CACAO AND ITS ALLIES

A TAXONOMIC REVISION OF THE GENUS THEOBROMA

JOSE CUATRECASAS

Introduction

"Celebrem etiam per universam Americam multique usus fructum Cacao appellatum."

CLUSIUS, 1605.

"Cacao nomen barbarum, quo rejecto Theobroma dicta est arbor, cum fructus basin sternat potioni delicatissimae, saluberrimae, maxime nutrienti, chocolate mexicanis, Europaeis quondam folis Magnatis propriae (*βρωμα των θεων*, Vos Deos feci dixit Deus de imperantibus), licet num vilior facta."

LINNAEUS, Hort. Cliff. 379. 1737.

Theobroma, a genus of the family Sterculiaceae, is particularly noteworthy because one of its members is the popular "cacao tree" or "cocoa tree." The uses and cultivation of this outstanding tropical plant were developed in the western hemisphere by the Mayas in Central America a long time before Europeans arrived on the continent. The now universally used name *cacao* is derived directly from the Nahuatl "cacahuatl" or "cacahoatl," just as the name of the popular drink, chocolate, is derived from "xocoatl" or "chocoatl." The economic importance of cacao has given rise to great activity in several fields of development and research, especially in agronomy. Historians and anthropologists have also been very much interested in learning the role played by cacao in the economy and social relations of the early American populations. There exists today an extensive literature devoted to the many problems related to cacao.

I saw cacao for the first time in Colombia in 1932, but became actually interested in the genus in 1939 and the years following, when I found cacao trees growing wild in the rain forests of the Amazonian basin. I was fascinated by the unique structure of the flowers of the cocoa tree, and its extraordinary fruit. My explorations from 1942

to 1947 at the service of the Government of the Valle del Cauca, mainly in the dense, humid forests of the Pacific coast of Colombia and western slopes of the Andes, offered me the opportunity to become better acquainted with wild species of *Theobroma*. I published the descriptions and illustrations of four new species found in that region, and at the same time gathered material for a monograph of the genus. Subsequently in Chicago and Washington I continued these studies, using the collections of the museums there and loans received from important European herbaria. The steadfast cooperation of V. M. Patiño has been of great value to me in several respects, and his explorations have furnished two new species. Jorge León from Turrialba sent me specimens of an outstanding new species. Collections sent to me for identification by the members of the English Colombian Cocoa Expedition (1952–1953) very much helped to broaden my knowledge of many of the species and their distribution. In 1954, I had the opportunity to study the important *Theobroma* collections at the British Museum (Natural History), London; the Royal Botanic Gardens, Kew; and the Muséum d'Histoire Naturelle, Paris, where many *Theobroma* types are preserved. In 1961 (July 11–15) I was allowed to examine several European collections, at that time on loan at the Harvard Botanical Museum, which I felt desirable to see before publishing this revision. On my way to Colombia in 1961 for a general collecting trip, I also visited the living *Theobroma* collection of the Imperial College of Agriculture in Trinidad where some 14 species and several hybrids and varieties are cultivated. I was thus able to supplement my data on the growing system and fruits of some of the species I had not seen living before. For the same purpose I visited the cacao stations of the Interamerican Institute of Agronomic Sciences at Turrialba, Costa Rica.

This publication is restricted to the taxonomy of the genus. Many binomials (see the index) have been published in the past, and there is great confusion with regard to the names in the herbaria and literature. A critical revision was necessary in order to establish the validity of the species and to list synonymy. Although a complete study of the genus would require much more exploration, because of the great gaps existing in the herbarium collections, the present revision of all available materials seems justified. Three critical treatments of the genus have previously been published; Bernoulli (1869) recognized 18 species, and Schumann (1886) 11. Chevalier, in 1946, acknowledged 13 species and a few subspecies; he united some species which should be held separate and on the other hand listed as different others which are actually synonyms. Twenty-two species are recognized in the present work. The number of species in the genus will probably increase in the future, because new explorations

in Central as well as South America will undoubtedly bring about the discovery of new ones.

This revision is based on the classical method of comparative morphology. I have to a large extent used the structure of the fruit and the vegetative characters which I found were basic features in the definition and taxonomy of *Theobroma*. For a better understanding of the genus, some new concepts are also contributed by G. Erdtman in pollen morphology (pp. 442–446), F. W. Cope in cytology and incompatibility in cacao (pp. 446–449), and by W. L. Stern in anatomy (pp. 439–442). These contributions may help in the understanding of the taxonomic problems of *Theobroma*, especially those derived from cultivated varieties. In regard to *T. cacao*, the classification of the various cultivars is provisionally presented in a conservative way; an understanding of the innumerable existing forms of cacao will only be possible after long-term genetic research. Dr. Cope and Dr. Bartley in Trinidad are working in this direction. Dr. Soria in Turrialba, Costa Rica, is engaged at this time in an ambitious project of this kind, largely supported by the American Cocoa Research Institute of Washington.

Due to the nature of this paper, the historical sketch is limited to the works which have contributed basic new data related to the taxonomy of *Theobroma*. The relationships with other groups and within the genus itself have so far as possible been treated objectively, with few hypothetical speculations. The specific descriptions are accompanied by original analytical drawings of the flowers, fruits, and leaves of almost all the species, and the illustrations, carefully supervised by the author, can be considered complementary to the written descriptions. Because of the relatively small number of existing collections, I think it useful to publish the information on herbarium specimens given by collectors; these data, except in special cases, have been translated into English whenever written in another language. However, the numerous herbarium collections of *Theobroma cacao*, mostly from cultivated plants, cannot be identified as to the variety and are therefore not included in the text but simply listed in the index. For the citations of herbaria the abbreviations of Lanjouw's "Index Herbariorum" have been used. The abbreviation Photo F.M. is used to indicate the photographic series of the Chicago Natural History Museum.

The artistic work for most of the illustrations has been carried out by the artists Christopher Reinecke, Maria Luisa Biganzoli, and Gil Cuatrecasas. Their work, consisting of about 35 plates, has been sponsored by the American Cocoa Research Institute; a few other plates had formerly been made by Gustavo Rojas, artist of the

Comisión Botánica del Valle, Colombia, and by Paula Gerard, Chicago.

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I wish to express my thanks to the directors and curators of the herbaria for their aid in the loan of collections and granting of work facilities, particularly to Dr. Albert C. Smith, Assistant Secretary of the Smithsonian Institution; to staff members of the Museum of Natural History, U.S. National Museum, who have checked the manuscript: Dr. Jason R. Swallen, head curator of botany, Dr. Lyman B. Smith, curator of phanerogams, and Conrad V. Morton, curator of ferns; to Dr. E. P. Imle, director of Research of the American Cocoa Research Institute; the Ministry of Agriculture of Colombia; to Mr. N. Y. Sandwith of the Royal Botanic Gardens, Kew, who helped on several occasions with important data and collaborated in the typification of a few species; as well as to Mr. J. E. Dandy, of the British Museum, whose advice was of great help in the typification of *T. cacao* L. Likewise, I extend my thanks to Dr. W. Robyns of Brussels, Dr. H. Melchior of Berlin, Prof. H. Humbert, Prof. A. Aubreville, and Dr. A. Lourteig of the Museum National d'Histoire Naturelle, Paris, Drs. J. Pablo Leyva and A Fernández Pérez of the Instituto de Ciencias Naturales, Bogotá; to my collaborators in *Theobroma* studies, Dr. Victor M. Manuel Patiño, Ing. Humberto Guerrero, Dr. Ovidio Barros and Mr. Luis Willard, all of Colombia, and Dr. L. Aristeguieta, of the Instituto Botánico, Venezuela. I further thank Drs. Cope and Bartley of the Imperial College of Trinidad both of whom were helpful in many ways, and Drs. León and J. Soria of Turrialba, Costa Rica.

