# BRANCHING AND FLOWERING HABITS OF CACAO AND PATASHTE.

By O. F. Cook.

## INTRODUCTION.

Cacao and patashte are tropical trees of the family Sterculiaceae. The cacao tree is familiar to botanists under the name *Theobroma cacao*.[1] The patashte is closely related to the cacao, but has been placed recently in a different genus, receiving the name *Tribroma bicolor*.[2] Both trees are widely cultivated among the Indians of Central and South America for the sake of their edible seeds, those of the cacao tree affording the raw material for the manufacture of chocolate.

Features of general botanical interest are presented by these trees in their peculiar habits of branching and floral specializations. The branching habits of the patashte are similar to those of the cacao and in some respects are even more peculiar, so that they afford one of the most striking illustrations of the phenomenon of branch dimorphism. But notwithstanding this general agreement in manner of branching, cacao and patashte differ widely in their habits of flowering and fruiting and the structures of their floral organs.

Though the patashte tree had always been treated botanically as very closely related to the cacao, a detailed comparison of the two trees in eastern Guatemala in 1906 showed so many differences that it seemed necessary to look upon the patashte as the type of a distinct genus. Another visit to Guatemala, in 1914, afforded an opportunity of repeating the observations and of securing additional specimens and photographs. A preliminary account of the genus Tribroma was published in 1915.[3]

The patashte tree, as well as the cacao, produces gourdlike elliptical pods filled with large fleshy seeds, which are used in the same manner

---

[1] L. Sp. Pl. 782. 1753.

[2] **Tribroma bicolor** (Humb. & Bonpl.) Cook, Journ. Washington Acad. Sci. **5**: 288. 1915.

*Theobroma bicolor* Humb. & Bonpl. Pl. Aequin. **1**: 94. *pls. 30a, 30b*. 1808.

[3] Cook, O. F. Tribroma, a New Genus Related to Theobroma. Journ. Washington Acad. Sci. **5**: 287–289. 1915.

as cacao among the native Indians of Guatemala. Though not considered the equal of cacao in quality, patashte is bought readily by the Indians and would undoubtedly find a place in commerce if it could be produced cheaply. Cacao and patashte are among the few articles that can be sold to the Indians for money. But not much cacao is grown in Guatemala and the coffee planters are often obliged to import cacao from the West Indies or from Ceylon to sell to their Indian laborers. The scanty production of cacao seems the more remarkable because the early accounts show that the Spanish conquerers found this tree in cultivation on a rather extensive scale by the Indians of Guatemala. A statement by Acosta, published near the end of the sixteenth century, makes it plain that Guatemala was recognized at that time as the chief center of production of cacao:

> The tree whereon this fruite growes is of reasonable bignesse, and well fashioned; it is so tender, that to keep it from the burning of the Sunne, they plante neere unto it a great tree, which serves only to shade it, and they call it the mother of Cacao. There are plantations where they are grown like to the vines and olive trees of Spaine. The province where there is greatest trade in cacao is Guatimala. There grows none in Peru, but this country yields Coca, respecting which there is another still greater superstition.[1]

Since the patashte grows much more rapidly than cacao and develops eventually into a much larger tree, the possibility of securing profits from plantations of patashte has not altogether escaped the attention of enterprising landowners in Central America. That the patashte might serve as a shade tree in cacao plantations was an especially attractive idea, since most of the trees used for shade purposes yield nothing of direct value to the planter. The largest experiment in the planting of patashte known to us is in the Senahú district of the Department of Alta Verapaz, in eastern Guatemala, on the Trece Aguas Estate of Don Ricardo Fickert-Forst. Agriculturally speaking, the patashte plantation has not met expectations, the soil conditions having proved rather unfavorable, but the experiment afforded an unusually favorable opportunity of comparing the behavior of the two trees under the same conditions of growth.

Another possibility, as yet apparently untried, is that patashte might prove useful as a stock for the vegetative propagation of superior varieties of cacao. The greater vigor of growth shown by the patashte tree might make budding easier and more successful. Trees grafted on patashte might also grow more rapidly or be better adapted to special conditions, or to higher altitudes. At Trece Aguas the patashte trees seemed to have thriven better in the coffee plantations at altitudes of over 600 meters than in the lower valleys where they were planted with cacao.

---

[1] The Natural and Moral History of the Indies, 1590. Hakluyt Society edition **1**: 245. 1880.

## MORPHOLOGICAL AND ECOLOGICAL COMPARISONS.

### DIMORPHISM OF BRANCHES.

The crown of the patashte tree, like that of the cacao, is made up of two entirely distinct kinds of branches. These may be distinguished as uprights and laterals. The tree appears to consist of a main trunk bearing clusters of lateral branches, but when the stages of growth are observed it is seen that all of the primary lateral branches have at first a terminal position, standing at the end of an upright shoot. (See pls. 44–46.)

Though the trunk increases in length by the growth of upright shoots, these shoots do not form a continuous axis, but are strictly self-limiting. This is because each shoot, instead of carrying up a terminal bud to continue its growth, has the terminal bud replaced by a cluster of buds, and these give rise to a whorl of lateral branches. The specialization is very definite. Each of the upright shoots ends with a whorl of lateral branches and no lateral branches are produced except in this way—in whorls at the ends of the upright shoots. The lateral branches are capable of subdivision, but the divisions are always of the nature of laterals, uprights never being produced from laterals.

New upright shoots are formed only from dormant buds on the sides of the old uprights, below the terminal whorls of lateral branches. Thus the trunk is formed by a succession of upright shoots and is not only strictly sympodial but represents a very extreme type of sympodial structure.

As a result of this peculiar method of growth the whorls of lateral branches, though always formed in terminal positions, are brought eventually into lateral positions and appear as lateral clusters of branches instead of as whorls. When a new upright develops just below a whorl of branches the thickening of the trunk, as it were, incorporates the whorl, which remains in its original horizontal position, or nearly so, whereas when an upright starts several inches below the whorl the subsequent enlargement of the trunk throws the whorl over into an oblique position. Doubtless the result is influenced somewhat by the time when the new upright begins to grow. A whorl that had enlarged and formed a thickened woody base would be more difficult to push over into the oblique or lateral position.

---

EXPLANATION OF PLATES 44–46.—Pl. 44, end of an upright shoot of cacao, with a whorl of 5 lateral branches. Pl. 45, uprights and lateral branches of cacao, the leaves of the uprights with long petioles and those of the laterals with short petioles, one of the uprights ending in a whorl of 6 small lateral branches. Pl. 46, upright shoot of patashte ending in a whorl of 3 lateral branches; some of the leaves are removed to give a better view of the petioles.

## PRACTICAL SIGNIFICANCE OF DIMORPHIC BRANCHES.

Attention has been called in a previous publication [1] to the bearing of dimorphism upon cultural problems. After a further opportunity of studying the habits of branching it is still more apparent that the previous estimate of the practical importance of dimorphism is justified by the facts.

