll. 1976, cult. at SEL, flowered in cult. May 1979, *Madison 6944* (Holotype: SEL; Isotypes: QCA, F, K).

Species floribus femineis dense aggregatis et disco styli parvo a congeneribus diversa.

Terrestrial herb, the stems 1-2 cm thick, erect, cylindric, to 22 cm tall, clothed in marcescent remains of leaf bases, the internodes 1.5-3 cm long.

Leaves 2-3, the petiole erect, the lamina horizontal or drooping, the petiole 25-35 cm long, sheathing for ca. 2/3 its length, medium green or rose; the lamina sagittate to hastate, medium dull green above, pale below, 12-22 cm long, 7-14 cm broad, the primary lateral veins ca. 6 in number. Inflorescences 2-4 per monochasium, the peduncle 10-16 cm long, ca. 2 mm thick, the spathe 6-8 cm long, the tube pale green, ca. 2.5 cm long and 6-8 mm thick, the limb cream, cuspidate. Female part of the spadix pale yellow, ca. 2 cm long and 3-4 mm thick, the female flowers narrowed above, ca. 0.8 mm in diameter and 1.2 mm tall, a collar-like disc surrounding the narrow style, (2-) 3-4 locular with 4-6 ovules per loculus. Sterile flowers in 2 whorls only, cream; male part of the spadix ca. 4 cm long, 3-4 mm thick, white, the male flowers 3-4-androus, the pollen in tetrads. Berries white, ca. 3 mm in diameter, with 3-5 seeds per berry, the seeds 1.5 mm long, ovoid, striate.

Additional collection: Ecuador: Morona-Santiago: Cordillera de Cutucú, ca. 28 km SE of Logroño, elev. 1600-1800 m, Nov. 1976, *Madison et al. 3530* (SEL, US).

Etymology: The name refers to the Cordillera de Cutucú, where the species is native.

In this species, one of two found on the eastern slopes of the Andes, the discoid part of the style is of small diameter and is fused to the ovary, but morphologically it is still identifiable by its texture and abundant red chromoplasts. The female flowers are more closely crowded together than in other species of *Chlorospatha*, and in this feature and the large pollen tetrads the species is somewhat closer to *Xanthosoma*. Nonetheless, in the totality of its characters it seems best placed with *Chlorospatha*, though it extends the concept of that genus.

It is notable that although there are 12-16 ovules per ovary in *Chlorospatha cutucuensis*, the berries are mostly 3-seeded, or sometimes 4-5-seeded. This situation is suggestive of recent evolution toward increased seed size/decreased seed number, a situation found in also in *Caladium*, *Scaphispatha*, *Aphyllarum* and other Caladieae.

9. Chlorospatha ilensis Madison

Chlorospatha ilensis Madison, sp. nov.

Type: Ecuador: Pichincha: Montañas de Ila (La Centinela), elev. 600 m, *Dodson, Gentry & Duke 7547* (Holotype: SEL; Isotypes: MO, RPSC).

Species a *C. dodsonii* et *C. atropurpurea* foliis nitidis, stigmate sessili dignoscenda.

Terrestrial herb, the stem 3-4 cm thick, cylindric, brown, to 24 cm tall, clothed with marcescent remains of cataphylls to 20 cm long. Petiole to 1 m long, sheathing in the lower ¼-½, purple-punctate at the base, solid dark purple for most of the length, green apically, with a glaucous bloom. Lamina hastate, nearly trifoliate, the three lobes each held horizontal-arching from the petiole, shiny medium green above, shiny pale green below, the central lobe 20-30 cm long and 12-16 cm wide, the lateral lobes 17-26 cm long, 7-10 cm wide. Inflorescences 5-6 per monochasium, erect, the peduncle 1-2 mm thick, weak, held in the leaf sheath, 30-52 cm long; spathe green, cream at the tip, 9-12 cm long, the tube ca. 6 mm in diameter. Female part of the spadix 4-5 cm long, adnate to the spathe for less than half its length, the female flowers cylindric with a yellow-green discoid style and sessile, white stigma;

sterile flowers comprising ca. 1 cm of the spadix, prismatic, cream-colored; male part of the spadix 3-4 cm long, ca. 6 mm thick in the center tapering to the tip, male flowers cream, subprismatic, 3-5-androus.

Additional collection: Ecuador: El Oro: 11 km W of Piñas on new road to Santa Rosa, elev. 850 m, Oct. 1979, *Dodson, Gentry & Schupp 9135* (SEL, MO).

Etymology: Named for Montañas de Ila, the type locality.

This species was first collected at La Centinela, Montañas de Ila, a region noted for a high level of endemism. It occurs there together with *Chlorospatha dodsonii*, with no evidence of hybridization. The second locality, in El Oro province, represents the southernmost range of the genus.

Chlorospatha ilensis is a robust species, standing more than a meter tall. It is distinguished by the shiny texture of the nearly trifoliate leaves and by the large inflorescences lacking the bright colors that characterize other *Chlorospatha* species. From *C. dodsonii* and *C. atropurpurea* it differs by the cylindric ovaries truncate at the apex, with no indication of a narrowed style.

10. Chlorospatha castula (Madison) Madison

Chlorospatha castula (Madison) Madison, comb. nov.

Caladiopsis castula Madison, Contr. Gray Herb. 208:98. 1978.

Type: Ecuador: Pichincha: vicinity of Chiriboga, wet montane forest, elev. 1200 m, *Madison 4141* (Holotype: SEL; Isotypes: QCA, K).

Terrestrial herb, the stem erect, fleshy, 2-4 cm thick, to 50 cm tall, giving rise along its length to scattered bulbils ca. 1 cm long. Cataphylls triangular, 8-11 cm long, marcescent. Petiole 35-50 cm long, 6-10 mm thick, purple punctulate, vaginate for about one half its length. Lamina glabrous, deep green above, green with purplish veins below, sagittate, 25-35 cm long, 7-11 cm wide, the anterior lobe 16-20 cm long, the posterior lobes 12-15 cm long, their costae denudate at the base on the outer side for 1-1.5 cm. Peduncles terete, weak, 1-2 mm thick, 25-35 cm long. Spathe cucullate, 7-8 cm long, the tube dark purple, the lamina cream, hardly opening. Female part of the spadix adnate to the spathe, ca. 1.7.cm long, white, the discoid part of the style ca. 3 mm broad and spreading beyond the ovary walls, deliquescing at anthesis. Sterile part of the spadix ca. 1 cm long, the flowers fungiform, cream with purple margins. Male part of the spadix cream, 2.2 cm long.

Additional collection: Ecuador: Carchi: Peñas Blancas, 20 km below Maldonado, elev. 900 m, May 1978, *Madison et al. 4596* (SEL, MO, QCA).

Etymology: Latin *castula*, 'petticoat,' referring to the spreading style which covers the ovary.

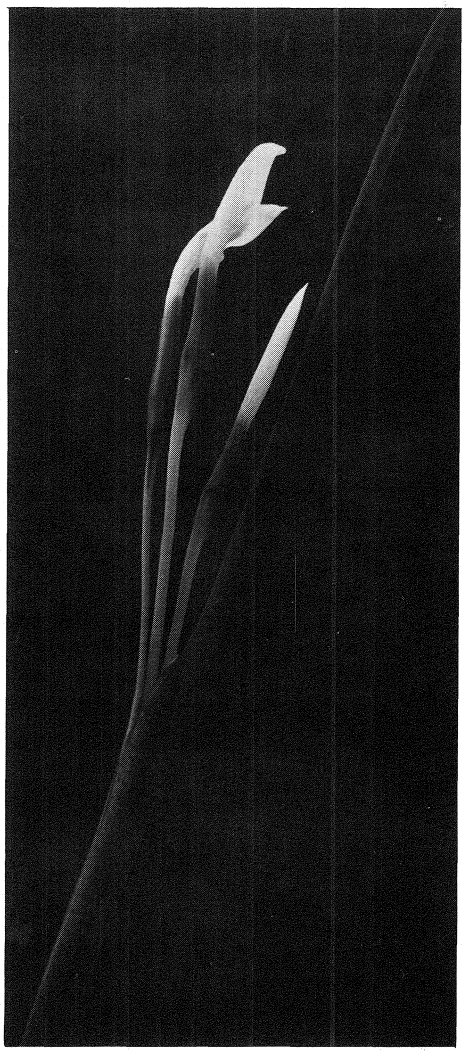
Chlorospatha castula is distinguished by the purple spathe tube and by the extreme development of the stylar disc, which is up to three times the diameter of the ovary.

11. Chlorospatha lehmannii (Engler) Madison

Chlorospatha lehmannii (Engler) Madison, comb. nov.

Caladiopsis lehmannii Engler, Bot. Jahrb. Syst. 37:140. 1905.

Type: Colombia: Cauca: thick rain forest west of Popayan, elev. 1500-1800 m, *Lehmann 5315* (B, non vidi, Isotypes: K, F).



Chlorospatha castula - inflorescence

Terrestrial herb to 0.8 m tall. Stem 2-3 cm thick, erect, to 15 cm tall, clothed in marcescent cataphylls to 15 cm long. Petiole 30-50 cm long, vaginate for ¼ to ½ its length; lamina velvety deep green, elegantly sagittate, the anterior lobe narrowly triangular, to 18 cm long and 6 cm wide, the posterior lobes 7-10 cm long and 1.5-3 cm wide. Peduncle 15-27 cm long, 2-3 mm thick. Spathe ca. 10 cm long, the tube green, the lamina cream, the tube ca. 5 mm thick. Female part of the spadix completely adnate to the spathe, 3-5 cm long, the ovaries subglobose, contracted to a narrow style bearing a capitate stigma; sterile flowers in 1-2 whorls, the synandrodia subprismatic, fertile male part of the spadix 2.8-4 cm long and ca. 0.5 cm thick, the synandria of 3-4 stamens subprismatic.