The collections used for this revision are the following:

Arnold Arboretum, Harvard University, Cambridge, Mass. (A).
Botanical Museum, Harvard University, Cambridge, Mass. (AMES).
Botanisches Museum, Willdenow Herbarium, Berlin (B).
Bailey Hortorium, Ithaca (BH).
British Museum (Natural History) London (BM).
Jardin Botanique de l'Etat, Bruxelles (BR).
Botanical Museum and Herbarium, Copenhagen (C).
Instituto de Ciencias Naturales, Bogotá (COL).
Edinburgh Royal Botanic Garden (E).
Chicago Natural History Museum (F).
Conservatoire et Jardin Botaniques, Genève (G).
Göteborg Botaniska Trädgärd, Göteborg (GB).
Gray Herbarium, Harvard University, Cambridge, Mass. (GH).
University of Glasgow, Dept. of Botany (GL).
Systematisch-Geobotanisches Institut der Universität Göttingen (GOET).

Staatsinstitut für Allgemeine Botanik, Hamburg (HBG).
Instituto Agronómico do Norte, Belem do Pará (IAN).
Royal Botanic Gardens, Kew, Surrey (K).
Rijksherbarium, Leiden (L).
Botanical Museum and Herbarium, Lund (LD).
Komarov Botanical Institute of the Academy of Sciences, Leningrad (LE).
Botanische Staatssammlung, Munich (M).
Instituto de Biología, México (MEXU).
Museu Goeldi de Historia Natural, Belem do Pará (MG).
University of Michigan, University Herbarium, Ann Arbor (MICH).
Missouri Botanical Garden, St. Louis (MO).
New York Botanical Garden (NY).
Muséum d'Histoire Naturelle, Paris (P).
Naturhistoriska Riksmuseum, Stockholm (S).
Imperial College of Tropical Agriculture, Trinidad (TRIN).
Botanical Museum and Herbarium, Utrecht (U).
University of California, Berkeley (UC).
U.S. National Herbarium (US).
Facultad de Agronomía del Valle, Cali, Colombia (VALLE).
Instituto Botánico, Venezuela (VEN).
Naturhistorisches Museum, Wien (W).
School of Forestry, Yale University, New Haven, Conn. (Y).

Historical Sketch

1605: First citation of cacao in botanical literature, by Charles de l'Ecluse (Clusius) in chapter XXVIII, of his Exoticorum libri decem, under the name *Cacao fructus*. It refers only to the fruit and gives a poor illustration of cacao seeds. "Celebrem etiam per universam Americam multique usus fructum Cacao appellatum."

1623: K. Bauhin mentions for the first time in his books in his chapter "Amygdalus" the cocoa plant as "Amygdalis similis Guatimalensis Avellana Mexicana cujus fructum indigenae Cacao appellant," etc. (Pinax Th. Bot. 442).

1630: The first prints of the Hernandez's Rerum Medicarum Novae Hispaniae Thesaurus appear in which are given descriptions of the cocoa tree under its Mexican name *cacahoaquahuitl* and of four varieties called *quauhcacahoatl*, *mecacahoatl*, *xochicacahoatl* and *tlalcacahoatl* which are distinguished by the fruits diminishing in size from the first to the last, presumably representing cultivars; the pods were called *cacahoacentli* and the useful seeds *cacahoatl;* he also mentions *quauhpatachtli* which undoubtedly refers to *Theobroma bicolor*. His illustration of the first (fig. 223) is clearly cacao Criollo.

1658: W. Piso describes cocoa "De Arbore Cacavifera" and repeats the varieties cited by Hernandez in a long article on cocoa and chocolate. His drawing also represents the Criollo variety.

1688: John Ray, in his Historia Plantarum, gives much attention to cacao and its products in chapter VIII under the title: *Cacao* Ger. *Cacao sive Cacavate* Park. *Cacao Americae sive Avellana Mexicana* J. B. *Amygdalae similis Guatimalensis* C. B. *The Cacao Tree.* He explains that there are four kinds of cocoa trees and under the heading of *Cacava quahuitl* describes the tree, fruits, and seeds which he compares to almonds saying that they are white before ripening and red when fully ripe.

1696: Plukenet, in his Almagestum Botanicum, classifies cacao as an almond, under the name *Arvor cacavifera Americana,* the fruits of which (folliculi) contain some kind of almonds; in his plate 268, fig. 3, a leafy branch with a cacao fruit of the Criollo variety is represented.

1696: Sloane lists *Cacao* in his catalog of Jamaican plants, with a long series of quotations from previous authors and travel writers.

1700: The first taxonomic statement is made by Tournefort publishing the genus *Cacao:* "Cacao est plantae genus auctore clariss. Plumerio" with a single species "speciem unicam novi." He gives a short description and drawings sent to him by Plumier. They distinguish the 5 sepals, the strangulated petals, and a pistil surrounded by a laciniate girdle (staminodes) which develops into a ridged and pointed fruit filled with seeds.

1705: Sibilla Merian gives an illustration of Surinam cacao which proves to represent clearly the Criollo type (26, t. 26).

1710: Ray in his Methodus Plantarum copies Tournefort's description and data to define *Cacao;* there are no changes in the 1733 edition.

1725: Sloane publishes a long article on "The Cacao Tree" in his Voyage to Jamaica (vol. 2) giving the following botanical description (p. 15): "Out of the Body of the Tree, or Branch comes a very small Flower, standing on a half Inch long Footstalk, it is made up of 5 *Capsular* Leaves, 5 crooked Petals, several *Stamina,* and a Stylus, of a very pale Purple color, after which follows the Fruit, which when ripe is as big as one's Fist, bigger in the Middle than at the Ends, which are pointed, it has some *Sulci* and Asperities on its Outside, is for the most Part of a deep Purple colour, the Shell being about Half a Crown's thickness, and containing within it many Kernels of an oval Shape, each of which is as big as a *Pistachia* Nut, having a thin Membrane without which is a mucilaginous Substance in which it lies. The Nuts themselves are made up of several parts like an Ox's Kidney, some Lines being visible on it before broken, and is hollow within, its Pulp is oyly and bitterish to the Taste, made up of many Striae, which tend from the Circumference to the Center." The plate 160 illustrates a leafy branch with oblong-ovoid fruits, 10-ridged and strongly pointed; there are separate drawings of flowers

showing more or less clearly 5 sepals, some petals and (not well defined) 4 or 5 staminode laciniae at the center, but no stamens; seeds, one isolated, some others together covered with pulp are also illustrated. The article gives much information about cultivation, varieties, geographical distribution, and trade in cocoa, and many authors are cited.