The cacao tree takes widely different forms, and these can be controlled by pruning. Left to themselves, most of the trees will produce an open crown formed by a succession of upright shoots and whorls of lateral branches. But some of the trees show a thick, spreading crown of secondary lateral branches. Such trees are preferred for cultural reasons, because they are much more productive. Though now their occurrence is determined entirely by accident, there seems to be no reason why they should not be produced regularly by design. Probably the best course would be to leave only one or two of the whorl branches, or at most three. But the experiment would be worth making with one, for the whorl joint is essentially weak and unsuited to more than temporary existence. With one whorl branch developing secondary laterals, as it might be encouraged to do by pinching off the terminal bud, a low rounded tree can be developed. The formation of uprights would need to be guarded against at first, but after a rounded top has been formed there seems to be little tendency to produce uprights.

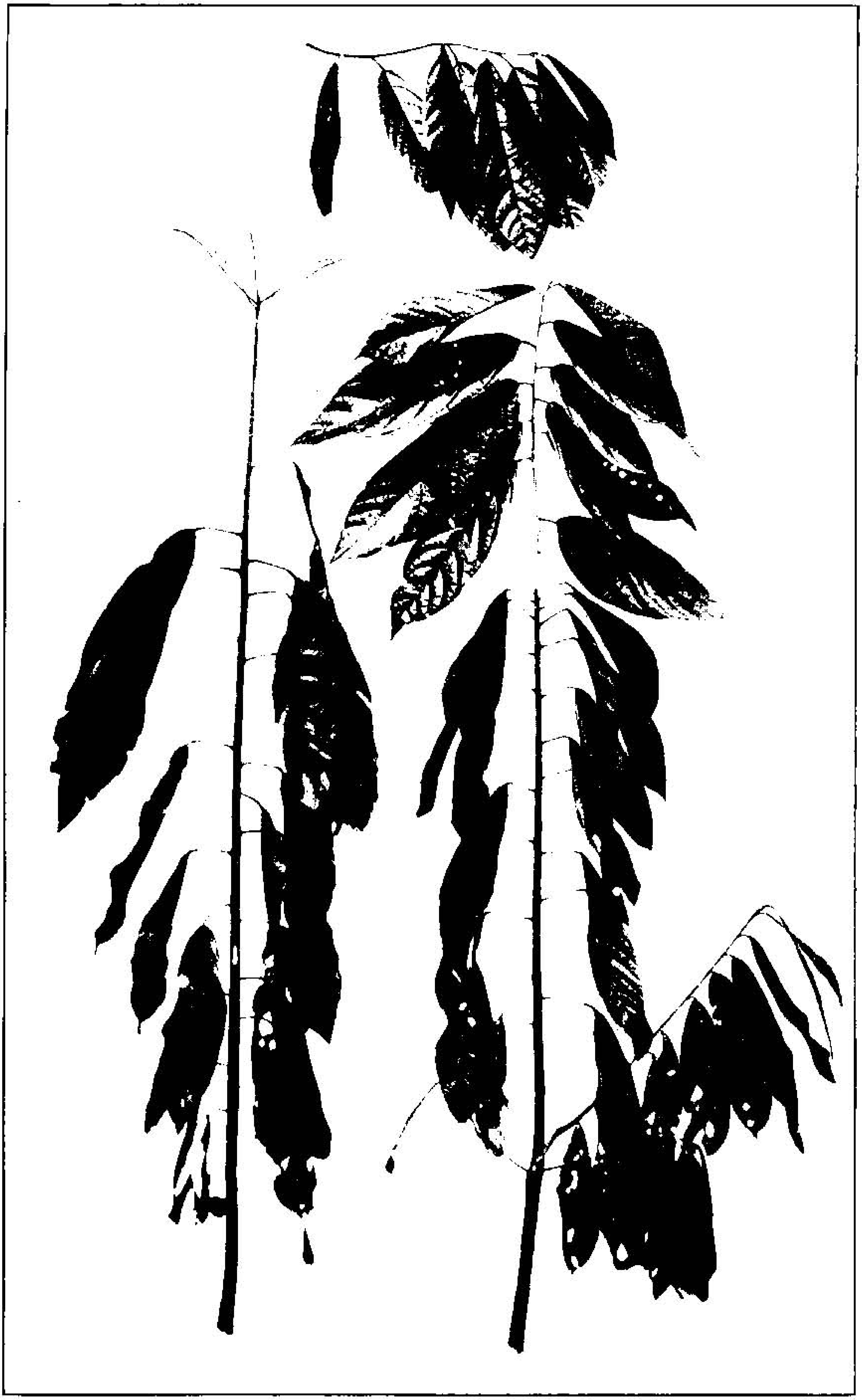
The still more striking specialization of branching habit in the patashte tree serves to emphasize the peculiarities of the cacao tree and to explain the nature of the whorl formation, illustrating also the contrasting forms of top obtainable by controlling the method of branching. But the caulocarpous habit of the cacao tree renders it entirely different from the patashte in many of its biological features. The classification of trees of such widely different habits as species of the same genus tends to obscure the significance of the facts. This difficulty is avoided by recognizing the patashte tree as representing a genus distinct from Theobroma. Unless such differences of habit are clearly recognized there is little hope of applying the facts in the solution of cultural problems.

## NUMBERS OF LATERAL BRANCHES.

Although cacao and patashte have the same method of forming lateral branches in whorls at the ends of upright shoots, there is a definite difference in the number of branches in a whorl. In patashte there are always 3 branches in a whorl, in cacao always more than 3 (pls. 44–46). The usual number in cacao is 5, but occasionally there are 4 or 6. If 6 branches were the normal number, it could be under-

[1] Cook, O. F. Dimorphic Branches in Tropical Plants: Cotton, Coffee, Cacao, the Central American Rubber Tree, and the Banana. U. S. Dept. Agr. Bur. Pl. Ind. Bull. 198. 1911.

UPRIGHT SHOOT OF CACAO.



UPRIGHTS AND LATERAL BRANCHES OF CACAO.

UPRIGHT SHOOT OF PATASHTE.

stood as representing two of the three-branched whorls of patashte. But a greater specialization must be admitted if 5 be considered as the normal number of branches in cacao.

The lateral branches of cacao are usually simple, at least at first, though afterwards producing many secondary laterals from axillary buds. In patashte the primary laterals often have a fork at the fifth or sixth internode from the base, as shown in plate 46. This forking results from the forcing of one of the axillary buds near the growing end of the branch, while the wood is still soft. The development of this bud appears to be almost simultaneous with that of the terminal, while buds of the other internodes remain dormant. The enlargement of the new shoot bends the smaller joints of the primary branch away from it, thus forming an apparently dichotomous fork. Apart from these forks near the base, the lateral branches of the patashte are usually simple, the tendency to produce secondary laterals from dormant buds being much weaker than in cacao, this difference being connected, no doubt, with the fact that the patashte produces its inflorescences on the new growth of the lateral branches, while cacao does not.