Additional collections seen: Colombia: Chocó: Corcovado region, Yeracui Valley, elev. 275 m, 1939 *Killip 35298* (US); El Valle: La Cumbre, elev. 1700-2100 m, 1922, *Hazen & Killip 11153* (US, NY); Huila; San Augustin, km 17 a Sta. Rosa, elev. 2420 m, 1958, *Idrobo et al. 2869* (P); Nariño: La Conga, Popayan, *Lehmann K389* (K); Cauca: Timbiqui, 1903, *Lehmann K390* (K); Ecuador: Carchi: vicinity of Maldonado, elev. 1800 m, 1977, *Madison 3988* (SEL, QCA, US).

Etymology: Named for F. C. Lehmann (1850-1903), prolific collector of north Andean aroids.

The specimens cited above are rather diverse, but as it is quite difficult to determine dried material in this group I have referred them all to this species recognizing the possibility that some other taxa are included. The typical form of *Chlorospatha lehmannii* is a diminutive plant with elegant, narrow sagittate leaves. It occurs in the altitude zone of 1500-2500 m, well above the other species of the genus. It differs from *C. castula*, to which it is closely related, by its lack of colors, by the paucity of sterile flowers, and by the narrow styles elevating the stigmas.

Xanthosoma Schott, Schott & Endlicher, Melet. Bot. p. 19. 1832.

Type species: *Xanthosoma sagittifolium* (L.) Schott, based on *Arum sagittifolium* L.

Synonyms: *Acontias* Schott, Schott & Endlicher, Melet, Bot. p. 19. 1832.

Type: *Acontias helliborifolius* (Jacq.) Schott, *Arum helliborifolium* Jacq.

Cyrtospadix C. Koch, Ind. Sem. Hort. Berol. App. 13. 1853.

Type: *Cyrtospadix striatipes* (Kunth) Koch, *Philodendron striatipes* Kunth.

Terrestrial herbs, the stems arborescent or subterranean, often with corms or tubers connected to the main stem by elongate rhizomes. Leaves erect, often large (to 2.5 m), cordate, sagittate, hastate, trisect, or pedatisect, rarely peltate. Inflorescences usually several in a monochasium, borne on short, stout peduncles. Spathe constricted below the center, forming a lower, more or less globose tube and an upper limb. Female part of the spadix free from the spathe, the female flowers 3-4 locular with axile placentation, at least at the base, sometimes unilocular with 3-4 deeply intrusive parietal placentae, the ovules ca. 20-100 per flower, the ovary capped by a tough discoid style coherent to styles of adjacent flowers. Sterile part of the spadix frequently very narrow with elongate, subprismatic sterile flowers. Male flowers 4-5 androus, subprismatic, the pollen shed in sticky threads; pollen in tetragonal tetrads.

Etymology: From Greek *xanthos*, 'yellow,' and *soma*, 'body,' referring to the yellow or orange interior of the stems of many species.

Xanthosoma is the largest genus of the Caladieae and includes well over half of the species. Its diagnostic features include the large pollen grains shed and transported in tetragonal tetrads, and the conspicuous stylar disc capping each ovary and coherent to the stylar discs of adjacent flowers. Both individual flowers and inflorescences are larger and more robust than those of other genera in the tribe.

A number of *Xanthosoma* species are sub-arborescent and inhabit the dark understory of wet and moist forests. Other species have adapted to permanently wet habitats with high light intensity, and probably from these both the cultivated and weedy forms have evolved. Still other xanthosomas, especially in section *Acontias*, inhabit seasonally dry habitats where they survive the dry season as leafless underground tubers, a situation parallel to that found in *Caladium*.

Several species originally described in the genera *Acontias* and *Caladium* are herewith transferred to *Xanthosoma*, in accordance with a rather narrow view of *Caladium* taken in this treatment. Since a complete revision of *Xanthosoma* is being prepared by Sue Thompson, no key is given here and the notes are restricted to new, newly transferred, or otherwise noteworthy species.

12. Xanthosoma viviparum Madison

Xanthosoma viviparum Madison, sp. nov.

A *X. weeksii* Madison pedunculis longioribus, floribus femineis minoribus, et venis marginalibus multioribus differt.

Type: Ecuador: Napo: Limoncocha, elev. 240 m, *Madison, Plowman & Besse 5429* (Holotype: SEL; Isotypes US, QCA, F, K).

Terrestrial herb of lowland forest understory. Stem brown, cylindric, creeping or erect, 1-2.4 cm thick, the internodes 1-2.2 cm long. In some plants, large numbers (to ca. 400) or bulbils ca. 1 mm in diameter are produced at each node in a crescent-shaped region opposite to the leaf insertion. Leaves

Xanthosoma viviparum with numerous bulbils.

several, erect, the petiole light green, 8-25 cm long, sheathing for 1/3 to 2/3 its length, terete above. Leaf lamina shiny deep green above, shiny pale green below with darker veins, ovate, cordate at the base, 8-24 cm long, 4.5- 14 cm broad, the primary lateral veins ca. 5 in number, the innermost arcuate, 0.8-1.5 cm from the margin, the margins undulate. Inflorescences solitary or paired, the peduncle green, terete, erect, 16-26 cm long, ca. 6 mm in diameter. Spathe 8-22 cm long, the tube green, comprising the lower 1/3-1/2, the limb cream, acute at the apex. Female part of the spadix 1.5-2.5 cm long, 4-7 mm

thick, the female flowers cream colored, ca. 1.8 mm tall, 4-locular with a broad discoid style. Sterile part of the spadix 1-2.3 cm long, narrowed apically. Male part of the spadix 3-4 cm long, the synandria 3-androus, white.

Distribution: Understory of wet or moist low elevation forest in the Amazon lowlands of Ecuador and Peru.

Additional collections seen: Ecuador: Napo: Limoncocha, 1978, *Madison et al. 5300* (SEL, QCA); along Río Napo, E of Puerto Misahualli, elev. 400 m, 1979, *Besse et al.1189* (SEL); Morona-Santiago: Río Namanagoza, at Logroño, elev, 450 m, Nov. 1980, *Madison 7291* (SEL). Peru: Loreto: Pebas, trail N from town, 1977, *Plowman et al. 6705* (GH); Pebas, trail to Pijuayal, 1977, *Plowman et al. 7021* (GH); Dept Madre de Dios: Prov. Manú, near Shintya, elev. 600 m, 1975, *Plowman & Davis 5063* (GH); Junín: Puerto Bermudez, elev. 375 m, 1929, *Killip & Smith 26626* (US).

Etymology: Latin *viviparus*, 'bearing active, live young,' in reference to the numerous bulbils produced on the stem which fall from the plant and readily sprout on the ground.

Xanthosoma viviparum is readily distinguished from other species of the genus by its shiny ovate leaves with lightly undulate margins and slightly cordate bases, It shares this feature with *Xanthosoma weeksii*, to which it appears to be closely related. The two differ in the following: *X. weeksii* is a montane species with short, stout peduncles, purple spathe tubes, female flowers 2 mm across, and lacking bulbils, whereas *X. viviparum* is a lowland species with elongate peduncles, green spathe tubes, female flowers ca. 1 mm broad, and often bearing numerous bulbils on the stems. Further, *X. viviparum* usually has 4 or 5 veins parallel to the leaf margins while *X. weeksii* has only 2 or 3.

Xanthosoma viviparum is variable in size, though usually of small stature. In the population from the Rio Namangoza, the leaves seldom exceed 10 cm in length, production of bulbils is prolific, and flowering has not been observed, while in the population at Limoncocha the plants are larger, production of bulbils is sporadic, and flowering is not uncommon. Evidently there is a shift in emphasis between vegetative and sexual reproduction between the two populations. Most of the Peruvian collections have few bulbils, but this may simply be a condition of plants in flower.

13. Xanthosoma fractum Madison

Xanthosoma fractum Madison, sp. nov.

Type : Peru: Huanuco: La Divisoria, collected live by Timothy Plowman, a.n., cult. at SEL, flowered in cult. March 1979, specimens prepared from cult. plants as *Madison 6747* (Holotype: SEL: Isotypes F, K, others to be distributed).

Species statura parva, petiolis transversaliter notatis, pedunculis elongatis, et floribus sterilibus roseis a congeneribus diversa.

Terrestrial herb, the stem irregularly cylindric, subterranean, 2-4 cm in diameter, 4-5 cm tall. The leaves 3-5 per plant, erect, the petiole 18-25 cm long, sheathing for about 1/2 its length, semi-transparent and marked by conspicuous transverse white lines. Lamina soft, velvety dark green above, shiny medium green below with darker veins, triangular-cordate, ca. 12 cm broad and 16 cm long, the primary lateral veins 5-6 in number, the collecting veins 3,

the innermost arcuate at 4-7 mm from the margin, the other two parallel to the margin. Peduncle terete, 3-5 mm in diameter, about equal in length to the petiole. Spathe tube deep green, ca. 3 cm long and 1.5 cm in diameter; limb ca. 6 cm long, cream colored, cuspidate. Female part of the spadix ca. 1.5 cm long, the flowers green and 1.2 mm broad, 1.8 mm tall with a tough discoid style, 4-locular. Sterile part of the spadix 2-2.5 cm long, the lowermost whorl of flowers purplish-red, the others white. Male part of the spadix 4-5 cm long, the flowers white, pollen grains in tetrads.