1737: Linnaeus (Genera Plantarum) introduces cacao into *Classis 18* of his classification, in *Polyadelphia pentandria* giving it a new name *Theobroma*—meaning "food for the Gods"; the name *Cacao* given by Plumier and Tournefort was rejected by Linnaeus as "barbarous." By the International Code of Botanical Nomenclature, Linnaeus' name prevails. The new genus *Theobroma* was published almost at the same time in the Genera Plantarum and in Hortus Cliffortianus; Linnaeus described the flowers as having 5 stamens, 5 petals and staminodes (folioli nectarii), but only 3 sepals and with 5-celled anthers instead of 4. Linnaeus probably used dried specimens and annotations sent to him by Sloane for his description. He included in *Theobroma* two species: one with "foliis integerrimis," *Cacao*, the other with "foliis serratis," *Guazuma*, both also differentiated by their fruits. In the Genera Plantarum, he gives as the only synonyms and citations Tournefort for *Cacao* and Plumier for *Guazuma*, but in the Hortus Cliffortianus he quotes for Cacao: *Clus.*, *Raj.*, *Tourn.*, *Sloane*, *Mer.*, *Hern.*, *Pluk.*, and *Bauh.* But Linnaeus found out by himself, with the help of Sloane, the number and kind of stamens typical of *T. cacao*. He writes in Hortus Cliffortianus: "Flores a nullo bene depicti, multo minus descripti sunt," and then: "Sloane mihi inspiciendi copiam fecit, videbatur structura exacte sequentis, ab aliis in universum omnibus diversissima." His original description of the stamens, given in the Genera Plantarum ("Filamenta subulata, longitudine nectarii, cui radiorum instar innata: singula apice quinquefida. Antheris in singulo stamine quinque, tectis petalo concavo"), was made on the basis of drawings or flowers sent to him by Sloane, for which reason the flowers of the Sloane herbarium have to be considered as the type of Linnaeus' description. But Linnaeus may have had very scanty material of the flowers, because he described the anthers as 5-celled instead of 4-celled.

1739: Weinmann writes extensively about cacao and chocolate and gives a plate (*277*) which is inspired by Tournefort's illustration using very much imagination in painting it. *Plate 278*, devoted to *Cacao minor*, depicts a very deformed kind of pod.

1739: Elizabeth Blackwell depicted cacao (*pl. 373*) using Miller's specimens and suggestions. The fruit is figured as elongate, pointed

and 10-ridged, although slightly verrucose; it represents the Criollo type.

1741: Geoffroy in his De Vegetabilibus Exoticis has a long article (XIX) *De Cacao* giving detailed descriptions of the tree, fruits, seeds, and their preparations. He calls the attention to the variability of the species in size or thickness of the different organs (especially the leaves and fruits).

1747: Catesby publishes a magnificent colored plate of the cocoa tree in his Appendix to the Natural History of Carolina, etc. (p. 6, pl. 6); the buds are colored red, the petals yellow, the staminodes red, and the fruits orange, obovoid-oblong, 10-ridged and warted, and very pointed; clearly it is the Criollo type. There is a long description of the tree with observations taken from Dampier; of the fruit it is said: "Fruit about the bigness of a swan's egg, but longer, more tapering, and ending in a point. The fruit hangs pendant, and when ripe, has a shell of a purple color, in substance somewhat like that of a pomegranate, and furrowed from end to end, containing in the middle many kernels of the size of acorns, inclosed in a mucilaginous substance . . ." In a later edition (1771) the color of the fruit was changed to dark violet.

1749: Linnaeus, in his Materia Medica, includes *Theobroma foliis integerrimis* (p. 364) with the previous definition and classification; he attributes to it the qualities and virtues of *pinguis, subamara, nutriens, aphrodisiaca, calefaciens.*

1753: Linnaeus gives a binomial name to cacao in his first edition of the Species Plantarum (p. 782): *Theobroma Cacao*, with the short specific diagnosis "*foliis integerrimis.*" He also names a second species *Theobroma Guazuma* with the diagnosis "*foliis serratis.*" To the bibliographical citations are added: "*Mat. Med.* 364," "*Geoffr. Mat.* 409," and "*Catesb. car.* 3. p. 6. t. 6." Inasmuch as the first edition of Linnaeus' Species Plantarum is the official beginning publication date for phanerogams by the Code of Nomenclature, *Theobroma cacao* receives here its official nomenclatural start, the generic name being in accordance with the diagnosis given in the corresponding edition (fifth) of Linnaeus' Genera Plantarum.

1754: Linnaeus, in the fifth edition of Genera Plantarum, defines *Theobroma* and gives it the same classification (Polyadelphia pentandria) as in the first edition. Linnaeus did not improve his knowledge of the genus nor change his concepts of it in later works. In the third edition of Species Plantarum (1764), and also in the twelfth edition of Systema Naturae (2: 508. 1767) he keeps the same treatment of *Theobroma* as in his earlier publications.

1754: The generic name *Cacao* is validated, according to the present Code of Nomenclature, by Miller in his fourth abridged edition of

"The Gardeners Dictionary." As in his popular sixth (1752) and eighth (1768) and other later editions of the Gardeners Dictionary, Miller publishes, without or with slight variations, a long article on "Cacao," "The Chocolate Nut." He explains that "This genus of plants was constituted by Father Plumier, who communicated the characters, which he had drawn in America, to Dr. Tournefort, who has inserted it in the Appendix of his Institutions. Dr. Linnaeus has joined this to the *Guazuma* of Plumier, under the title of *Theobroma*, but as the fruits of these plants are very different from each other, I shall keep them under different genera. We have but one species of this plant, which is Cacao."

1763: Adanson separates *Cacao* (*Theobroma*) from *Guazuma*, but, while the latter is kept in the family "Les Tilleuls," *Cacao* is placed in the family "Les Pistachiers," side by side with *Diosma*, *Triopteris*, *Acaju*, *Hugonia*, etc., far away from its true relationships.

1765: A disciple of Linnaeus, Antonius Hoffmann, presents to the Swedish Royal College of Medicine the first doctoral thesis ever proposed dealing with a *Theobroma* subject, "Potus Chocolatae." It is an excellent review of the knowledge about the composition and ways to prepare the chocolate at that time and the nutritional and medical importance of it. Hoffmann gives a more detailed description of the cacao plant and the fruit than did Linnaeus, probably inspired in Geoffroy; he writes: "Fructus magnitudinem et figuram refert Melonis, sed verrucosus est, decem angulis instructus et superne acuminatus; dum maturescit, fit colore coccineus atque maculis variegatus flavis; intus continet nucleos circiter triginta, qui magnitudine Olivas aemulantur ac *pulpa* obteguntur albida, subdulci et amaricante. Olei magna scatent hic nuclei copia, quod expressum vocatur *Pinguedo de Cacao*." (1769, p. 257.)

1775: A disciple of Linnaeus, Jacobus Alm, in his doctoral dissertation Plantae Surinamenses republished ten years later in Amoenitates Academicae, emends the Linnaean description of the cacao flowers. He recognizes sterile stamens ("stamina alia 5, castrata") in what Linnaeus called "nectaria," alternate with the other "stamina fertilia solitaria"; he corrects Linnaeus also in seeing the calyx "pentaphyllus" and the anthers "quadriplici."