### ARRANGEMENT OF LEAVES ON BRANCHES.

Cacao and patashte have the same phyllotaxy, five-thirteenths on the upright shoots and one-half on the lateral branches. This means that there are 13 rows of leaves on the upright shoots, but only 2 rows on the lateral branches. The number 5 in the phyllotaxy represents the number of times that the leaf spiral encircles the stem in passing from any leaf to the next that is directly above it. But it is not obvious that the number of turns in the spiral could have any practical relation to the number of branches developed to form a whorl.

### DIMORPHISM OF LEAVES.

In connection with the dimorphism of branches there is a dimorphism of leaves, the leaves of the upright shoots being consistently different from those of the lateral branches. In cacao the difference is not very striking, being apparent only in the greater lengths of the petioles on the upright shoots. Usually the petioles are about an inch long on the lateral branches and 3 to 4 inches long on the upright shoots (pls. 44, 45). In patashte the disparity in lengths of petioles is much greater. With about the same length of 2.5 cm. for the petioles of the lateral branches, the leaves of upright shoots have petioles often attaining a length of 30 to 33 cm. (pls. 46, 47).

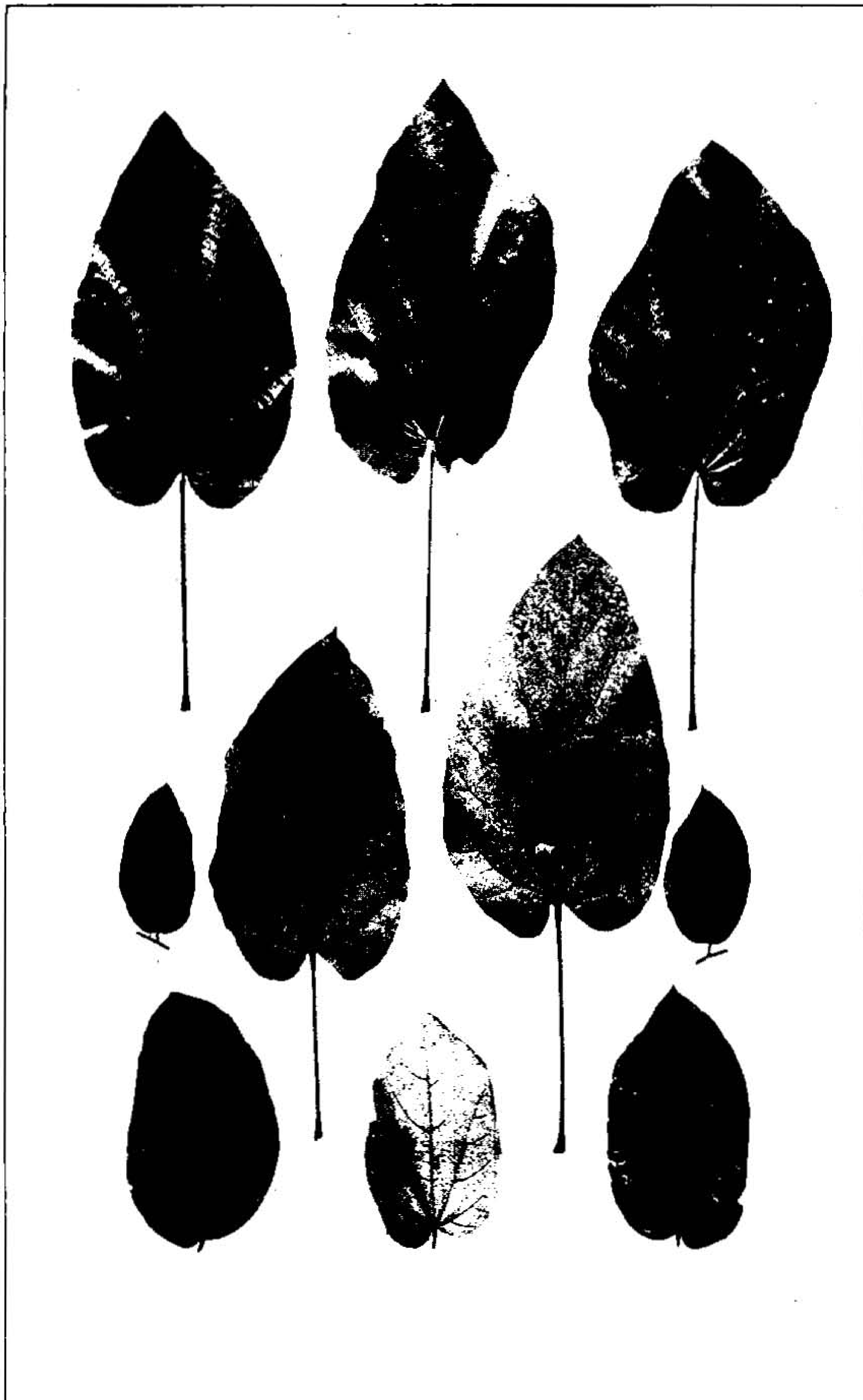
Along with this disparity in lengths of the petioles of patashte there are differences in the sizes and shapes of the blades of the leaves, those of the upright shoots being of a more broadly oval or cordate form, while those of the lateral branches are more nearly oblong or elliptic (pl. 47). Furthermore, the leaves of the uprights have the blades flat, while the blades of the lateral branch leaves are strongly convex above and hollowed beneath. The lateral branches being generally horizontal, the leaves usually hang in a more or less drooping or pendent position, while the leaves of the upright shoots are usually held out flat, or nearly so, at the ends of their long stiff petioles. The position can be changed in accommodation to the exposure, for the petioles have two pulvini, the basal rather small and the terminal very large. If we consider the pulvini as organs distinct from the petiole, the difference between the two kinds of leaves of the patashte appears somewhat greater, in view of the fact that what has been looked upon as a petiole in the case of the lateral branch leaves is entirely of the nature of the pulvini, with nothing to represent the petiole proper, the structural element that intervenes between the basal and apical pulvini of the leaves of the upright shoots. A comparison of the petioles shown in natural size in plates 48 and 49 will make this point clear. From the difference in texture between the petioles and the pulvini it can be seen even from the photograph that the lateral branch leaves have only pulvini and not true petioles. While it would be overtechnical to describe the lateral branch leaves as sessile, instead of as having short petioles, the differences are really greater than the descriptive language implies.