Etymology: Latin *fractus*, 'fractured' or 'cracked,' referring to the irregular transverse white lines marking the petioles and representing plexuses of the laticiferous system.

This diminutive species, less than 50 cm tall, is notable by the semi-transparent petioles with irregular white transverse lines that appear as cracks or fractures. The elongate peduncles, equal to the petioles, and the deep red color of the lowermost whorl of sterile flowers are also diagnostic. In these features *Xanthosoma fractum* differs from the related species *X. striolatum* (Mart.) Schott, a native of lowland Amazonian Brazil.

14. Xanthosoma pubescens Poeppig

Xanthosoma pubescens Poeppig, in Poeppig & Endlicher, Nov. Gen. et Spec. Pl. 3:89 t. 299. 1845.

Type: Peru: Hunauco: Quebrada de Cassapi, Poeppig s.n.; the illustration serves as the type.

Caladium pubescens N. E. Brown, Bot. Mag. T. 8402. 1911.

Type. Peru: San Martin: Moyobamba district, Forget legit., live to Kew via Sanders & Son., *N. E. Brown s.n.* (K).

Xanthosoma buchtienii Engler, Das Pflanzenreich IV 23 E: 54. 1920.

Type. Bolivia: Antahuacana, elev. 750 m, 1909, *Buchtien 2345* (B, non vidi, photo US, Isotype NY).

Distribution : Peru and Bolivia

There has been considerable confusion concerning the generic identity of the several pilose or pubescent Andean caladioids. N. E. Brown described a plant sent by Forget from Peru as *Caladium pubescens* N. E. Brown and in the same publication transferred *Xanthosoma pilosum* C. Koch and *X. holtonianum* Schott to *Caladium*. Evidently Brown was unaware of *X. pubescens* Poeppig, since he makes no mention of it and clearly indicates that *Caladium pubescens* N. E. Brown is a new species based on the Forget collection and not a transfer of Poeppig's name. It is only by chance that the same specific epipthet was selected for the two species, which prove to be synonymous. Engler and Krause (1920) recognized both species, each in its own genus, and the descriptions provided are quite similar.

In the construction of the female flowers *Xanthosoma pubescens* is clearly a *Xanthosoma*; the ovaries are 4-locular with axile placentation and a thickened discoid style is present. The shedding of the pollen grains in tetrads confirms this generic assignment. *Xanthosoma pubescens* is distinguished from *X. pilosum* most readily by the large number (10-18) of primary lateral veins in the leaf, while *X. pilosum* has but 4-6 primary lateral veins.

15. Xanthosoma trichophyllum K. Krause

Xanthosoma trichophyllum K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11:622, 1932

Type: Peru: Loreto: Soledad on Rio Itaya, elev. 110 m. 1929, *Killip & Smith 29640* (B, non vidi, Isotype: US)

Additional collections seen: Peru: Loreto: Pebas, April 1977, *Plowman et al. 7029* (GH), San Martin: Tarapoto, Aug. 1967, *Martin & Plowman 1822* (GH); Quebrada Shilcayo, near Tarapoto, Sept. 1977, *Schunke 9821* (MO)

This species is quite similar to *Xanthosoma pubescens* Poeppig, and Krause distinguished it chiefly by its leaves, which are much narrower and often acute or truncate at the base rather than cordate as in *X. pubescens.* In addition the inflorescences of *X. trichophyllum* are only about half the size of those of *X. pubescens*, and the spathe tube is proportionately larger in comparison to the limb. These differences may well succumb to the future discovery of intermediates, in which case the relationship of the two species must be reassessed, but the collections now available readily sort into two groups which seem sufficiently distinct to merit specific recognition.

Both *Xanthosoma trichophyllum* and *X. pubescens* are evidently related to *X. viviparum*, with which they share the more or less ovate leaves with undulate margins that are unusual in the genus as well as the prolific productions of tiny bulbils which vegetatively serve to reproduce the plant.

16. Xanthosoma pilosum C. Koch & Aug.

Xanthosoma pilosum C. Koch & Aug., Ind. Sem. Hort. Bot. Berol. App. 2, 1855.

Caladium pilosum (C. Koch & Aug.) N. E. Brown, Bot. Mag. t. 8402, 1911
Type: Based on a sterile plant cultivated by Augustin and obtained from Linden; the description serves as the type.

Xanthosoma holtonianum Schott, Oestrr. Bot. Zeitschr. 9:39, 1859
Caladium holtonianum (Schott) N. E. Brown, Bot. Mag. t. 8402, 1911
Type. Columbia: Magdalena, Dec. 1852, *Holton 216* (K)

Caladium puberulum Engler, Bot. Jahrb. Syst. 37:136, 1905
Type: Columbia: Antioquia: Valparaiso, elev. 1300 m, Oct. 1883, *Lehmann 3262* (B, non vidi, photo F, US).

The slight differences in leaf shape used by Engler to distinguish these species seem hardly adequate, as the variants may be found on a single plant. It is possible that this species, which ranges from Colombia to Costa Rica, will prove to be synonymous with *Xanthosoma mexicanum* Liebm. of Mexico and Guatemala, in which case it will go by its oldest name, *X. mexicanum.* As with *X. pubescens* floral and pollen morphology indicate the placement of this species in *Xanthosoma* rather than *Caladium.*

17. Xanthosoma riopalenquense (Madison) Madison

Xanthosoma riopalenquense (Madison) Madison, comb. nov.

Caladium riopalenquensis Madison, Selbyana 2: 24. 1977.
Type. Ecuador: Los Rios: Rio Palenque Science Center, *Dodson 6681* (Holotype: SEL, Isotypes: MO, RPSC).

Additional collections: Ecuador: Pichincha: El Centinela, elev. 550 m, Feb.

1979 *Gentry et al. 24703* (MO); same locality, April 1977, *Madison 3808* (SEL, QCA); Esmeraldas: environs of Lita, elev. 550 m, June, 1978, *Madison et al. 5068* (SEL); El Oro: Km 16 on road Pinas-Santa Rosa, elev. 620 m, Oct. 1979, *Dodson et al. 8952* (SEL, MO).

This species was described from dried material to provide a name for an undescribed plant in the Flora of Rio Palenque, at that time in press. The recent observation that the pollen is presented in tetrads stimulated me to reexamine the floral morphology using liquid-preserved materials I had meanwhile collected in the wild. While some ovaries are 2-locular, the majority are 3 to 4-locular and a discoid style is evident in the flowers in spirits, though difficult to discern in the dried collections. These character-states suggest that the species properly belongs with *Xanthosoma.* In the original description I noted a similarity to *Caladium pilosum*, which also has proved to be a species of *Xanthosoma*.

A unique feature of *Xanthosoma riopalenquense* which is quite striking in the living plants, (once one is aware of it, it is also evident in dried specimens), is the presence of an aerenchymatous layer below the abaxial surface of the leaf. The leaf from below appears to be full of bubbles, and in being torn, it has the texture and quality of a thin sheet of styrofoam.

Collections of *Xanthosoma riopalenquense* made in the last few years extend the range to most of western Ecuador in wet or moist premontane forest at altitudes close to 500 m.

18. Xanthosoma stenospathum Madison

Xanthosoma stenospathum Madison, sp. nov.

Type: Peru: Huanuco: La Divisoria, collected live by Timothy Plowman, cult. at SEL as SEL 78-1615, flowered in cult. July, 1979, specimens distributed as *Madison 6969* (Holotype: SEL; Isotypes to be distributed: F, K, USM, US).

Species spatha angusta, spadice in dimidio inferiore spathae adnato a congeneribus diversa.

Stem erect, 3-4 cm thick, to 20 cm tall, solitary or branched, brown, covered with marcescent or fibrous remains of old leaf bases and cataphylls. Petiole 40-48 cm long, solid green, 8 mm thick at the base, tapering to 4 mm thick at the apex, smooth, terete, sheathing for less than ¼ of its length. Lamina sagittate, the anterior lobe ca. 20 cm long, 11 cm wide at the base, triangular, the posterior lobes 15 cm long, ca. 5.5 cm wide, dull medium green with veins furrowed above, shiny pale green with veins prominent and darker below, thin. Inflorescences 3-4 per monochasium, erect, the peduncle green, smooth, ca. 12 cm long, 5 mm thick, biconvex-flattened. Spathe ca. 10 cm long, the tube green, 2.5-3 cm long and 8-12 mm in diameter, the limb cream, cuspidate, twisting-reflexing at anthesis before the pollen is shed. Carpellate part of the spadix ca. 2.5 cm long and 4-5 mm broad, adnate to the spathe for more than half its length, the flowers pale green, coherent to one another, 3-locular. Sterile part of the spadix about 1 cm long, greenish, the flowers prismatic and tightly packed. Male part of the spadix white, about 3 cm long and 5 mm in diameter, the flowers 5-6-androus.

Etymology: From the Greek *steno-*, "narrow," and *spatha*, "spathe," referring to the unusually slender spathe tube.

In several of its features this species is unique in *Xanthosoma* while being

similar to species of *Chlorospatha*, most notably in that the inflorescence is very slender and the female part of the spadix is adnate to the spathe for half or more of its length. However, in the structure of the flowers the species clearly pertains to *Xanthosoma*; both fertile and sterile flowers are prismatic and tightly packed on the spadix in contrast to the lax-flowered condition of *Chlorospatha.* In cultivation *X. stenospathum* has flowered on an annual cycle despite nearly uniform greenhouse conditions.