1775: Aublet, in his explorations in French Guiana, found wild species of *Theobroma*, which he describes extensively in his Histoire des Plantes de la Guiane. He names them *Cacao guianensis* (pl. 275) and *Cacao sylvestris* (pl. 276); he quotes "cacao" as a Caribbean name used. To the cultivated cacao, which he also found, he gives the new name *Cacao sativa*. It is unfortunate that Aublet mixed up elements of three species in describing his two new species; *Cacao sylvestris* was pictured from concordant parts of foliage and fruits

which agree well with the species at present known as *T. subincanum*, but the flowers mentioned in his description were from *T. cacao*. *Cacao guianensis* was described and depicted from branches and foliage identical to *Cacao sylvestris* (= *T. subincanum*) and its flowers were taken from specimens of *T. cacao;* the fruit is the only different part, belonging to a third species. Aublet's descriptions and drawings are detailed, this being the first publication giving an accurate idea of the cacao flowers and of the fruits of some wild *Theobroma*.

1785: Lamarck, in his famous Encyclopédie Méthodique, lists *Cacao* as belonging to the family of *Cacaoyers* characterized by hermaphrodite and complete flowers with 5 petals, 5 or 10 stamens and superior, usually 5-celled ovary; other genera of the family were: *Ambroma, Guazuma, Ayenia, Buttneria*, and *Kleinhovia*. He points out its close relation to *Hermannia, Tilia*, and the Malvaceae. He describes three species: *Cacao sativa, C. sylvestris*, and *C. guianensis* with the remarks mostly taken from Aublet.

1789: A. L. Jussieu (Genera Plantarum) places *Theobroma* in Classis XIII, Ordo XIV (Malvaceae), of his system including it in his section V, (bis!) characterized by mixed fertile and sterile stamens connate at base; here *Theobroma* is associated with *Pentapetes* L., *Abroma* Jacq., *Guazuma* Plum., *Melhania* Forsk., *Dombeya* Cav., *Assonia* Cav., and *Byttneria* L.

1791: Gaertner, in his remarkable book on fruits and seeds, gives a good description of cacao and drawings of its fruits and seeds, which represents a Criollo form; undoubtedly, Gaertner had at hand a dried specimen, for the section of the pod is drawn relatively thin and he describes it with "cortex sublignosus." The specific name used by Gaertner, *Cacao minus*, is a nomenclatural synonym of *Theobroma cacao;* Gaertner mentions *Theobroma foliis integerrimis* Linn., besides Sloane and Blackwell.

1791: Schreber, in the eighth edition of Linnaeus' Genera Plantarum, divides Classis XVIII in two subclassis, Decandria and Dodecandria. He places *Theobroma* in Decandria, a new concept, while *Bubroma* (a new name for *Guazuma*) and *Abroma* are brought into the *Dodecandria*. Schreber points out as differences between *Theobroma* and *Bubroma*, that the first has "laminae subrotundae acuminatae" and "antherae in singulo filamento duae," while *Bubroma* has "laminae semibifidae," "antherae in singulo filamento tres," and "capsula non dehiscens muricata."

1791: Gmelin, in the 13th edition of Linnaeus' Systema Naturae (vol. 2, p. 1151), includes *Theobroma* in Polyadelphia Decandria together with the genus *Abroma*. He still lists *T. Cacao* and *T. Guazuma* as species of *Theobroma*, adding another: *Theobroma guianense*, a new combination based on Aublet's *Cacao guianensis*.

1796: Salisbury publishes *Theobroma celtifolia*, which is a synonym of *Guazuma ulmifolia*.

1796: Lamarck (Tableau Encyclopédique) publishes illustrations of *Theobroma Cacao, fig. 1* representing flowers, copied from Aublet's plate, *fig. 2* the smaller form of *T. cacao* illustrated by Gaertner, and *fig. 3* a correct drawing of flowering and fruiting branches of a Criollo cacao (not *T. guianense* as stated).

1802: Willdenow, in his edition of Linnaeus' Species Plantarum, follows the treatment of Schreber, including *Theobroma* in Polyadelphia Decandria and *Bubroma* and *Abroma* in Dodecandria. Still only two species are considered: *T. cacao* and *T. gujanensis*.

1806: Humboldt and Bonpland, in Plantae Aequinoctiales, a magnificent work, publish the first perfect botanical description of a species of *Theobroma*. It is supplemented with two plates illustrating leafy and flowering branches, fruits, seeds, and flowers of *Theobroma bicolor*, found by the authors cultivated in Colombia. The drawings show details of the embryo; the staminodes are wrongly figured as pointed instead of obtuse.

1808: De Tussac, in Flora Antillarum, writes extensively on the cacao tree, its cultivation and uses, under the heading *Cacao Theobroma*, giving "Le Cacaoyer Theobrome" as the French and "The Chocolate Tree" as the English name. There is a plate in folium (pl. XIII) showing illustrations of orange yellowish, 10-ridged fruits, attenuate at both ends, foliage, floral details, and the embryo. De Tussac is so enthusiastic about the use of chocolat that he says "le chocolat est au corps, ce que le café est à l'ésprit" (p. 103).

1811: Poiret, in the supplement to Lamarck's Encyclopédie, makes the new binomial *Cacao bicolor*, a combination based on the Humboldt and Bonpland species.

1812: Stokes, in his Botanical Materia Medica, publishes a new name, *Theobroma integerrima*, for *T. cacao* L.

1823: Kunth, in Humboldt, Bonpland, and Kunth, Nova Genera et Species Plantarum, gives a good description of the genus *Theobroma* and of the two species *T. cacao* and *T. bicolor;* the description of the androecium is entirely correct: "Filamenta 10, basi in urceolum connata; quinque petalis opposita dianthera; quinque alterna sterilia, lineari subulata. Antherae didymae biloculares, in petalorum cavitatae reconditae." Kunth gives a good description for the family Büttneriaceae R. Brown and for the five sections in which it is divided (Sterculiaceae, Büttneriaceae verae, Lasiopetaleae, Hermanniaceae and Dombeyaceae). *Theobroma* (jointly with *Guazuma, Abroma, Glossostemon, Büttneria, Ayenia,* and *Commersonia)* are placed in the Büttneriaceae verae which have the stamens "10–30. Filamenta magis minusve connata; quinque, laciniis calycinis opposita,

antheris destituta, alius formae. Antherae didymae, longitudinaliter dehiscentes."

1824: De Candolle, in his Prodromus, accepts also family status for the Byttneriaceae (as Ordo XXVI) and follows the classification of Kunth, except for calling the sections divisions. In the tribe Byttneriaceae he includes the same seven genera, plus another doubtful one. In his treatment of *Theobroma* he includes five species, three already known, *T. cacao*, *T. guianensis*, and *T. bicolor* and two new ones, taken from the Mexican flora of Mociño and Sessé: *T. angustifolia* and *T. ovatifolia*. Mociño and Sessé had written an unpublished Flora of Mexico supplemented by a series of illustrations, which were copied at Geneva by artists hired by De Candolle.