In the case of the cacao there appears to be less in the way of structural differences between the petioles of the two classes of leaves. The petioles of the uprights are not so long and those of the lateral branches are not so short, and there is a definite constriction in the middle, between the thickened ends that represent the pulvini.

## MEASUREMENTS OF PETIOLES AND LEAF BLADES.

The petioles on the upright shoots of the patashte attain a length of 34 cm., or about 13½ inches. Usually the length is about 30 cm. The blades of such leaves are sometimes 50 cm. long by 30 cm. wide, or nearly 20 inches by 11½, the base being broadly cordate, with a rather narrow sinus 5 to 6 cm. deep. Toward the ends of the upright shoots, below the whorls of lateral branches, the leaves are often much reduced in size and the petioles are much shorter. Usually these reduced upper leaves are about 30 cm. long by 20 cm. wide, with petioles 8 to 9 cm. long, but a leaf from just below a whorl was only 22 cm. long and 16.5 cm. wide. The petiole was 5 cm. long and the shallow basal sinus only about 1 cm. deep. These reduced leaves form an apparent transition to the form of leaves shown on the lateral branches as far as size and reduction of length of petiole are concerned, but there is no true overlapping, for very much larger leaves on the lateral

EXPLANATION OF PLATES 47-49.—Leaf characters of patashte. Pl. 47, 5 leaves from an upright shoot, with long petioles, and 5 from a lateral branch with short petioles, to show the general difference in form and size of the blades. Pl. 48, section of upright with base and summit of petiole and lower part of blade, to show the pulvini and the insertion of the veins. Pl. 49, portion of a lateral branch showing petioles and bases of 3 leaves to compare with corresponding parts of upright shoot, plate 48. Pls. 48 and 49 natural size.



LEAVES OF PATASHTE FROM UPRIGHT AND FROM LATERAL BRANCHES.

SECTION OF UPRIGHT SHOOT OF PATASHTE WITH PARTS OF PETIOLE.

PORTION OF LATERAL BRANCH OF PATASHTE.

branches have shorter petioles than even the smallest leaves of the upright shoots. Thus in the shoot represented by plate 46 lateral branch leaves with blades 34 to 36 cm. by 20 to 22 cm. had petioles only 2.5 cm. long, or only half as long as the smallest leaves of the upright shoot.

In the case of cacao, where the petioles are less unequal, larger series of measurements are required to represent the differences. A series of leaves from the uprights shown in plate 45 measured (in centimeters) as follows:

| Petiole length. | Blade length. | Blade width. |
|---|---|---|
| 6. 8 | 33 | .... |
| 8 | 39 | .... |
| 5. 8 | 30 | 8 |
| 5. 5 | 23. 5 | 7 |
| 7 | 30. 5 | 10 |
| 7 | 32 | 9. 8 |
| 6 | 27. 5 | 10 |
| 8. 2 | 44 | 13 |
| 5. 5 | 29 | 8 |
| 5. 5 | 26 | 8. 5 |
| 5. 5 | 26. 1 | 7. 8 |

For comparison with these the following records were taken from the lateral branches shown at the top of plate 45. The uppermost branch, which was 35 cm. long, produced leaves as follows, beginning at the base:

| Petiole length. | Blade length. | Blade width. |
|---|---|---|
| 2. 5 | 26. 5 | 8. 7 |
| 2. 3 | 23. 5 | 8 |
| 3. 5 | 27 | 9. 3 |
| 3. 3 | 33 | 12 |
| 3. 1 | 32. 5 | 11. 3 |
| 3 | 31 | 12 |
| 2. 2 | 25 | 10. 2 |
| 1. 9 | 22 | 8 |

The leaves of another lateral branch, the second from the top of plate 45, were also measured, and the series is interesting for comparison with the preceding, because, although the leaves are very large for a lateral branch, the petioles are shorter than on the other less luxuriant branch:

| Petiole length. | Blade length. | Blade width. |
|---|---|---|
| 2. 4 | 31 (about) | 12 |
| 2. 2 | 33 | 11 |
| 1. 5 | 24 | 9 |
| 1. 4 | 19. 5 | 7 |
| 1. 8 | 26 | 8. 8 |
| 1. 9 | 40. 5 | 12. 5 |
| 2 | 33. 5 | 12 |
| 2. 2 | 41 | 14. 3 |
| 1. 6 | 33 | 12. 6 |
| 1. 6 | 29. 5 | 12 |
| 1. 3 | 24. 5 | 9. 2 |

## VENATION OF LEAVES.

In connection with the greater degree of dimorphism shown by the leaves of patashte, there is another difference. The blades of patashte leaves not only have broader outlines, but show a different arrangement of the veins. The venation of patashte is palmate, while that of cacao is pinnate. Instead of a single strong primary vein or midvein which gives rise to all of the secondary veins, as in cacao, the leaf of patashte has several larger secondary veins, inserted directly on the basal pulvinus, which is broadened at the end to receive them. The structure of the pulvinus and the arrangement of the veins are shown in plates 48 and 49. With several of the veins in direct relation with the pulvinus, one side of the leaf may be raised in advance of the other whereas in cacao the entire leaf blade must be moved as a unit.

The palmate venation of patashte suggests a comparison with the related genus Herrania, which has palmately divided leaves, somewhat like those of the horse-chestnut (Aesculus). But there is little agreement with Herrania in other respects. The leaves of patashte might also be compared with those of some of the American species of Sterculia, such as *S. carthaginensis*.

## POSITIONS OF INFLORESCENCES.

Another very striking contrast is that cacao flowers are borne on the oldest wood, while the flowers of patashte are confined to the new growth, as shown in plates 50 and 51. It is not merely that cacao is caulocarpous while patashte is cladocarpous, but the very extremes of these habits are shown. The cacao tree flowers most abundantly and persistently on the main trunk itself, and more sparingly on the old wood of the larger and smaller branches, but never on the new growth. The contrast could not be made more complete; the cacao tree begins flowering at the base of the main trunk and never bears its flowers in the places where all of the flowers of patashte are borne, at the ends of the growing branches with the new leaves.

In the cacao tree the positions of the flowers in relation to the leaf scars may be studied, although the leaves fall long before the inflorescences appear. It has been learned in this way that the first inflorescences usually arise somewhat above the middle of the leaf scar, in the same relative position as the inflorescence of the patashte. But inflorescences that seem to be truly adventitious are found in other positions, and especially around the swollen bases of

---

EXPLANATION OF PLATES 50, 51.—Pl. 50, inflorescences of patashte at flowering stage, with new leaves near the growing ends of branches. Pl. 51, trunk of cacao tree, producing flowers and fruits directly from the old wood, contrasting thus with patashte, as shown in plate 50. Pl. 50 natural size; pl. 51 reduced.

INFLORESCENCES OF PATASHTE.