19. Xanthosoma aristeguietae (Bunting) Madison

Xanthosoma aristeguietae (Bunting) Madison, comb. nov.

Caladium aristeguietae Bunting, Acta. Bot. Venez. 10:282. 1975.
Type: Venezuela: Guarico: 2 km N of Ortiz, July 1971, *Bunting 4495* (MY, non vidi)

Xanthosoma riedelianum Schott var. *brancoanum* Engler, Das Pflanzenreich IV 23 E:132. 1920. Type. Brazil: Rio Branco: San Marcos, *Ule 7753* (B, non vidi, photo: SEL, Isotype:K)

Cormous herb forming colonies in open swampy areas by means of rhizomatous spread; corms to 4 cm thick, rhizomes ca. 0.5 cm thick and to 50 cm long. Petiole spongy, to 90 cm long, vaginate for ½ its length, bright green with cream striate markings, especially in the lower half, the non-vaginate part D-shaped in cross section. Leaf blade erect, white-spotted, hastate, to 35 cm long and 38 cm broad. Peduncle to 72 cm long. Spathe tube 10.5 cm long, 3 cm wide, limb cream, ca. 15 cm long. Spadix to 24 cm long.

Additional collections seen: Venezuela: Guarico: near Ortiz, July 1960 *L. Aristeguieta 4290* (VEN, MO); same locality, Aug. 1967, *Bunting 2201* (VEN); Carabobo: near El Paito, Aug. 1967, *Bunting & Trujillo 2237* (VEN); *Bunting & Trujillo 2226* (VEN); Cojedes: alrededores de San Carlos, Aug. 1971, *Bunting 4521* (VEN).

This striking species is notable by its large, hastate, spotted leaves held stiffly erect with the posterior lobes also folded upward, and by the elongate inflorescences. It is closely related to *Xanthosoma striatipes*, differing chiefly by its greater size, broadly hastate rather than lanceolate to slightly sagittate leaves, and much larger inflorescences. With considerable chromosomal diversity being discovered in the tribe it is possible that *X. aristeguietae* will prove to be a polyploid based at least in part on *X. striatipes.*

Though placed originally in *Caladium*, the 3 to 4-locular ovary with axile placentation and thickened discoid style clearly indicates *Xanthosoma*. Shedding of pollen in tetragonal tetrads further substantiates the transfer.

20. Xanthosoma striatipes (Kunth) Madison

Xanthosoma striatipes (Kunth) Madison, comb. nov.

Philodendron striatipes Kunth, Ind. Sem. Hort. Bot. Berol. ? 11. 1848.
Cyrtospadix striatipes (Kunth) C. Koch & Bouche, Ind. Sem. Hort. Berol. App. 13. 1853.
Caladium striatipes (Kunth) Schott, Synopsis Aroidiarum 51. 1856.
Acontias striatipes (Kunth) Schott, Prod. Syst. Aroid. 192. 1860.
Type: Brazil. Minas Gerais: *Sellow 1206* (B, non vidi, destroyed? tracing of Koch's sketch of type at K)
Caladium heterotypicum S. Moore, Trans. Linn. Soc. London, Bot. 4:500. 1898.

Type: Brazil: Mato Grosso: 1891. *S. Moore 691* (NY)

Caladium angustifolium Engler, Das Pflanzenreich IV 23: E:26. 1920.
Type: Brazil: Mato Grosso: Las-Pes Caceres, 1909, *Hoehne 1197* (B, non vidi, illustration of type in Das Pflanzenreich IV 23 E:26)

Terrestrial herb, the tubers subglobose, 2-3.5 cm in diameter, produced annually directly above the tuber of the previous year, which often persists so that the caudex consists of 2 or 3 vertically superposed subglobose tubers, the tubers yellow to orange within, giving rise to numerous, succulent, spreading roots. Leaves 2-3 per plant, erect, the petiole spongy, 22-35 cm long, 4-6 mm in diameter at the midpoint, sheathing for slightly more than half its length, sometimes marked with elongate cream or white striations. Leaf lamina held stiffly erect and slightly folded at the midrib with the two halves deflected toward the adaxial surface, variable in shape, narrowly lanceolate to ovate, 1.5-7 cm broad, 16-36 cm long, the tip acute, the base attenuate, acute, truncate, rounded, or auriculate, the primary lateral veins 4-6 in number, arising at a narrow angle (10-25°) from the midrib, the marginal veins 3 or 4, the innermost 3-7 mm from the margin. Inflorescence typically solitary, erect, appearing with the leaves or without them, the peduncle exceeding the petiole, 25-45 cm long, 4-8 mm thick. Spathe tube green, 1.5-2.5 cm in diameter, 3-6 cm long, the limb white, 5-11 cm long. Carpellate part of the spadix 1.2-2.6 cm long, 6-8 mm in diameter, obliquely attached to the spathe, the stigmas yellow; sterile portion of the spadix with 1-2 whorls of approximately isodiametric synandrodia directly above the female flowers, above which is a very narrow section of elongate (to 1.3 cm) sterile flowers 3-3.5 cm long; staminate part of the spadix 4-6 cm long, 5-7 cm thick. In fruit, the spathe tube persists, nutant. Berries subglobose, 4-6 mm in diameter, the seeds 1.5-2 mm long.

Etymology: From the Latin *striatus*, "striate," and *pes*, "foot," referring to the striate markings on the petioles.

Distribution. Paraguay, Brazil, the Guianas, Venezuela, and Colombia.

Representative collections: Colombia: Boyaca: El Yopal, July 1963, *Blydenstein & Saravia 1162* (US); Meta: Menegua, June 1937, *Garcia 5307* (US); Rio Meta, July 1897, *Lehmann 8846* (K); Vichada: Maypures, June 1854, *Spruce 3741* (K, P).

Venezuela: Bolivar: Gran Sabana, elev. 1065 m, Oct. 1944, *Steyermark 59257* (F); Morichal, elev. 300 m, Oct. 1963, *Maguire et al. 35920* (US, NY); Sta. Rosalia, Feb. 1970, *Velasquez 1082* (VEN); Amazonas: Puerto Ayacucho, July 1977, *Huber 896* (VEN); San Carlos de Rio Negro, Sept. 1975, *Berry & Brunig 1483* (VEN). Guarico: Calabozo, July 1967, *Tamayo 7200* (VEN); same locality, Aug. 1962, *Blydenstein 463* (VEN).

Guyana: Rupununi savanna, 2 mi S of St. Ignatius, elev. 100 m, Sept. 1963, *Goodland & Persaud 736* (NY)

Fr. Guiana: Cayenne, 1846, *Leprieur s.n.* (P).

Brazil: Goias. 25 km SW of Caiaponia, elev. 800 m, May 1973, *Anderson 9568* (F, K, NY, US); 15 km N of Corumba, elev. 1150 m, Jan. 1968, *Irwin et al. 18658 (F, K, NY, P); 12 km S. of*
win et al. 18658 (F, K, NY, P); 12 km S. of Guara, elev. 550 m, March, 1968, *Irwin et al. 21564* (NY); Minas Gerais: Caldas, Jan. 1876, *Mosen 4402* (P), Caranday, Feb. 1886, *Glaziou 16490* (P); Mato Grosso: S. Antonio de Leverger, Feb. 1975, *Harschbach et al. 36095* (NY); Guaporé:

Río Guaporé, viz. hort., 1976, *Bogner 1279* (M); Pará: Braganca, April 1955, *Pires & Silva 4848* (US).

Paraguay: Villa Rica, Nov. 1874, *Balansa 977* (K, P); Villa Rica, April 1931, *Hassler 4023* (US, F).

Xanthosoma striatipes grows in seasonally wet or swampy areas at the margins of gallery forest or along streams, in open grasslands, and in sandy savannas. There is marked periodicity to its growth evident both in flowering times (corresponding to onset of flooding) and in the incremental growth of the tuber which results in a vertical chain of attached subglobose tubers with a new one added each year above the others.

Xanthosoma striatipes is widespread in S. America and may be divided into a southern range extending from Minas Gerais to Paraguay and a northern range extending from Pará and the Guianas to eastern Colombia. These two regions are separated by the forested areas of the Amazon basin, leaving a gap of about 1000 km between the two. The northern and southern populations are differentiated morphologically chiefly in the structure of the ovary. Specimens from the north have (2-) 3 to 4-locular ovaries with 10-22 ovules, while those from the south have 2 to 3-locular ovaries with 4-12 ovules. The southern populations, which have slightly larger seeds, may be undergoing selection for increased seed size/decreased seed number, a trend parallel to that seen in *Caladium* and *Aphyllarum*. At present the species is not sufficiently differentiated in the two regions to merit division into two taxa, though the situation appears to be one in which such a divergence could occur in the future.

Leaf shape in *Xanthosoma striatipes* is variable, with simple ovate or lanceolate laminae most common. The base may be acute, truncate, or auriculate, and several collections with subhastate leaves seem best interpreted as extreme variations of leaf shape within the species, rather than as separate taxa. There is no discernible pattern in the geographic distribution of leaf shapes, and the auriculate and subhastate forms occur sporadically throughout the range of the species. A species closely related to *X. striatipes*, but with spreading hastate leaves and much greater size, is *X. aristeguietae*, q.v. *Xanthosoma conspurcatum* and *X. riedelianum* also appear very similar to *X. striatipes*, and may prove to be conspecific.