1826: Sprengel, in the sixteenth edition of Linnaeus' Systema Vegetabilium, keeps *Theobroma* in Polyadelphia (Classis XVIII) and divides it in three genera: *Theobroma* with 2-antheriferous stamens and *Bubroma* and *Abroma* with 3-antheriferous stamens. He lists five species in *Theobroma: T. cacao*, *T. bicolor* Humb., *T. speciosum* W. herb., *T. ovatifolium* Sess., and *T. guianense* W. The genus *Bubroma*, considered synonymous with *Guazuma* Poir., comprises five species: *B. Guazuma*, *B. tomentosum*, *B. polybotryon* W., *B. grandiflorum* W. herb., and *B. Invira* W. Of these *B. grandiflorum* is actually a *Theobroma*. In *Abroma*, Sprengel included two species: *A. augustum* L. suppl., and *A. fastuosum* Salisb. New *Theobroma* species in this publication are *T. speciosum* and *B. grandiflorum*.

1827: Descourtilz, in his picturesque Flore Médicale des Antilles, dedicates much space to the description of the cacao tree "Cacaoyer cultivé," to its origin, cultivation, varieties, uses, etc. Plate 266 represents a leafy branch with flowers, seeds, and a fruit which is of the Criollo type (10-ridged, very warty, and acute).

1828: Voigt publishes a description of a *Theobroma guianensis* without mention of *Cacao guianensis* Aublet ("fol. acuminatis cordatis sublobatis inaequaliter eroso-dentatis, subtus tomentosis, ramis petiolisque ferrugineo-hirtis, corymbo terminali. Flores albi, parvi). According to some of the features given (corymbo terminali, flores albi), the plant described does not belong to *Theobroma*.

1830: Sweet, in Hortus Brittanicus, listed four species under *Theobroma* mentioning a new binomial, *T. caribaea*, with no description. It is undoubtedly a name for a form *T. cacao*.

1830: Martius, who observed and collected many Theobromas on his trips throughout Brazil, says that more species may be found growing wild in tropical forests; he gives an account with short descriptions of the species found by him in Brazil, of which three are new species: *Theobroma subincanum* Mart., *T. sylvestre* Mart., and

T. microcarpum Mart.; the other species listed are *T. cacao* L. (=*T. sativum* Lam.), *T. speciosum* Willd. ?, and *T. bicolor* H. et B.

1831: Don, in A General History of the Dichlamydeous Plants, places *Theobroma* in the family Byttneriaceae, tribe Byttnerieae DC. He gives good descriptions of these groups and of *Theobroma*, and short definitions for six species with some special attention to *T. cacao*. The other species listed are: *T. guianensis*, *T. bicolor*, *T. angustifolia*, *T. ovatifolia*, and *T. sylvestris*, the last being a new combination for *Cacao sylvestris* Aubl.

1831: Martius, in his Reise in Brasilien (p. 1127), explains that the cocoa from Pará and Rio Negro is of a lower, more bitter quality, because it comes more often from wild cacao trees than from cultivated trees. He also says that he found *T. bicolor* growing wild in Barra do Rio Negro, in Manacurú, and Yapurá.

1840: Endlicher, in his Genera Plantarum, gives excellent descriptions for the Ordo CCXI Büttneriaceae and its six tribes, two of them being new: Eriolaenae and Philippodendrae; the other four are the same as those of Kunth and De Candolle, except for the Sterculiaceae which are treated as an order apart united with Bombacaceae and Helicteraceae. He includes in *Büttnerieae* DC. the genera *Rulingia*, *Commersonia*, *Abroma*, *Büttneria*, *Ayenia*, *Theobroma*, and *Guazuma*. The genus *Glossostemon* is placed in the Dombeyaceae.

1847: Dietrich, in his Synopsis Plantarum, describes briefly nine species of *Theobroma* and gives a new name, *Theobroma Martiana*, for *T. sylvestris* Mart.

1856: Karsten describes *Theobroma glaucum*, a new species from eastern Colombia.

1861–1870: Baillon studies the development of the parts of the flower in *T. cacao*. The primordia of the sepals appear successively one after another, emerging above a common basal annulus. The petal primordia appear simultaneously and have the same aspect as in flowers of most other plants, but when they develop, there appears a strangulation which divides them into two articulated parts; the basilar parts are valvate, the upper parts contorted. The staminode primordia, opposite to the sepals, appear before those of the fertile stamens, which are opposite to the petals, and develop a simple filament which divides into two, each branch having an anther whose two thecae become superimposed. The five primordia of the carpels opposite to petals have a half-moon shape; they become connate and develop alternate growths at the joints which are the primordia of the walls; these are centripetal and progressively divide the ovary into five cavities. Primordially, the placentation is parietal, becoming axile when the carpelar walls reach the axis; the ovules develop two integuments, become anatropous and placed in two rows in each

cavity, with the raphe, outside facing each other, horizontal. The embryo at first has ovate-orbicular entire, flat cotyledons; later these develop folds becoming corrugated. The initial transparent albumen is absorbed and at the end disappears.

1862: Triana and Planchon, in Prodromus Florae Novogranatensis, list three species of *Theobroma* for Colombia (*T. cacao*, *T. bicolor*, and *T. glauca*) and three species of *Herrania* (*H. pulcherrima*, *H. albiflora*, and *H. laciniifolia*). *T. cacao* is only given as cultivated.

1862: Bentham and Hooker (Genera Plantarum 1: ix, 216), following basically the lines of De Candolle, although using other terms, classify *Theobroma* in the series Thalamiflorae, cohors VI Malvales, ordo XXXII Sterculiaceae and tribus VI Buettnerieae. The chief characters for the tribe are the hermaphrodite flowers, concave petal base, and anthers 1–3 alternating with staminodes; it is divided into two groups: *) the fertile stamens with 2-∞ anthers (*Glossostemon*, *Abroma*, *Theobroma*, *Herrania*, *Guazuma*), **) the fertile stamens with a single anther (*Ayenia*, *Buettneria*, *Rulingia*, *Commersonia*). With the main characters of most of the genera already known, good defining descriptions are given for each of them.

1869: Bernoulli attempts the first monograph of *Theobroma*. After a long time of field study in Central America and using the herbarium collections preserved at Berlin, Kew, and Munich, Bernoulli became so well acquainted with the genus that he was able to draw a very good natural classification of it. The five sections established by him, based on flower and fruit characters, may be entirely kept today, strongly reinforced by other more recently known characters. When he started the study, there were only four or five species known besides *T. cacao;* and he writes, "Actually nobody knew these species, because the extremely short diagnoses of the old species were completely insufficient to determine them, for which reason there was the greatest confusion in the nomenclature in the herbaria that I had the opportunity to see." Bernoulli found that flowers and fruits give constant characters, whereas the leaves only give some secondary characters, especially the basal nervation; he also noticed that in some species there is great variation in the shape and pubescence of the leaves, with all transitions from one to another form when abundant material is compared. The basic characters used by Bernoulli for his system are: petal appendix or ligula sessile, subsessile or stipitate; staminodes erect or reflexed in bud, subulate, claviform, or petaloid; stamens 2-antheriferous or 3-antheriferous; fruit, when it was known; calyx 5- or 3-parted with narrow or broader lobes. With combinations of these features the following five sections (the descriptions here abridged) result.