TRUNK OF CACAO WITH FLOWERS AND FRUITS.

secondary branches, or on internodes at intermediate points between the insertions of the leaves, and this on shoots that appear to have made regular growth. The question is complicated by the fact that the leaves are often suppressed on some of the internodes, especially toward the ends of the upright shoots, and on the bases of the lateral branches, as shown in plate 45. Yet the suppression of the leaves can not be taken as proof that inflorescences would not be borne afterward in the axillary position, instead of being altogether adventitious. All that can be said with certainty is that the inflorescences often appear in places where no leaves have developed.

In patashte it can be seen that the inflorescences do not come from a strictly axillary position, but appear at one side of a dormant axillary bud, the side that is above the bud when the lateral branch is in its normal horizontal position. But in order to bring all of the inflorescence buds above the axillary buds they have to be placed on different sides of the axillary buds from the standpoint of phyllotaxy, and this must be reckoned as another very specialized feature of the lateral branches.

### PERIODS OF FLOWERING.

In patashte only one inflorescence comes from a bud and only one crop of flowers is produced by each inflorescence. In cacao the floral buds are adventitious, with no apparent relation to the positions of the leaves, and an indefinite succession of new buds is produced from the same inflorescence. In Guatemala patashte seems to flower only during the dry season, consisting of the spring months, ending in May, but cacao produces a constant succession of flowers, though the crop is set rather irregularly, most of it late in the season in eastern Guatemala, after the period of heavy and frequent summer rains. In other districts the planters often speak of two or three crops at definite periods, but these may be determined more by favorable conditions for setting or developing the fruits than by interruptions of flowering.

### STRUCTURE OF INFLORESCENCES.

As might be expected from their different positions and periods of production of flowers the inflorescences are not of the same form. Those of patashte may be described as many-branched, pseudodichotomous panicles or dichasia, solitary in the axils of new leaves, near the ends of lateral branches. The pseudodichotomy consists in the fact that the branch is equal to the main stalk at each subdivision, and the branch and the stalk stand at the same angle to the internode below. The inflorescence as a whole is subtended by a rather large sheathing bract. The basal joints are rather short, and the terminal joints, to which the flowers are attached, are still shorter, both being greatly exceeded by some of the intermediate joints (pls. 50, 52).

In cacao the branching framework of the inflorescence is almost entirely eliminated, or reduced to a very short specialized twig or fruit spur. The joints are reduced to mere rudiments, except the terminal ones, and these are much longer than in patashte. The pedicels of the flowers are usually 2 or 3 times as long as the branches that bear them. For practical purposes the flowers of cacao might be described as almost sessile, on the short, simple branches of a rudimentary inflorescence. In patashte, on the other hand, there is a compound inflorescence with many joints exceeding the length of the pedicels of the flowers (pls. 52, 53).

## STRUCTURE OF FLOWERS.

Though the flowers of the two trees are built upon the same general plan, all of the details of construction seem to be different. The flowers of cacao are not only larger and more ample in all their parts, but each part seems to show a different line of specialization. The pedicels of cacao are longer, the sepals are longer, narrower, and more reflexed, the petals are very much larger with the parts differently proportioned, and the staminodes are of a different form, slender and attenuate in cacao, robust and clavate in patashte. The sepals, petals, and staminodes of cacao are brightly colored, light yellow tinged with pink, while the corresponding parts of the patashte are a dull deep red. Another general contrasting feature is that the inflorescences, pedicels, sepals, and pistils of cacao are beset with long, erect, gland-tipped hairs, the corresponding organs of patashte being very finely pubescent but the hairs appressed and not at all glandular (pls. 52, 53.)

More minutely studied, the floral structures present further differences. The sepals of the patashte, in addition to having a much more broadly triangular form, are not separated completely to the base and do not open as widely as those of cacao, but retain more nearly the same position as in the bud. The tips of the sepals become more strongly inflexed as the flowers begin to wilt, instead of remaining straight or becoming reflexed as in cacao.

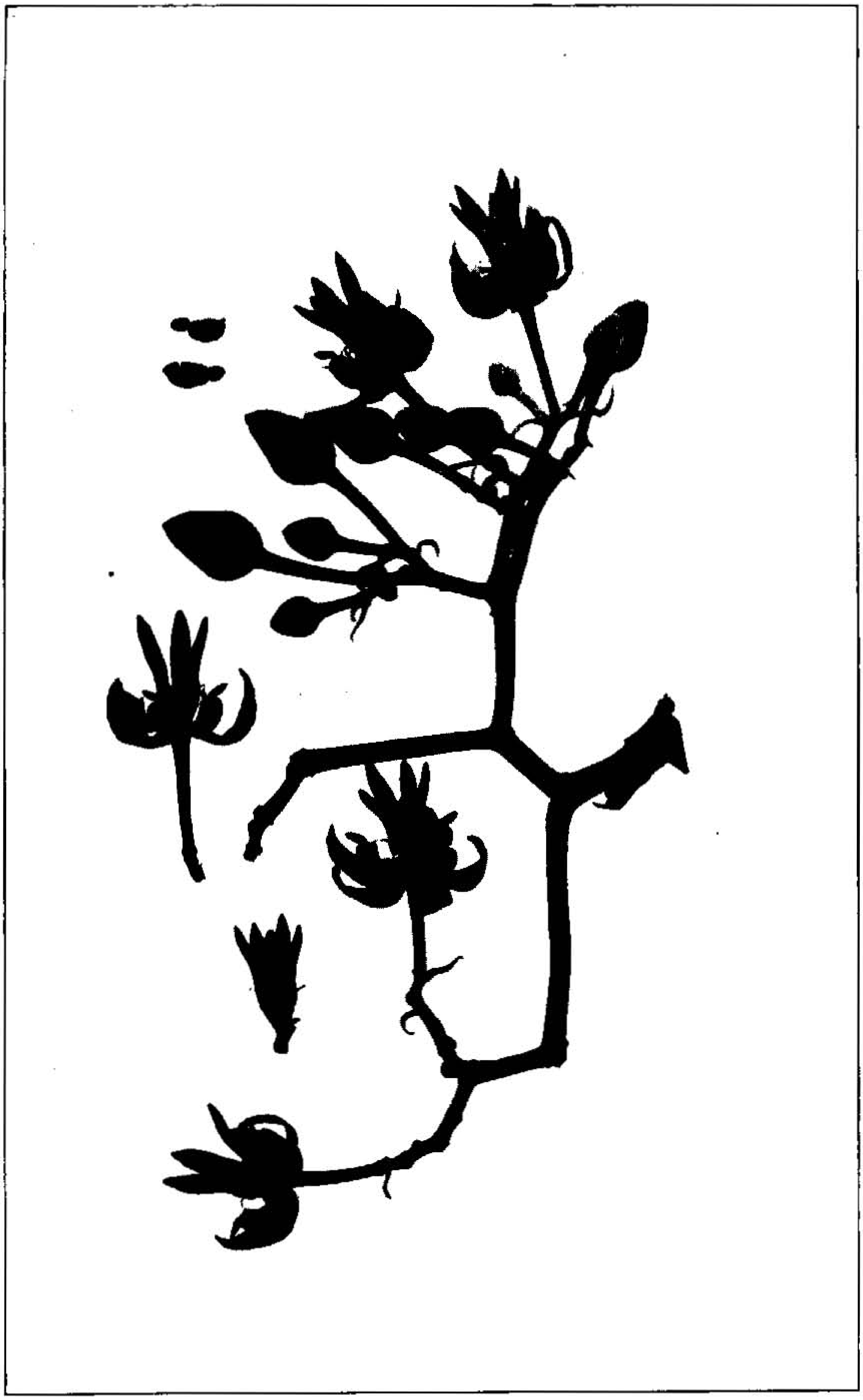
The petals of patashte are much shorter than the sepals, while those of cacao, if fully extended, would be much longer than the sepals. The petals of cacao are divisible into three parts about equal in length, the inflated basal hood for the reception of the anthers, a narrow,