The generic placement of *Xanthosoma striatipes* is difficult, and *Xanthosoma* is the fifth genus to which the species has been assigned. On the basis of ovary structure the Paraguayan specimens, with a two-locular ovary and 2-3 ovules per loculus, are close to *Caladium* or *Aphyllarum*. However, the thick discoid style and large size (2.5-3 mm broad) of the ovary indicate an affinity to *Xanthosoma*. The northern populations are much more palatable as *Xanthosoma* species in terms of the structure of their ovaries. The pollen, shed in tetragonal tetrads, is typical of *Xanthosoma*. Inclusion of the species in *Xanthosoma* stretches the interpretation of that genus to the point where it includes greater diversity than is found between other genera of the tribe. This is chiefly a reflection of the closely knit nature of the Caladieae and the number of parallel evolutionary lines included in it.

Caladium Vent., Descr. Pl. Nouv. Jard. Cels. 30. 1801.

Type species: *Caladium bicolor* (Aiton) Vent., *Arum bicolor* Aiton

Phyllotaenium Andre, Ill. Hort. 19:3. 1872.

Type species: *Phyllotaenium lindenii* Andre

Terrestrial herbs, the stem a flattened or subglobose tuber, fully subterranean. Leaves several, erect, often peltate, frequently variegated. Inflorescences solitary or a few in a monochasium, the peduncle elongate, often equalling the petiole. Spathe with a globose tube, usually green, and an ovate or lanceolate limb which is deciduous after anthesis. Female flowers less than 1.5 mm broad, prismatic, sometimes with a different texture in the upper part but lacking a well-defined style, 1-2-locular with 1-2 intrusive parietal or sub-basal placentae that may be fused in the center; ovules 2-20 in number. Male flowers mostly 3-4-androus, subprismatic. Pollen grains solitary.

Etymology: From a Malay word *keladi*, referring to an aroid, possibly *Colocasia esculenta.*

The genus *Caladium* as here interpreted includes a small group of species considered to have evolved from a *Xanthosoma*-like ancestor. The genus is distributed chiefly in the northern half of the Amazon basin and the plants occur mostly in regions with a pronounced seasonal climate. Many of the characteristic morphological features of *Caladium* may be interpreted as adaptations to a seasonal environment. These include specialization of the stem as a deeply buried subterranean tuber and intermittent above-ground vegetative growth. Selection for larger seeds which are hypothesized to be adaptive in a seasonal environment may lead to decrease in ovule number and associated changes in placentation as well as changes in pollen from tetrads to solitary grains.

Many of these specializations are paralleled in other Caladiinae that have colonized seasonal habitats, for example in the line leading to *Xanthosoma striatipes*, which makes generic identifications difficult. However, shedding of pollen in solitary grains in *Caladium* vs. tetrads in *Xanthosoma* remains an inflexible diagnostic character.

Key to species of *Caladium*

1. Leaves 3-lobed or trifoliate
   2. Leaflets ovate, fully separate at the base; berries 1-2 seeded ..... *C. ternatum*
   2. Lobes of the leaf lanceolate, confluent at the base; berries many-seeded ..... *C. macrotites*
1. Leaves ovate, cordate, or hastate, but not 3-lobed
   3. Leaf peltate
      4. Petiole to 2 mm thick, the leaves less than 10 cm long ..... *C. humboldtii*
      4. Petioles more than 4 mm thick, the leaves more than 12 cm long
         5. Leaves 12-25 cm broad, green or variegated with pink, red, or white ..... *C. bicolor*
         5. Leaves 40-60 cm broad, glaucous bluish above . . *C. coerulescens*
   3. Leaf not peltate
      6. Leaf sagittate ..... *C. lindenii*
      6. Leaf more or less ovate, lacking posterior lobes. .*C. schomburgkii*

21. Caladium ternatum Madison

Caladium ternatum Madison, sp. nov.

Type: Brazil: Amazonas: Caatinga at Porto Camanaus, Alto Rio Negro,

Oct. 1978, *Madison et al. 6418* (Holotype: INPA; Isotypes: SEL, US).

Species foliis ternatis et ovariis unilocularibus a congeneribus diversa.

Terrestrial herb, the tuber sub-globose, 1-3 cm in diameter, buried 12-26 cm in the ground, with numerous succulent roots extending from the upper surface. Leaves solitary or several, the petiole 8-26 cm long, sheathing in the lower 1/3 to 1/2, marked with transverse brown lines; lamina trifoliate in mature plants, the leaflets sub-equal, the central leaflet 11-20 cm long and 6-8 cm broad, the lateral leaflets slightly smaller, fully free at the base or joined by a narrow band of lamina, rarely the leaves hastate, and if so, usually in immature plants, the leaves dark to medium green above with or without scattered spots of lighter yellow-green, the marginal veins 2-3, the innermost 6-10 mm from the margin. Inflorescence solitary, erect, the peduncle 1/2 to 3/4 the petiole length. Spathe tube green, 2-3 cm long, the limb pale yellow, 4-5 cm long. Female portion of the spadix ca. 1.5 cm long, the flowers with yellow stigmas, unilocular with a single sub-basal parietal placenta bearing 4-5 ovules. Sterile portion of the spadix purplish, 1-1.3 cm long; male portion of the spadix cream, 2.5-3 cm long. Berry white, irregularly globose, 1- 2-seeded, the seeds smooth, 2.5-3.5 mm long.

Additional material seen: Brazil: Amazonas: road Camanaus-Uapes near Camanaus, Nov. 1971, *Prance et al 15987* (NY, US).
Colombia: Vaupes: Rio Negro, San Felipe, Oct. 1952, *Schultes et al. 18064* (US)

Etymology. Latin *ternatus*, "in threes," referring to the three leaflets of the leaf.

Caladium ternatum grows in white sandy soil in open woodlands on the upper Rio Negro in Brazil and adjacent Colombia. The leaves of small plants may be sagittate or hastate, but in vigorous mature plants the leaves are fully trifoliate.

The ovary of *Caladium ternatum* is unilocular with a single intrusive parietal placenta bearing 4-5 erect anatropous ovules at its base. The bilobed stigmas of the flowers, however, suggest that this condition is derived by reduction of a bicarpellate ovary, a situation presumably parallel to that of *Aphyllarum tuberosum* and *Scaphispatha gracilis.*

Caladium ternatum is most closely related to *C. macrotites*, differing in seed size and number and in the shape of the leaf. Tubers of *C. ternatum* in cultivation remain dormant for 6 or 7 months of the year despite uniform greenhouse conditions; perhaps the dormancy mechanisms are influenced by day length, but they seem to operate independently of moisture availability.

22. Caladium macrotites Schott

Caladium macrotites Schott, Oesterr. Bot. Wochenbl. 5:20. 1855.

Type. Brazil: Amazonas: Maypuré, Humboldt & Bonpland 880 (B, non vidi, photo NY!)
Caladium angustilobum Engler, Bot. Jahrb. Sept. 37:136. 1905.
Type: Colombia: Meta. Rio Meta at Orucue, July, 1897, Lehmann 8844 (Holotype B, non vidi, photo SEL, Isotypes K, F).

Terrestrial herb, the tuber globose, to 4 cm in diameter. Leaves 2-5 in number, erect, the petiole to 35 cm long, sheathing in lower ¼, terete above, 2-3 mm thick at its midpoint. Lamina hastate, slightly peltate, the anterior lobe

pointing up, 8-12 cm long, 1.5-2 cm broad, the posterior lobes slightly smaller than or equalling the anterior lobe, the marginal veins 2 or 3, the innermost ca. 3 mm from the margin. Inflorescence solitary, produced with the leaves, the peduncle slightly exceeding the petioles, ca. 3 mm in diameter. Spathe tube 4-5 cm long, the limb ca. 4 cm long. Female part of the spadix 1-1.5 cm long, 5-6 mm thick, the sterile portion ca. 1 cm long, the staminate portion ca. 4 cm long, 5 mm thick, claviform.

Etymology: From the Greek *macrotos*, "elongate" or "drawn out," in reference to the elongate narrow leaves.

Distribution: Colombia, Venezuela, and Brazil, close to the point where the three countries come together.

Additional collections seen. Venezuela: Amazonas: Isla el raton, June 1940, *Williams 13299* (US, VEN); Puerto Ayacucho, May 1940, *Williams 13101* (VEN); 35 km from Puerto Ayacucho on road to Sanariapo, July 1964, *Bunting et al. 3507* (MY); 25 km S of Sanariapo, June 1975, *Gentry & Berry 14602* (MO).

Caladium macrotites occurs in open sandy regions where it flowers in June and July. The species is readily recognized by the very narrow lobes of the hastate leaves and the upward pointing orientation of the anterior lobe. Several collections with broader leaves from around Puerto Ayacucho in Venezuela may also be referrable to this species, but the material available is insuffucient to determine this with certainty at present.

23. Caladium humboldtii Schott

Caladium humboldtii Schott, Oesterr. Bot. Wochenbl. 4:417. 1854.

Type: Brazil: Amazonas: San Carlos, n.v. "contra culevra," *Humboldt & Bonpland 985* (B, non vidi, photo NY).

Caladium argyrites Lem., Ill. Hort. 5:, t. 185. 1858.

Type. Ex hort., the illustration (t. 185) serves as the type.

Caladium myriostigma C. Koch, Wochenschr. Gärtnerei Pflanzenk.:135. 1862.