1. *Cacao:* Petal ligule stipitate; staminodes erect, subulate; stamens 2-antheriferous; calyx 5-parted, the laciniae equal. Fruit ovate-oblong.
2. *Oreanthes:* Petal appendix subsessile; staminodes erect, subulate; stamens 3-antheriferous; calyx 5-parted, the laciniae equal.
3. *Rhytidocarpus:* Petal appendix subsessile; staminodes erect, claviform; stamens 2-antheriferous; calyx 5-parted, the laciniae equal; fruit woody.
4. *Telmatocarpus:* Petal ?; staminodes erect ?, linear-subulate with broad base; stamens 3-antheriferous; calyx 5-parted, the laciniae equal; fruit ovate, lacunose.
5. *Glossopetalum:* Petal ligule stipitate; staminodes reflexed, petaloid; stamens 3-antheriferous; calyx irregularly 3-5-fid, "foliaceous"; fruit sublignose.

Bernoulli describes 18 species, some of them extensively, others very briefly, according to the material he had at his disposal. Of these, 12 species are described as new. In sectio *Cacao* he includes 4 species: *T. cacao* L. and 3 new ones: *T. pentagona,* "cacao lagarto" from Guatemala; *T. leiocarpa,* "cumacaco" from cultivation in Guatemala; and *T. saltzmanniana* from Bahia, Brazil. In sectio *Oreanthes* he includes *T. speciosa* Willd. ex Spreng., and 2 new species: *T. quinquenervia* and *T. spruceana,* both from Brazil. Sectio *Rhytidocarpus* with one species, *T. bicolor* Humb. & Bonpl. (synonym, *T. ovatifolia* DC.), and, as doubtful, also *T. glauca* Karst. In sectio *Telmatocarpus* there is a single species, *T. microcarpa* Mart. In the sectio *Glossopetalum,* the largest, he describes in some detail *T. angustifolia* DC., *T. subincana* Mart., *T. sylvestris* Mart., and as new species *T. macrantha* from Brazil, *T. ferruginea* from Peru, *T. obovata* from Brazil, *T. alba* from British Guiana, and *T. nitida* from Brazil. About "Cacao guyanensis" Aublet, he writes "bleibt somit eine vollstandig ungewisse Art. Sie scheint auch von keinem weiteren Autor gesehen worden zu sein, sondern immer nur nach Aublet citiert zu Werden." Bernoulli quoted *Herrania* as a genus differing from *Theobroma* in the habit of the plant and in the 5-6-foliolate digitate leaves. Bernoulli's work is illustrated with several drawings. This monograph was published by the Swiss Society for Natural Sciences in its new serial of Memoires, vol. 24, no. 3, in 1871. However, a reprint was issued previously in pamphlet form in 1869, which is the effective date of publication. (See Pritzel, 1872; Sargent, 1912).

C. G. Bernoulli was born in Basel, Switzerland, Jan. 24, 1834, and died in San Francisco, Calif., while returning home, May 18, 1878; he lived in Guatemala from 1858 until 1878 and collected plants and animals extensively in Central America.

1873: Baillon publishes excellent comparative descriptions of the genus based on *T. cacao* in his Histoire des Plantes. He includes it in the family Malvaceae which includes the Sterculiaceae and Bomba-

caceae; the family is divided into twelve series, the sixth being the *Buettnerieae* with 12 genera: *Buettneria, Ayenia, Commersonia, Rulingia, Theobroma, Herrania, Guazuma, Scaphopetalum, Leptonychia, Abroma, Maxwellia,* and *Glossostemon.* The main characters given for the tribe are the usually hooded petal base, the fertile stamens opposite the petals, the staminodes alternate with the petals, the bilocular anthers (rarely 3-locular), the plurilocular ovary, and the capsular or carnose fruit.

1882: D. Morris of Jamaica, in his well-known book on cultivation of cacao, after describing the cacao plant and fruit, publishes the first known classification of its varieties based upon the nomenclature of some of the best estates of Trinidad. He distinguishes two great classes (p. 12), the second being divided into several varieties:

> Class I. Cacao Criollo (Red).
> Class II. Cacao Forastero.
> var. *a.* Cundeamor verugoso amarillo (yellow), (rough yellow Cerasee)
> *b.* Cundeamor verugoso colorado (red), (rough red Cerasee)
> *c.* Liso amarillo (yellow), (smooth yellow)
> *d.* Liso colorado (red), (smooth red)
> *e.* Amelonado amarillo (yellow), (yellow Melon)
> *f.* Amelonado colorado (red), (red Melon)
> *g.* Calabacillo amarillo (yellow), (yellow Calabash)
> *h.* Calabacillo colorado (red), (red Calabash)

This is the first valid publication in the nomenclature of the cultivars of *Theobroma cacao.* Morris goes on to say that before the "blast" or plague that almost exterminated cacao plantations in Jamaica before the end of the seventeenth century, the Criollo class was the only kind cultivated there. Since then, the Criollo has been entirely discarded for the hardier Forastero, the Criollo being "now chiefly confined to the mainland (Venezuela) where its yield, though small, is considered of great value" (p. 13). This assertion determines that the nomenclatural type of the Criollo cultivar is the Venezuelan Criollo. Of the Forastero varieties the best are the Cundeamor, the yellow kind being preferred for yielding a larger proportion of seeds. The seeds of Cundeamor "are mostly of the true almond shape—large, plump and full, of a pale crimson colour in the interior, and ferment easily." The Liso variety is closely allied to the former. The Amelonado is intermediate between Cundeamor and Calabacillo, and is considered as of good quality. The Calabacillo is the lowest quality and, Morris says, "never cultivated by a judicious planter; its fruits are small, the seeds flat, angular, intensely bitter and of dark crimson colour."

1886: Schumann, in his Vergleichende Blüthenmorphologie, makes an accurate morphological analysis of eleven genera of Büttnerieae,

especially of *Büttneria, Ayenia, Commersonia, Rulingia, Guazuma, Theobroma,* and *Abroma,* and tries to figure out the existing relationships between them and other Sterculiaceae genera. He concludes that the genera treated have a very close relationship and constitute a very natural group. Schumann sees in the Sterculiaceae two series, one of which is the main series (Hauptreihe), with a floral diagram C_5, P_5, Std_5, A_5, G_5, where P.A.G. are opposite; these elements are either normally developed or modified by division or abortion; to this series belong as the leading tribe, the Büttnerieae, followed by Sterculieae, Helictereae, Lasiopetaleae and part of Hermannieae (*Melochia, Dicarpidium, Waltheria*). The other division of the Sterculiaceae differs in having a floral diagram with the carpels opposite the sepals, this includes the Dombeyeae and *Hermannia.* He sees very close relationships between Büttnerieae and Lasiopetalae, which have to be artificially separated, and also between *Büttneria* and *Ayenia,* between *Theobroma* and *Guazuma,* and between the last and *Scaphopetalum* and *Leptonychia.* There is no direct relationship between the two series of the Sterculiaceae, the Dombeyeae being close to the Malvaceae. Schumann does not see a way to explain this and decides not to draw any evolutionary hypotheses.

Schumann describes the calyx of *Theobroma* as pentamerous or with three divisions, the sepals often concave and slightly cucullate, the petals sessile or shortly unguiculate. The inner glands of the receptacle are pluricellular and stipitate-globose or flagelliform; their function is unknown. The staminodes are more or less carnose. The ovules are in 2 rows in the ovary cells, but the seeds become uniseriate. The pulp of the seeds is mucilaginous and includes fine, curled, spiralish fibres.