---

EXPLANATION OF PLATE 52.—Inflorescence of patashte, with buds and open flowers and, detached, a flower with part of the sepals and petals removed, and with a cluster of staminodes and 2 petals. Scale about 2½.

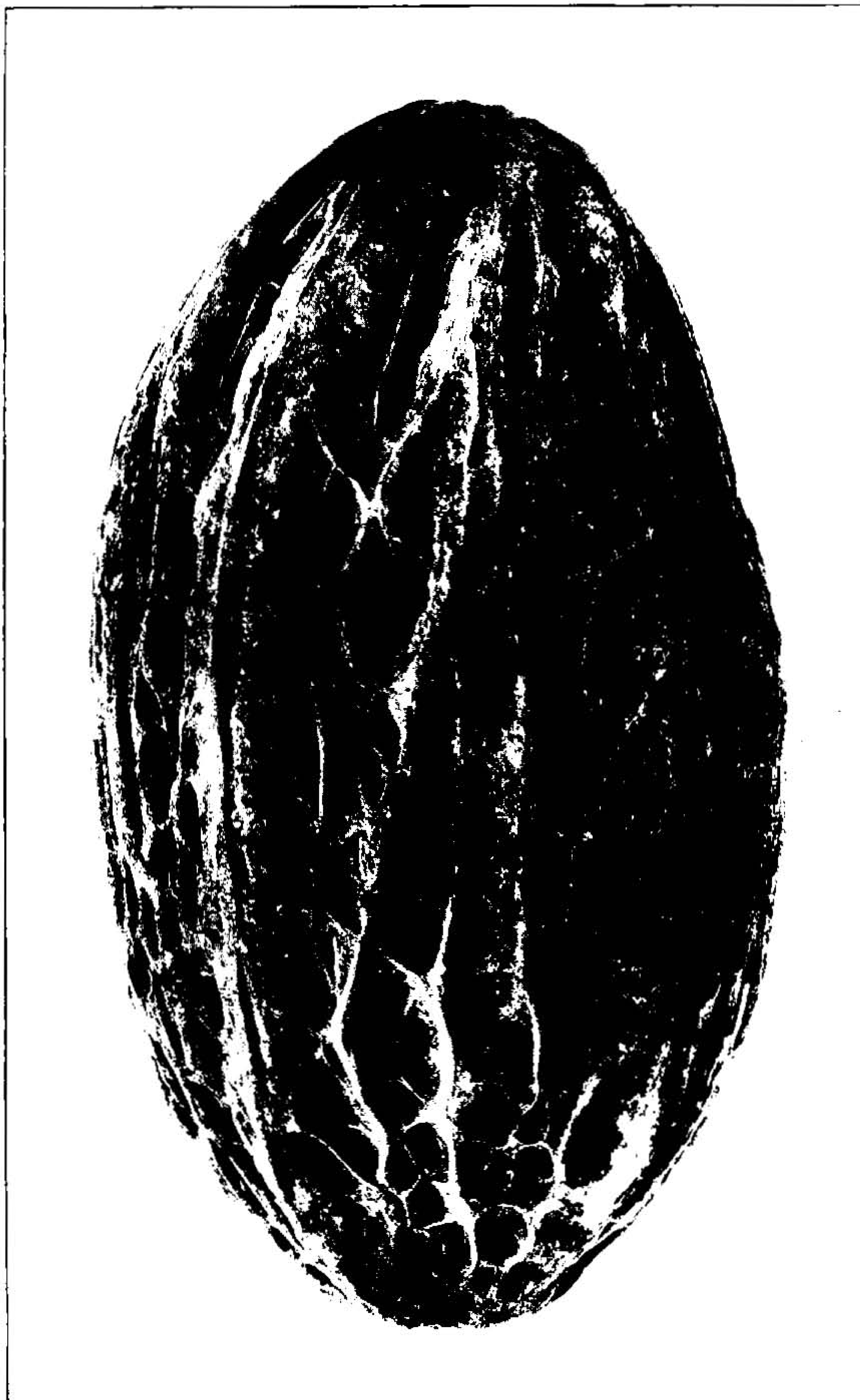
EXPLANATION OF PLATE 53.—Inflorescences of cacao, with buds and open flowers and, detached, 2 complete flowers, a flower with part of the sepals and petals removed, and 2 petals. Scale about 2½.

EXPLANATION OF PLATE 54.—Fruit of patashte, from Hope Botanical Garden, Jamaica. Natural size. Photograph by Mr. G. N. Collins.



INFLORESCENCE OF PATASHTE WITH DISSECTED FLOWERS.

FLOWERS OF CACAO.



FRUIT OF PATASHTE.

strongly reflexed middle portion, or isthmus, and a broadly diamond-shaped terminal expansion, or wing, with rounded lateral angles and an acute, sharp-pointed tip. The hood is strengthened at the base by two prominent parallel ribs, deep red in color, with a short median rib above, but not reaching the base. In patashte the petals are only about half as long as the sepals, the claw and wing being rudimentary and represented by minute paddle-shaped appendages of the hood. The appendage is oval in form, rather thick and fleshy, and with the surface pubescent, while in cacao all of the parts of the petals have naked surfaces. The form of the hood is also different, being much less curved, and the base is strengthened by a single median rib, divided above into three short branches.