C. humboldtii var. *myriostigma* (C. Koch) Engler, D. C., Monogr. Phan. 2:468. 1879.

Type: Ex hort., the description serves as the type.

Caladium lilliputiense Rodig., Ill. Hort. 42:363, t. 47. 1895.

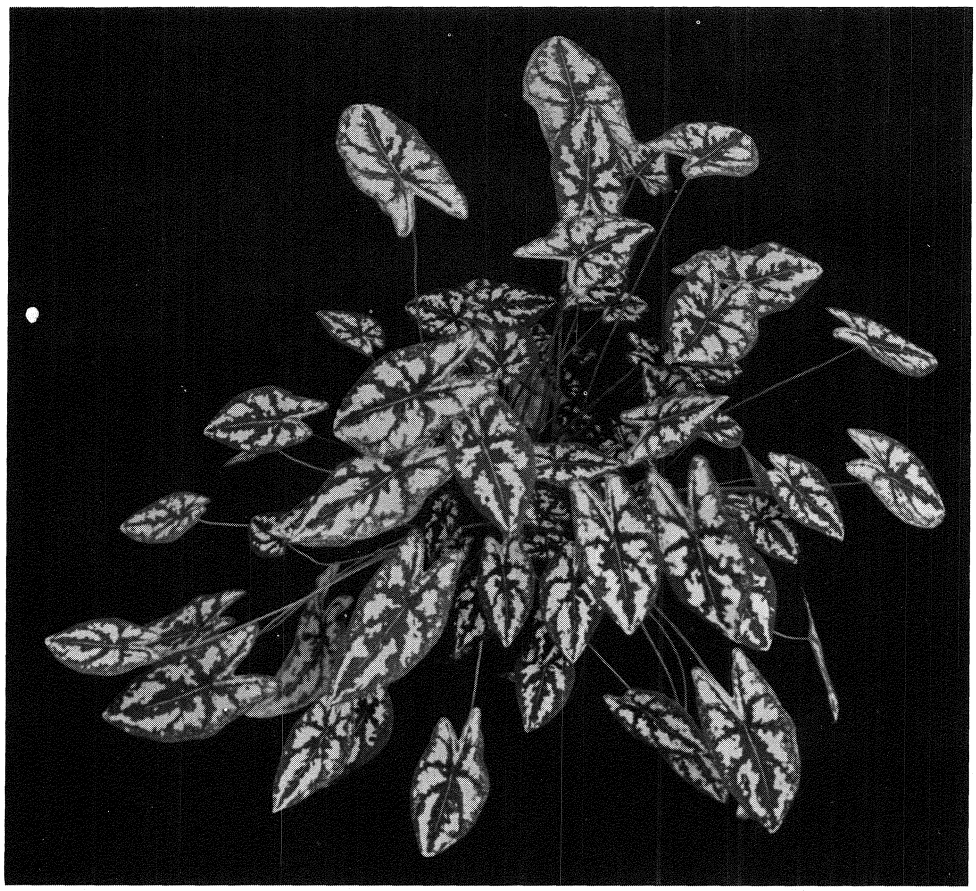
Type: Venezuela: cult. in Belgium, the illustration (t. 47) serves as the type.

Diminutive terrestrial herb with a subterranean globose tuber 1-2 cm in diameter and yellow within, suckering freely. Leaves several, erect, the petioles terete, 10-24 cm long, 1-1.5 mm in diameter. Lamina ovate, membranaceous, peltate, 5-9 cm long and 2-4.5 cm broad, dull deep green with white blotches and spots above, paler below. Inflorescences unknown.

Distribution: Brazil and adjacent Venezuela in the Casiquieres district.

Additional collections seen: Brazil: without locality, cult. at Kew, 1878, *N. E. Brown s.n.* (K); Venezuela: Amazonas: Casiquieres, near Yativa, 1969, *Bunting, Akkermans & VanRooden 3846* (MY).

Caladium humboldtii is distinguished from *C. bicolor* only by its consistently dwarf stature, its freely-suckering habit, and its lack of inflorescences. Even large and vigorous clumps of *C. humboldtii* in cultivation do not pro-



Caladium humboldtii

duce flowers. It is possible that the species will prove merely to be a chromosomal race of *C. bicolor* once its cytology becomes known.

Caladium humboldtii is a very attractive little plant and has been widely cultivated for more than a century, but only a few wild collections of the species have been made. The species may not be as rare as this implies since in its typically non-flowering condition, most collectors would pass it by.

24. **Caladium bicolor** (Aiton) Vent.

Caladium bicolor (Aiton) Vent., Descr. Pl. Nouv. Jard. Cels. t.30. 1801.

Arum bicolor Ait., Hort. Hew. 3: 316. 1789.

Type: Cult. at Kew, introduced to England in 1773 by Messrs. Kennedy and Lee from material cultivated in Madeira; the description serves as the type.

Caladium adamnatinum Linden, Ill. Hort. 37: 71. 1890.
Caladium argyrospilum Lem., Ill. Hort. 5: 59. 1858.
Caladium barraquinii Lem., Ill. Hort. 7, t. 257. 1860.
Caladium belleymei Lem., Fl. des Serres 2nd. Ser., 13: t. 1377. 1858.
Caladium brogniartii Lem., Ill. Hort. 5: 58. 1858.
Caladium chantinii Lem., Ill. Hort. 5: 58. 1858.
Caladium concolor C. Koch, Berliner Allg. Gartenzeitung 1857: 135.

Caladium devosianum Lem., Ill. Hort. 9: t. 322. 1862.
Caladium enkeanum C. Koch, Wochenschr. Gaertnerei Pflanzenk. 1861:267.
Caladium firmulum Schott, Oesterr. Bot. Wochenbl. 4: 417. 1854.
Caladium haematostigma Kunth, Enumer. Pl. 3. 42. 1841.
Caladium hastatum Lem., Ill. Hort. 5:61. 1858.
Caladium hortulanum Birdsey, Cultivated Aroids 42. 1951.
Caladium houletii Lem., Ill. Hort. 5: 59. 1858.
Caladium laucheanum C. Koch, Wochenschr. Gaertnerei Pflanzenk. 1861: 266.
Caladium lemaireanum Barraquin, Ill. Hort. 9, t. 311. 1862.
Caladium macrophyllum Lem., Ill. Hort. 9, t. 316. 1862.
Caladium marginatum C. Koch, Ind. Sem. Hort. Bot. Berol. App. 6. 1854.
Caladium marmoratum Mathieu, Ind. Sem. Hort. Bot. Berol. App. 6. 1854.
Caladium medio-ratiatum Lind. & Rodig., Ill. Hort. 37, t. 528. 1890.
Caladium mirable Lem., Ill. Hort. 10, t. 354. 1863.
Caladium neumannii Lem., Ill. Hort. 5:58. 1858.
Caladium pallidum C. Koch & Bouche, Ind. Sem. Hort. Bot. Berol. App. 3, 1853.
Caladium perrieri Lem., Ill. Hort. 8, t. 294. 1861.
Caladium picturatum C. Koch, Wochenschr. Gaertnerei Pflanzenk. 1862: 135.
Caladium poecile Schott, Melet. Bot. p. 18. 1832.
Caladium porphyroneuron C. Koch, Wochenschr. Gaertnerei Pflanzenk. 1861. 8.
Caladium purdieanum Schott, Oesterr. Bot. Zeitschr. 9: 38. 1859.
Caladium regale Lem., Ill. Hort. 9, t. 316. 1862.
Caladium sagittatum Lind. & Rodig., Ill. Hort. 37, t. 538. 1890.
Caladium smaragdinum C. Koch & Bouche, Ind. Sem. Hort. Berol. App. 3. 1853.
Caladium sororium Schott, Oestrr. Bot. Zeit. 9: 38. 1859.
Caladium spruceanum Schott, Oestrr. Bot. Zeit. 9: 38. 1859.
Caladium stangeanum C. Koch, Wochenschr. Gaertnerei Pflanzenk. 1861: 136.
Caladium steudneriifolium Engler, Arac. Exsicc. et Illustr. 134. 1885.
Caladium surinamense Miq., Delect. Sem. Hort. Amst. 1853.
Caladium troubetzkoyi Chantin, Fl. des Serres 2nd Ser. 13, t. 1379. 1858.
Caladium vellozianum Schott, Bonplandia 7: 163. 1859.
Caladium verschaffeltii Lem., Ill. Hort. 5: 59. 1858.

Terrestrial herb, the tuber starchy, fully subterranean or with the apex at the soil line, flattened, subglobose or subcylindric, 2.5-6 cm across, 2-12 cm long, white or yellowish within. Leaves several, erect, the petiole 30-95 cm long, 4-8 mm thick, sheathing in the lower part, terete above, green or marked with small purplish or reddish striations, with a glaucous surface. Lamina peltate, ovate to elliptic, 18-46 cm long, 12-25 cm broad, the posterior lobes round, divergent or fully fused, the lamina dark green to medium green with or without white, pink, or purplish spots, zones, and splotches, paler and glaucous abaxially. Inflorescences solitary or borne two or three together. Peduncle 16-60 cm long, somewhat shorter than the petiole, terete, galucous green or marked as the petiole. Spathe tube green, 2-3 cm long, lamina white, 4-8 cm long. Female part of the spadix 4-6 mm thick, 1-3 cm long, the stigmas often yellowish, the ovary sub-bilocular with two placentae and 10-20

ovules. Sterile flowers largest at the base, more elongate in the narrowed part of the spadix, the sterile part 1-2.4 cm long; male part of the spadix white, 2.5-6 cm long.