1886: Schumann, in the Flora Brasiliensis, gives a synopsis of *Theobroma,* describing with detail and accuracy its recorded species. But he does not follow the well-based system of Bernoulli. Schumann includes the genus *Herrania* in *Theobroma* as section *Herrania,* leaving the other species as section *Eutheobroma.* He uses the shape of the petal lamina and the staminodes and the number of anthers in a single stamen as secondary characters to classify the species using as the primary character the many-flowered or few-flowered inflorescence, a very vague feature in many instances. The keyed species in the first group are *T. Cacao, T. bicolor,* and *T. speciosum,* and in the second group, *T. microcarpum, T. grandiflorum, T. subincanum,* and *T. angustifolium.* Four species are listed outside of the key as "dubiae": *T. glaucum* Karst., *T. silvestre* Mart., *T. Martii* Schum., and *T. album* Bern. Two excellent illustrations are given for *T. Cacao* and *T. grandiflorum.* Schumann reduces to *T. Cacao* three Bernoulli species, *T. leiocarpum, T. pentagonum,* and *T. salzmannianum,* which

he thinks were based on insignificant variations of fruits or petals of this polymorphic species. Also he considers the flowers of *Cacao guianensis* Aublet as being *T. Cacao*, whereas the foliage and fruit is possibly *T. subincanum*. Bernoulli's *T. quinquenervium* and *T. spruceanum* are reduced by Schumann to varieties of *T. speciosum*. Schumann transfers *Bubroma grandiflorum* Willd. to *Theobroma*, citing as a synonym *T. macranthum* Bern. *T. obovatum* Kl. ex Bern. was not well known to Schumann, who makes it a synonym of *T. subincanum*. In short, the 18 species listed by Bernoulli are reduced by Schumann to 11, four of these being dubious to him.

Schumann places *Theobroma* in the family Sterculiaceae, tribe IV Büttnerieae, characterized mainly by cucullate petals. This is divided into two subtribes, corresponding exactly to the two groups made by Bentham and Hooker, but Schumann gives them names: a) Theobrominae, defined as having 10 or 15 stamens and the base of petals cymbiform, and b) Büttnerinae, distinguished by having 5 stamens and the petal cucullus incurved at apex. *Theobroma* is the principal genus of the first, differing from *Guazuma* by its baccate fruit, lack of perisperm, and scarce, mucilaginous endosperm; *Guazuma* has lignose fruits, a developed perisperm, and lacks endosperm.

1890: Schumann in his treatment of the Sterculiaceae for Engler and Prantl's Die Natürlichen Pflanzenfamilien divides *Theobroma* into three sections: 1) *Herrania*, 2) *Eutheobroma* (2-antheriferous stamens) with *T. cacao* and *T. bicolor*, and 3) *Bubroma* (3-antheriferous stamens) with *T. angustifolium*, *T. ovatifolium*, *T. grandiflorum*, and *T. subincanum*. There are good illustrations. Schumann divides the family into eight tribes, *Theobroma* belonging to the fifth, Büttnerieae, characterized by hooded petals. It is divided into subtribe Büttnerinae with single stamens and Theobrominae with bundled stamens; the first includes *Rulingia*, *Commersonia*, *Büttneria* and *Ayenia*, and the second *Glossostemon*, *Scaphopetalum*, *Leptonychia*, *Abroma*, *Theobroma*, and *Guazuma*.

1890: Gómez de la Maza publishes *Theobroma tomentosa*, based on *Guazuma tomentosa*.

1892: Hart modifies the Morris classification of the varieties of *T. cacao*, removing Calabacillo from the Forastero group and making with it a third class, as follows:

Class I. Criollo or fine thin-skinned.
1. var. *a*. Amarillo
2. var. *b*. Colorado

Class II. Forastero or thick-skinned cacao.
3. var. *a*. Cundeamor verugosa amarillo.
4. var. *b*. Cundeamor verugosa colorado.
5. var. *c*. Ordinary amarillo.
6. var. *d*. Ordinary colorado.

7. var. *e*. Amelonado amarillo.
8. var. *f*. Amelonado colorado.

Class III. Calabacillo, or small-podded, thick, smooth-skinned, flat-beaned.

9. var. *a*. Amarillo.
10. var. *b*. Colorado.

Hart makes extensive and sound comments on the characteristics and qualities of each variety, saying, among other considerations, that "The finest cacao is by general consent admitted to be produced by the Criollo variety, and this is assumed to be identical or similar in character to that called the Caracas variety." (pag. 48). "The characteristics of the Criollo cacao are the thinness of its pod, its rounded beans and pale colour of the interior of the bean on section. The leaves of the tree are small when compared with the Forastero varieties, and the tree itself is not nearly so sturdy and thriving, and does not produce such regular and abundant crops as the Forastero and Calabacillo varieties. The skin of the bean itself is thinner, and the interior has but a small proportion of that bitter flavour which is characteristic of the unfermented bean of Forastero and especially that of Calabacillo. The flattest beans are those produced by pods of the Calabacillo type. The beans of Forastero are intermediate between these and the rounded form of the Criollo." (p. 51). Hart illustrates his important pioneer work with not too good illustrations of pods and its sections of Amelonado, Calabacillo, Forastero and Criollo, and with three diagrammatic sections of typical seeds of Criollo, Forastero and Calabacillo. He adds, however, that there will be found intermediate forms hardly reconcilable with any of the figures, so that "these are to be taken as representative only of the typical varieties with some latitude."

Hart's illustrations are not representative of the concepts for which the same nomenclature is generally used outside Trinidad: For instance, the figure given as Criollo represents the type Cundeamor, and the models he used to illustrate Calabacillo were not well selected. These facts explain the comments made some years later by Preuss about Hart's somewhat confusing nomenclatural concepts.

1898: John Donnell Smith describes a new *Theobroma* with yellow flowers and smooth cylindrical pods which Pittier and Tonduz discovered in the mountains of Costa Rica, *T. simiarum*.

1899: Jumelle publishes an excellent monographic compilation on cacao with a long chapter devoted to the botany following an interesting account of its history. Disregarding the work of Bernoulli, Jumelle follows Schumann in his treatment of the Sterculiaceae in the Flora Brasiliensis, declaring that "C'est certainement l'étude la plus complète et la plus consciencieuse qui ait été faite sur les *Theobroma*." Then he gives in French Schumann's complete key for seven

species. He recognizes that several species have been published before, based on weak characters, probably due to variations caused by cultivation or changes of soil or climate. Jumelle devotes much attention to the description of *T. cacao* and its different varieties. He follows in this the works, experiences, and classification of Hart. Chapters with descriptions and accounts are also devoted to *T. bicolor* (and separately *T. ovatifolium*), *T. angustifolium*, *T. subincanum*, *T. grandiflorum*, *T. speciosum*, *T. microcarpum*, and *T. glaucum*. Short notes are given to *T. sylvestre* Mart., *T. Martii* Schum., and *T. album* Bernoulli. Although excellent as a compilation, Jumelle's publication offers nothing original with regard to the systematics of *Theobroma;* its many illustrations were taken from Bernoulli, Schumann, and Hart.