The staminodes also show several contrasting characters, being slender, tapering, and needle-like in cacao, while in patashte they are robust, clavate, and blunt-pointed. In cacao there is a lateral compression of the staminodes, in patashte a dorsiventral compression, with shallow grooves on the inner and outer faces. In cacao the lateral faces of the staminodes are hirsute along the middle, while the outer and inner faces are smooth and shining. In patashte the whole terminal portion of the staminode has a close, short pubescence, but not the basal portion. The color of the staminodes is a very deep purplish red in patashte, while in cacao the lateral faces are white and the other faces show bands of purple, though the color is not decurrent upon the staminal tube. In patashte, on the other hand, the darker color of the staminodes is decurrent in broad bands upon the staminal ring. The surface of the ring is naked in patashte, but covered with a whitish pubescence in cacao. The ovary of cacao is rounded and beset with short glandular hairs, while that of patashte is distinctively 5-angled and densely covered with short, nonglandular pubescence. The style of patashte is 5-grooved and more tapering than that of cacao and also somewhat longer, extending beyond the middle of the staminodes.

As mentioned in the introduction, the fruit of the patashte is an ellipsoid pod, large, and large-seeded. For comparison of this with the fruit of cacao see the generic descriptions, page 624, and the illustrations, plates 51, 53.

## FLORAL ADAPTATIONS.

The structure of the flowers of both trees indicates a very definite adaptation for cross-fertilization. Only half of the stamens are functional, the others being modified into large erect staminodes. The functional stamens are not erect but are bent far outward away from the stigma, being held by a notch in the rim of a large inflated hood-like cavity at the base of the petal. Thus the anthers are completely covered and kept from any possibility of contact with the stigma. But in spite of their agreement in this feature of holding the stamens away from the pistil, the floral biology of the two trees is apparently very different.

The caulocarpous habit, shared by cacao with many tropical trees, has been looked upon as an adaptation to favor cross-fertilization by ants or other small crawling insects, but the striking form and conspicuous coloration of the cacao flowers, as well as their highly specialized structure, suggests that flying insects are attracted. The glandular pubescence of the calyx and sepals may also be considered as an adaptation that tends to discourage the attention of small crawling insects.

With the patashte the case is obviously different. The petals, instead of being conspicuous and bright-colored, are greatly reduced, or even rudimentary. The dull color of the flowers and their altogether different position on the tree make it evident that they are not adapted to attract the same class of insect visitors as the flowers of the cacao. The patashte flowers are carried up to the light and are probably visited by bees or other sun-loving, day-flying insects that might never go down into the darkness to find the flowers of cacao. The nonglandular character of the pubescence of the patashte flowers may be significant from this point of view.

A new interpretation of the floral biology of cacao is presented in a recent work by Dr. C. J. J. van Hall. The fact of variation among cacao seedlings is brought forward as evidence that crossing is of frequent occurrence, and the following explanation is given:

This strong intercrossing indicates that the pollen can be transported from one tree to another. The transport might be effected in two ways, either by wind, or by flying insects such as butterflies, wasps, bees, flies—but not by thrips, aphides, or ants, none of which fly at all, and of which thrips and aphis can only move very slowly.

The question whether pollination takes place by wind or by flying insects seemed at first difficult to answer, because the flower of the cocoa does not appear to be adapted to wind-pollinisation, and flying insects were never found. Accordingly, the whole question for long remained a puzzle. Happily, however, a thorough investigation has lately been carried out by Dr. von Faber at Buitenzorg (Java), and this investigation solved the question.

Dr. von Faber has kindly given the present writer a short summary of his results, with permission to incorporate it here. He writes as follows:

"Though the structure of the flower seems to eliminate the possibility of self-pollination, this is really not so. The long and supple flower stalk facilitates the swinging to and fro of the hanging flower by the wind. Experiments proved that by this movement pollen easily falls from the anthers on the pistil of the same flower, and it could be demonstrated that isolated flowers were easily self-pollinated in this way. Self-pollination may therefore be regarded to be the rule in the cocoa-flower. When, however, neighbouring trees stand close to each other, it is also possible that the pollen falls from the hanging blossoms and settles on the pistil of flowers of the neighbouring tree. In this way cross-fertilisation is possible when the trees stand in close proximity, as is the case in all plantations." [1]

[1] Van Hall, C. J. J. Cocoa 54. (London, 1914.)

One can only regret being unable to share the confidence of Dr. van Hall in the statement just quoted. Indeed, it is hard to believe that this account can relate to cacao. It suggests, rather, the question whether there is another tree in Java that could have been mistaken for cacao. As may be seen by reference to the photographs reproduced in plates 51 and 53, the flower stalks of cacao are neither long nor "supple," nor do the flowers hang in a pendent position that would enable them to swing in the wind. The most drooping or nearly pendent flowers often have their petals in contact with the surface of the bark. No doubt some of the flowers might be made to flutter by a strong breeze, but there could be no "swinging to and fro" unless the pedicels were wilted. The stalks are strong enough to hold the flowers rather firmly in place. It may not be impossible that grains of pollen would reach the stigma if the flowers were sufficiently beaten about, but the preference of the tree for moist, sheltered situations and its peculiar habit of producing its flowers in the most sheltered positions are opposed to the idea that it is normally dependent on wind pollination. Even stronger reasons against this view are afforded by the structure of the flower itself, with its reduced number of anthers and the very small quantity of pollen. In several other respects the flowers are as highly specialized as those of orchids, asclepiads, or other groups that are known to be dependent on insects. It would be difficult to find adaptive functions for these specializations under a theory of wind pollination. Indeed, this theory may be said to dismiss the problem of the cacao flower, instead of giving a solution.

The theory that seems most worthy of consideration, on the basis of present information, is that proposed by Uzel, that the pollen may be carried by thrips, a suggestion dismissed by van Hall because thrips is injurious to cacao. Yet this hardly excludes the possibility of a beneficial function being performed by the same insects, or by other members of the same order. Some of the Thysanoptera are very active, free-flying insects, a fact that van Hall seems to overlook. The small size of the chambers that shelter the anthers may be taken to indicate that they are to be entered by small insects. The fact that the stamens are held in a notch of the petals naturally gives an impression that they are to be released or "tripped" by a large insect such as a butterfly, bee, wasp, or fly, but this may prove not to be the case. A small insect could enter the petal hood from the side and bring out pollen without disturbing the stamens. The staminodes also would appear more likely to have a function in relation to small insects, since these organs form a complete ring around the pistil and are hirsute on their lateral faces as if to keep small insects from passing between.

## QUESTION OF NATIVITY.

Obviously, the pollination problem needs to be investigated in the forests of tropical America rather than in Java or elsewhere in the East Indies. The identity of the insect visitors and the true meaning of the floral and other specializations can hardly be determined satisfactorily until the trees can be studied in their native habitats, which are still to be ascertained. The present wide distribution of cacao and patashte, from Mexico to Brazil, is probably due to human agency. The patashte tree was described originally from Colombia, and is said to grow wild in the Amazon Valley. The cultivation of cacao extends along the eastern slopes of the Andes into southern Peru and Bolivia, but in these countries is not supposed to be ancient. There appears to be no native name for cacao in the Quichua language. Nevertheless, one of the varieties of cacao cultivated about Santa Ana in the lower Urubamba Valley in the Department of Cuzco is known as "cacao chuncho," or cacao of the forest Indians, from whom it is supposed to have come.