Distribution: The species ranges from Panama to Bolivia and eastward to the Atlantic coast of Brazil. It is naturalized at many localities throughout the tropics.

Representative collections: Panama: Darien: headwaters of Río Chico, June 1947, *Allen 4629* (MO); San Blas: Molia, Playon Chico, May 1975, *Stier 34* (MO).

Colombia. El Valle: Santa Rosa, Dagua Valley, 1922, *Killip 5359* (NY, US); Tolima: La Union, *Lehmann 6117* (K); Antioquia: Medillin, 1930, *Archer & Aguilar 844* (US); Santander: La Gomez, 1944, *Fassett 25065* (US); Cuncinamarca: La Aguadita, 1958, *Garcia-Barriga 16014* (US). Putumayo: 25 km above Mocoa, 1972, *Madison 881* (GH); Caqueta. 41 km N of Florencia, 1974, *Gentry et al. 9174* (MO); Vaupés: Rio Apaporis, Jirijirimo, 1952, *Schultes 15949* (US).

Ecuador: Napo: Auca Oil Fields, 1976 *Balslev & Madsen 10614* (AAU); Los Ríos: Buena Fe, 1976, *Boeke 507* (MO); Morona-Santiago: Cordillera de Cutucú, 1976, *Madison et al. 3358* (SEL).

Peru: Junín: Pichis trail, 1929, *Killip & Smith 26119* (NY, US); Amazonas: Huampami, Quebrada Pantamentsa, 1973 *Kayap 872* (MO, US), Huanuco: Puente Durand, 1938, *Stork & Horton 9441* (UC, K). Cuzco: Atalaya, 1960, *Vargas 13405* (US); Loreto: Puerto Arturo, below Yurimaguas, 1929, *Killip & Smith 27841* (US, NY),

Bolivia: Isapuri, 1901, *R. S. Williams 678* (NY, K); Charopampal Mapiri, 1907, *Mang 1290* (US, NY).

Venezuela: Amazonas: Santa Barbara del Orinoco, 1975, *Berry 640* (MO); Delta Amacuro: Sierra Imataca. 1960, *Steyermark 87314* (VEN); Sucre: El Merey, 1973, *Steyermark et al. 95002* (VEN); Bolivar: Sta. Maria de Erebato, 1974, *Steyermark et al. 109850* (VEN); Miranda: Cerro de Bachiller, 1978. *Steyermark & Davidse 116309* (VEN, MO); Portuguesa: Agua Blanca, 1966, *Steyermark & Rabe 96477* (VEN); Yaracuy: between Salom & Temeria, 1977, *Steyermark et al. 100356* (VEN); Carabobo: Valencia, 1920, *Pittier 9395* (US).

Guyana: NW slopes of Kanuku Mts., Moku-moku creek, 1938, *Smith 3375* (P, K, NY); Pomeroon district, Moruka River, 1927 *de la Cruz 4574* (MO, US, NY); Potaro River Amatuk, 1959, *Whitton 343* (K).

Brazil. Pará: Belem, 1942, *Archer 7486* (US); Ceara: Guaramiranga, 1945, *Cutler 8304* (US, F).

The extensive synonymy cited above is by no means complete; I have omitted a great many subspecific taxa as well as horticultural names from the last century which technically may be validly published by virtue of notes in nursery catalogues or gardening magazines. However, the major synonyms are included.

Caladium bicolor ranges from the Andes to coastal Brazil and north to the Guianas and the Darien region of Panama. It is cultivated throughout the tropics for its showy foliage, and frequently is naturalized near sites of former cultivation. Naturalization of cultivated plants probably accounts for the presence of *Caladium bicolor* in the Antilles.

Most of the high Andean populations of *Caladium bicolor* differ from the eastern South American populations in several respects. The Andean

plants often have perfectly elliptical leaves with the sinus between the posterior lobes completely filled in; plants of this type previously were known as *C. steudneriifolium* Engler. In addition, these populations have more elongate, erect tubers and the leaf laminae are either entirely green or green with scattered white spots. In contrast the plants from Pará and the Guianas have flattened tubers, pronouncedly divergent posterior leaf lobes, and complicated color patterns frequently with red or pink variegations. While the extremes are quite distinct, well over half of the specimens examined in this study are geographically and morphologically intermediate, and it is impossible to subdivide the group meaningfully. Several clones of *C. bicolor*-like plants in cultivation fall rather far from the descriptions given here, but in the absence of any authentic wild-collected specimens I have chosen not to give them formal recognition.

25. Caladium coerulescens Bunting

Caladium coerulescens Bunting, Acta Bot. Venez. 10:284. 1975.

Type: Venezuela: Edo. Trujillo: 10 km above Biscucuyo, 1971, *Bunting 4370* (Holotype: MY, non vidi, Isotype. VEN!)

Terrestrial herb, the corms 4-8 cm thick and ca. 4 cm tall, yellow within, bearing numerous small offsets in the upper part. Leaves 1 or 2, the petioles to 108 cm long and 1.8 cm thick; lamina broadly ovate, ca. 60 cm long and 57 cm broad, peltate, the posterior lobes rounded, united for about 60 % of their length, green to blue-green and glaucous on both surfaces. Peduncle less than half the petiole length. Spathe to 14.5 cm long, the tube ca. 4.8 cm long and 3.3 cm broad, purplish green, the limb white. Spadix ca. 12.5 cm long, the female part ca. 1.8 cm long and 1.3 cm thick, the female flowers with round yellow stigmas. sterile part ca. 4 cm long; fertile male part ca. 6.7 cm long, white.

Distribution: Venezuela, evergreen forest at the slopes of the Andes in the states of Tachira, Barinas, Portuguesa, and Trujillo.

Additional collections seen: Venezuela: Barinas: San Miguel, April 1969, *Bunting et al. 3363* (VEN); Cano Barragan, 1967, *Bunting 2256* (VEN, MO); Tachira: Bramon, on Rubio-Las Delicias road, 1971, *Bunting 4399* (VEN); Portuguesa: Rio Saguas, El Amparo, 1969, *Bunting 3328* (VEN); Trujillo: near Boca del Monte, 1969, *Bunting 3183* (VEN).

Caladium coerulescens is a geographically well-defined variant of *Caladium bicolor* differing from that species chiefly by its much greater size in every dimension and by its glaucous, bluish leaf surfaces.

26. Caladium lindenii (André) Madison

Caladium lindenii (André) Madison, comb. nov.

Phyllotaenium lindenii André. Ill. Hort. 19, t.88. 1872.
Xanthosoma lindenii (André) Engler, Fl. Bras. III, 2:191. 1878.

Type: Colombia, living plant collected by Wallis, cultivated in Belgium by Linden, the illustration accompanying the description (t.88) serves as the type.

Terrestrial herb, the stem more or less globose and fully subterranean. Leaves numerous, the petiole flattened above, to 40 cm long, green with elongate

purple stripes, sparsely covered with a tangled reddish-brown scrufy indument. Lamina sagittate, not peltate, the anterior lobe 12-20 cm long, 6-12 cm broad, the posterior lobes 4-9 cm long, the veins of the leaf variegated, cream to pale green above. Inflorescences solitary or paired, the peduncle 4-8 cm long. Spathe green, ca. 7.5 cm long. Female part of spadix ca. 1.8 cm long, the pistils cylindric with pale yellow bi-lobed stigmas; sterile part of the spadix white, ca.2 cm long, male part ca. 2 cm long, white.

Other material seen: Florida, cultivated, from the nursery trade, *Madison 5916* (SEL).

Though known in horticulture as *Xanthosoma lindenii*, this species has typical *Caladium* floral structures and large solitary pollen grains, indicating its transfer to *Caladium*. The freely suckering habit and handsome variegated leaves make *Caladium lindenii* a much sought after horticultural subject.

27. **Caladium schomburgkii** Schott

Caladium schomburgkii Schott, Oesterr. Bot. Zeitschr. 8:122; 1858.

Type: Guyana: Warapoota, *Schomburgk. s.n.* (K).

Alocasia erythrea C. Koch, Wochenschr. Gaertnerei Pflanzenk. 8. 1861.
Caladium schomburgkii var. *erythraeum* (Koch) Engler, Fl. Brasil. III, 2:160. 1878.
Alocasia argyroneura C. Koch, Wochenschr. Gaertnerei Pflanzenk. 8. 1861.
Caladium schomburgkii var. *argyroneurum* (Koch) Engler, Fl. Brasil. III, 2.160. 1878.
Caladium schmitzii Lem., Ill. Hort. 8, t. 297. 1861.
Caladium schoelleri Lem., Ill. Hort. 8, t. 297. 1861.
Caladium subrotundum Lem., Ill. Hort. 5:60. 1858.
Caladium rubescens N. E. Brown, Gard. Chron. Ser. 3, 14:86. 1893.
Caladium venosum N. E. Brown, Gard. Chron. Ser. 3, 14.86. 1893.

Terrestrial herb, the stem subterranean, subglobose. Leaves several, erect, the petioles 16-23 cm long, dark green or purple; lamina ovate to broadly lanceolate to sub-rhombic, not peltate, often pink or white variegated, with 3-4 pairs of primary lateral veins arising near the base and 1-2 additional pairs arising from the costa, the lamina margins often ruffled. Inflorescence usually solitary, erect, the peduncle 18-26 cm long; spathe ca. 7 cm long, green or reddish below, white or mottled above. Spadix ca. 5 cm long, 5-6 mm thick.

Distribution: The Guianas and adjacent Venezuela.