It does not seem reasonable to believe that trees with such habits would attain extensive distributions through natural agencies. In Guatemala it is supposed that both the cacao and patashte grow wild in the woods, but the trees occur only sparingly and perhaps only in districts that were formerly occupied by the Indians. On the peninsula of Nicoya, on the Pacific side of Costa Rica, wild cacao is more abundant, but still in places that may have been cleared and cultivated by the Indians a few generations ago.

## ECOLOGICAL SIGNIFICANCE OF DIFFERENT HABITS.

The behavior of the patashte at Trece Aguas would seem to indicate that this tree has habits very different from those of the true cacao. It appears to be much less tolerant of shade and better adapted for growing long uprights every year and thus keeping above the surrounding vegetation. The flowers and fruits are carried up to the light on the new growth, instead of being borne on the old wood down in the deep shade. As might be inferred from these habits of growth, the lateral branches seem to be of a temporary nature and apparently live only a few years, producing a few annual crops of flowers, like the lateral branches of coffee. The lateral branches lose their functions as soon as they are covered by new vegetation above. Thus, while the tree might become very tall if growing in the forest, it would probably have only a small crown of a few branches alive at any one time. The trunk would serve only as the support of the few branches and would probably remain very slender. But in open places with favorable soil conditions a more spreading habit is assumed, the lateral branches grow longer, and the uprights are more numerous and divergent. But any tree with these habits of growth would probably be short-lived, for the constant succession of dead branches invites fungous diseases and insect pests.

## LATERAL BRANCHES CONSIDERED AS INFLORESCENCES.

The positions and functions of the inflorescences need to be taken into account in dealing with problems of the origin or nature of the dimorphic branches. In other plants that have specialized lateral branches, such as Gossypium, Coffea, and Castilla, it seems not unreasonable to look upon these branches as inflorescences that are being made to serve vegetative functions in addition to bearing the flowers. The form of the inflorescence, as determined by its method of branching, is closely analogous to that of the lateral branch. It might be easier, from a morphological standpoint, to think of the leaves of the lateral branches as representing large floral bracts than as direct specializations from the form of leaves produced by the upright shoots.

In the case of cacao it seems rather difficult to apply this theory, since it involves the assumption that the cacao tree, or its ancestors, after developing the lateral branches as inflorescences in the manner of patashte, at a later stage of development transferred the flowers to the trunk and other parts of the old wood. This would amount to saying that the cacao tree had removed the flowers from the inflorescences, so that only vegetative purposes are now served by the parts of the tree that were specialized originally for the production of the flowers and fruits in the manner still shown in the patashte. If this view of the caulocarpous habit be adopted, the cacao tree must be taken to represent a more advanced stage of evolution than the patashte.

The fact that the lateral branches of cacao have become more similar to the uprights, both in function and in form of leaves, than those of patashte, could be taken as another indication of more advanced evolution, since it would seem to represent a greater departure from a condition in which the lateral branches functioned as inflorescences. It is quite possible that the nature and extent of the specializations will be found to differ in the other species and varieties of Theobroma, and that these differences will prove useful in classification as well as in the solution of cultural problems. The differences between cacao and patashte that have been considered in the present paper are summarized in the following contrasted descriptions of the genera Theobroma and Tribroma.

## DESCRIPTIONS OF THE GENERA.

### THEOBROMA L.

*Theobroma* L. Sp. Pl. 782. 1753. PLATES 44, 45, 51, 53.

Low, shade-tolerant trees of tropical undergrowth, the lateral branches formed in terminal clusters of 5, rarely 4 or 6.

Leaves elliptic-obovate, narrowed toward the base, pinnately veined, naked on both surfaces, the petioles and young shoots hirsute with stiff erect bristles; leaves of lateral branches of the same form as those of the upright shoots, the petioles somewhat shorter, but the pulvini distinct at each end.

Inflorescences reduced to minute fleshy twigs, only the terminal joints distinct and these shorter than the pedicels of the flowers, produced from adventitious buds on old wood of the main trunk or the larger branches appearing long after the leaves.

Flowers larger than in Tribroma, the sepals and petals both conspicuous, light-colored, widely expanded; sepals narrow, tapering, and reflexed; petals longer than the sepals, strongly curved or folded in the bud, the basal hood with two strong parallel ribs, the limb longer than the hood and with a slender base folded down around the end of the hood; staminodes slender, naked, and tapering above, laterally compressed below, with bands of long hairs on the lateral faces; ovary rounded, covered with glandular pubescence like the sepals and the pedicel.

Fruits obovate or fusiform, with a thick fleshy rind, longitudinally ridged and furrowed, the surface smooth or tuberculate.

### TRIBROMA Cook.

*Tribroma* Cook, Journ. Washington Acad. Sci. 5: 288. 1915. PLATES 46–50, 52, 54.

Slender, erect trees, with strong upright shoots, each ending in a whorled cluster of three lateral branches.

Leaves of upright shoots with long petioles and broadly ovate-cordate blades, palmately veined, naked above, clothed underneath with a very fine dense appressed stellate pubescence, like the surfaces of the branches and petioles; leaves of lateral branches broadly ovate-oblong, subsessile, the petioles very short and representing only the confluent pulvini.

Inflorescences with pseudodichotomous branching, bracted at the articulations, forming a broad loose panicle or dichasium, produced near the ends of the lateral branches, above the axillary buds of the young leaves, entirely confined to the new growth.

Flowers small, inconspicuous, dark-colored, dull reddish purple, the petals minute and the sepals only partly opened; sepals broadly triangular, inflexed; petals much shorter than the sepals, the basal hood with a single median rib, the limb rudimentary, represented by a minute oval, reflexed, nearly sessile appendage; staminodes robust, clavate, clothed above with short pubescence, naked below; ovary 5-angled, finely pubescent like the pedicels, sepals, petals, and staminodes, but none of the pubescence glandular.

Fruits ellipsoid with a very hard woody shell, the surface broken by deep irregular lacunæ.

These descriptions relate, of necessity, to the forms of cacao and patashte that are cultivated in eastern Guatemala, where the comparison was made. It is not to be expected that all of the contrasted features will be shared in the same degree by all of the members of the genera. Some forms of cultivated cacao are less caulocarpous than others, and some have the inflorescence branches along the trunk developed into stout woody twigs. Several of the species now referred to Theobroma are only imperfectly known. Some of them differ widely from the cacao, but apparently without approaching nearer to the patashte. It may be that a more definite recognition of the differences between these two will facilitate the study and classification of the other members of the group by affording a larger series of diagnostic characters.