Additional collections seen: Surinam: Marowijne River, Albina, 1956, *Jonker-Verhoef & Jonker 374* (U, A, NY); Fr. Guiana: Karouany, 1856, *Sagot 612* (K, U); Venezuela: Bolivar: Juan Infante, Río Aparuren, 1953, *Steyermark 76073* (NY).

Caladium schomburgkii is readily identified by its ovate, non-peltate leaves, frequently with ruffled margins, and by most of the primary lateral veins arising from the lamina base. The species is sparingly cultivated, and has been hybridized with *Caladium bicolor* to produce some intermediate forms, notable for their crispate leaf margins.

Scaphispatha Brongn. ex Schott, Prodr. Syst. Aroid. 214. 1860.

Type species. *Scaphispatha gracilis* Brongn. ex Schott.

Tuberous herb. Leaves several, erect, ovate-sagittate and peltate. Peduncle long and slender, spathe constricted. Spadix shorter than the spathe, with female flowers in lower part, each ovary unilocular with several basal ovules; male flowers in the upper part of the spadix mostly comprising 4-merous synandria. Pollen grains solitary.

Etymology: Greek *skaphos*, "bowl," or "boat," and *spatha*, "spathe," referring to the shape of the spathe.

The genus consists of a single species, *S. gracilis*, of Bolivia and Brazil.

28. **Scaphispatha gracilis** Brongn. ex Schott

Scaphispatha gracilis Brongn. ex Schott, Prodr. Syst. Aroid. 214. 1860.

Type. Bolivia: Chiquitos. between San Rafael and Santa Ana, *d'Orbigny 1043* (Holotype: P, Isotype L, non vidi).

Tuber subglobose. 2.3-5 cm in diameter, fully subterranean. Petiole 10-28 cm long, 2.5-4 mm thick; lamina ovate-sagittate, 7-15.5 cm long, 4-7.5 cm wide, light green. Peduncle 23-40 cm long, 2.5-3 mm in diameter. Spathe constricted, 4.5-6 cm long, outside light green with white margins, inside white. Female part of spadix ca. 1 cm long, 4 mm thick, obliquely adnate to the spathe, the flowers ca. 2.8 cm long; male part of spadix ca. 1.3 cm long, yellowish.

Additional material seen: Brazil: Ceara: Serra do Araripe, near Crato, Oct. 1934, *Luetzelburg 25984* (M); same locality, Nov. 1976, *Bogner 1211* (K, M).

An excellent and thorough account of *Scaphispatha* has recently been provided by Bogner (1980), from which the following observations are taken. *Scaphispatha gracilis* inhabits open grassy areas that are temporarily flooded during the rainy season. It is dormant much of the year, showing aboveground growth during the rainy period, usually with the inflorescences appearing before the leaves.

Scaphispatha is somewhat isolated in the Caladieae by its lack of sterile flowers, its rather open spathe at anthesis, and its verrucose pollen. The unilocular ovaries with several basal ovules, but only single-seeded berries, are quite similar to those of *Caladium ternatum*. *Scaphispatha* is probably most closely related to *Caladium* and *Aphyllarum*, representing a parallel series of adaptations to a seasonal environment.

Aphyllarum S. Moore, Trans. Linn. Soc. London , Bot. 4:501. 1895.

Type species: *Aphyllarum tuberosum* S. Moore.

Terrestrial herb with a subterranean tuber. The leaves several, erect, peltate, with 3 parallel marginal veins. Inflorescence erect, the spathe constricted, the female flowers with the ovary unilocular and with 1-2 ovules borne at the base of an intrusive parietal palcenta. Pollen grains solitary.

29. Aphyllarum tuberosum S. Moore

Aphyllarum tuberosum S. Moore, Trans. Linn. Soc. London, Bot. 4.501. 1895.

Type: Brazil: Mato Grosso: Santa Cruz, Nov. 1891, *S. Moore 678* (K).

Herb arising from a subcylindric tuber, the tuber erect, 2-4 cm in diameter, 3-7 cm tall, giving rise to numerous fleshy white roots 3-5 mm thick. Leaves borne after the inflorescences or together with them, erect, the petiole 16-40 cm long, sheathing in the lower 1/4-1/3, 3-8 mm thick in the middle. Lamina medium green above, glaucous below, peltate, sub-sagittate-triangular, nutant from the erect petiole, the posterior lobes equalling or somewhat shorter than the anterior lobe, the tip of the anterior lobe rounded, blunt, or sometimes minutely apiculate, the posterior lobes rounded. Primary lateral veins 2-5 per lobe, marginal veins 3, one at the margin, one ca. 1 mm from the margin, the third 4-6 mm from the margin. Cataphylls erect, triangular, 3-12 cm long, marcescent. Peduncle solitary, erect, 20-80 cm long, exceeding or shorter than the petiole. Spathe 8-12 cm long, the tube green comprising 1/3-1/2 the length, the limb white. Spadix slightly shorter than the spathe, 7-11 cm long, the female portion 1.5-3 cm long, 6-11 mm thick, the flowers with broad, thick styles coherent to those of adjacent flowers; sterile part 1-2 cm long; staminate portion 4.5-6 cm long.

Distribution: Brazil, Mato Grosso

Additional collections seen: Brazil: Mato Grosso: Barra do Garcas, Oct. 1968, *Eiten & Eiten 9134* (US); Río Aripuana below Salto dos Dardenelos, Oct. 1973, *Berg et al. P18562* (NY); 90 km W of Xavantina, Oct. 1964, *Irwin & Soderstrom 6827* (US, NY); 12°49′ S, 51° 46′ W, Oct. 1968, *Harley 10477* (K), 15 km S of English base camp, Oct. 1968, *Sidney & Onishi 1126* (K, NY). 3 km E of km 259 Xavantina-Cachimbo, Nov. 1967, *Philcox et al. 3301* (K).

Aphyllarum tuberosum inhabits seasonally wet grasslands at forest margins in the Planalto of Brazil. Notes on Eiten & Eiten 9134 (US) describe the soil as moist with abundant humus in the wet season, and subject to burning in the dry season. The plants of *Aphyllarum* pass the dry season as dormant underground tubers, sending up inflorescences and foliage after the rains begin. All collections known were made in the months of October and November. In the type collection the inflorescences had appeared but the leaves had not yet expanded, hence the name *Aphyllarum*, 'leafless aroid.' In this the species resembles *Scaphispatha*, which grows in similar habitats. The majority of collections, however, have both leaves and inflorescences, so that the leafless inflorescence can hardly serve as a reliable generic character.

Aphyllarum appears to be closely related to *Caladium* and *Scaphispatha*, with which it shares the characters of large solitary pollen grains, seasonal dormancy, and a reduced number of ovules. From *Scaphispatha*, *Aphyllarum* is most easily distinguished by the well-developed synandrodial region of the spadix, which is lacking in *Scaphispatha*. The condition of the ovary in *Aphyllarum* with 1-2 basal or sub-basal ovules, is approached by *Caladium ternatum* which, however, does not consistently produce single-seeded fruits as does *Aphyllarum*. Because of this close similarity, the placentation characters in themselves do not seem sufficient to warrant generic status for *Aphyllarum*. However, the broad and thick styles coherent to the styles of adjacent flowers as found in *Aphyllarum* are quite alien to *Caladium* while being very similar

to *Xanthosoma*. This allows the interpretation that *Aphyllarum* may be an evolutionary line parallel to but distinct from *Caladium*, suggesting that the best course at present is to retain it as a monotypic genus. Future studies, especially of cytology, may give us a clearer idea of its true affinities.

Additional problematic species:

Caladium akkermansii Bunting, Acta Bot. Venez. 10.281. 1975.

Although I have not seen the type, I have examined two other collections from the type locality, both determined by Bunting, which presumably are conspecific. The morphology of their female flowers and the shedding of pollen in tetrads indicate that the species belongs with *Xanthosoma*. Since it seems to pertain to a particularly confusing array of *Xanthosoma* species, I will defer its correct determination to the specialist in that group. At any rate, it should be omitted from the roster of *Caladium* species.

A specimen at Kew, *Andre 2379*, is annotated *Caladium andreanum* Bogner, sp. nov. ined. The two sheets consist of inflorescences on elongate slender peduncles, and surely represent a species of *Chlorospatha*, though which one I cannot determine. The plants are described as leafless, quite peculiar for *Chlorospatha* since the peduncles are so weak that they cannot support the inflorescence except by being held in the leaf sheaths. The collection is from Colombia, Dept. Antioquia, further north than any other collections of the genus. It may represent an undescribed species.

Also from Colombia are several plants collected by E. Spear of Miami and cultivated at SEL, M, and elsewhere, which may represent undescribed species of *Chlorospatha;* however, they have not yet flowered and their identities remain unknown.

LITERATURE CITED

Bogner J. 1980. The Genus *Scaphispatha* Brongn. ex Schott, Aroideaea 3: 4-12.

Crisci, J. V. 1971. Flora Argentina: Araceae, Rev. Mus. la Plata 11: 193-284.

Engler, A. 1879. Araceae, in D.C., Monog. Phaner. II: 1-681.

———— **& K. Krause** 1920. Araceae-Colocasioideae, Das Pflanzenreich IV 23 E: 1-139.

Madison, M. 1976. *Caladium* and *Xanthosoma*, Phytologia 35: 103-107.

———— 1978. A synopsis of *Caladiopsis*, Contr. Gray Herb. 208:95-98.

Schott, H. 1858. Synopsis Aroidearum, Vindobonae.