1899: De Wildeman publishes a new binomial, *Theobroma Kalagua*, with a description and illustrations of leaves, flowers, and fruit. Unfortunately, this "new species" was based on separate elements belonging to different trees and different species from unknown localities, sent to de Wildeman by a Mr. Ch. Patin, at that time vice consul of Belgium in Panama. Although the specimens used for the description were claimed by Patin as having been collected from a single tree, Patin himself recognized later that they came from different trees and that the fruits were from *T. simiarum*. At that time, Panama was part of Colombia and that is the reason why the new species and the specimens were labeled as from Colombia.

1900: In a second work, Hart makes no alterations in his 1892 classification, stating that "after the lapse of some years I still see no necessity to revise the list." But he extended his comments on characteristics, variations, and properties of the cacao varieties with new considerations, as for instance: "Calabacillo is certainly as far removed from Forastero, as Forastero is from Criollo, as seen in plantations of the present day, when every intermediate form from Criollo down to Calabacillo can be seen linking the whole in one continuous chain of varieties. To properly classify Cacao, we must first know what the originals were like, and it is clear that at the present time, it is hard to decide exactly what were the forms assumed by the older types of Cacao fruit. There is an apparent consensus of opinion however which points to the thin-skinned and bottle-necked variety as the original Criollo (Spanish for Creole), and this is quite confirmed by the Criollo being discovered in the virgin forest of an uncultivated part of Trinidad" (p. 52).

The Criollo as well as the cacao of Java and Ceylon, the Criollo of Central America and *T. pentagonum* have the seeds white or almost white inside. The best quality Forasteros have the seeds slightly violet, and the Calabacillo strongly colored. He adds that the best

qualities of fruits of Venezuela (e.g., from Ocumare) are distinguished by the lightness of the seeds, and their shape, although the pod might belong to the type of Forastero. In Trinidad, in the Estates where certain strains of cacao from the continent had been introduced, we find the finest qualities of Forastero. The illustrations, with a similar nomenclature, are less clear than those of first edition.

1901: Paul Preuss publishes the first important field report ever written with keen observations on the varieties of cacao, conditions of cultivation, conditions and ways of preparation, and qualities of the products in several countries of South and Central America. It is the report of his trip made during 1899 and 1900, in order to obtain information on tropical crops for the Colonial-Economic Committee of the German government. From Surinam he names three varieties of *T. cacao* as cultivated: "Surinam," also called "Porcelaine" (corresponding to the Amelonado of Trinidad), "Aligator" (the Cundeamor of Venezuela and Trinidad), and "Caracas" (similar to Carupano or Forastero from Trinidad). He also observed mixed intermediate forms. From Trinidad and Grenada, where he saw extensive plantations, he describes several cultivars: "Amelonado," "Calabacillo," "Sangre de toro," "Forastero," "Criollo"; he mentions that Hart calls Criollo what is called Forastero in Venezuela and that Hart's Forastero is the Venezuelan Criollo. But according to Preuss, the formerly general use of the name Forastero in Trinidad applied to cacaos other than Criollo. At present, Forastero has the same meaning as Trinitario, which might have been introduced from the Venezuelan eastern coast or from the Orinoco region, after the earlier Trinidad plantations (all of the Criollo type) had been destroyed by some kind of disease. Preuss goes on to describe the three main Trinidad varieties using the concepts of Hart: "Forastero," "Amelonado," and "Calabacillo." He compares the yellowish variety of Amelonado to the Guayaquil cacao and the elongated form of Forastero to the Colombian cacao. Of Venezuela, Preuss says that it is the classic land of Criollo, producing large seeds with thin shell of the best quality. He distinguishes two main cacao varieties in Venezuela: 1) Cacao Criollo, 2) Cacao Trinitario. Preuss clearly distinguishes seven types, but there are also many intermediate forms.

1. Angoleta.
2. Cundeamor (Cundeamor legitimo, with red shell and Cundeamor amarillo, with yellow shell).
3. Carupano legitimo (Carupano grande, and Carupano mestizo, red with yellow).
4. Carupano parcho (yellow fruit).
5. Carupano Taparito (yellow or brownish).
6. Sambito (red or yellow, short, thick, rather smooth fruit).

7. Trinitario amargo or "Cojón de toro" (red or red brownish, smooth, blunt or shortly attenuate pointed fruit).

He describes the Criollo tree and mentions its three varieties: "Criollo legitimo" (the best quality) with deep red, "Criollo amarillo" with yellow, and "Criollo mestizo" with yellow and red shells. The seeds are white violet in the first and white in the second. Preuss sees in Ecuador a great uniformity in the cacao fruits as he had observed in no other country. They are of the Amelonado type, the same type being cultivated in the Cameroons, St. Thomé, Grenada, and Surinam; the Ecuadorian type has thicker shells. He mentions four varieties: "Arriba," "Balao," "Machala," and "Bahia." He says that cacao is frequent in the underlayer of the rain forests in Ecuador and that these wild trees, which cannot be distinguished from those of the plantations, also produce good fruits, which have very thick shells and roundish seeds in section. Preuss sees in this wild cacao the origin of the widespread plantations of the variety Amelonado (p. 247). *Theobroma bicolor* is also mentioned as a wild cacao ("cacao blanco," "bacao") in Ecuador.

From Central America he describes the native variety "Cacao Lagarto" (Alligator), the other native variety Criollo and two others introduced, the "Cauca" from Colombia, and "Trinitario" from Trinidad; in this Trinitario he distinguishes the three types Forastero, Amelonado and Calabacillo. There are intermediate forms between Lagarto and Criollo "Cacao del pais" difficult to separate one from another; they have red and yellow pods with a thin shell and white-violet or white cotyledons. The seeds of Nicaraguan Criollo are the largest of all varieties and of the best quality known. Mention is made and illustrations are given of *T. bicolor*, *T. angustifolium*, and *T. pentagonum* from Central America. Also drawings of fruits and seeds of five varieties of *T. cacao* (Nicaraguan and Venezuelan Criollo, Calabacillo, "Cundeamor Legitimo," and "Curupano grande") are reproduced.

1902: De Wildeman gives a taxonomic compilation of *Theobroma* in his book on tropical cultivated plants. Following Schumann he divides the genus in *Herrania*, *Eutheobroma*, and *Bubroma* and uses Schumann's key for the species (as in the Flora Brasiliensis), but adds another species, *T. simiarum* Donn. Smith, and accepts *T. pentagonum* as different from *T. cacao;* altogether, nine keyed species and four doubtful additional ones, as by Schumann, besides Herranias, are treated. For each species, summarized descriptions, native names and uses, geographic location, and miscellaneous comments, are given. Speaking of *T. simiarum* he writes: "Il faut rapporter en partie à cette espèce la plante que nous avons décrite, en 1899, sous le nom de *T. kalagua*, dont la description avait été fait sur de feuilles,

des fleurs et des fruits ne provenant pas de la même plante." Some attention is given to *T. cacao* and the differences between its seeds and those of *Herrania mariae*, based on anatomical sections and gross chemical analysis made by Heim. The varieties of *Theobroma cacao* are reduced to ten "series" distributed in three "grand" groups—I) Criollo with two varieties: 1) amarillo, 2) colorado; II) Forastero with varieties: 3) cundeamor verrugosa amarillo, 4) cundeamor verrugosa colorado, 5) amarillo, 6) colorado, 7) amelonado amarillo, 8) amelonado colorado; III) Calabacillo with varieties: 9) amarillo, and 10) colorado.

1904: Lignier, in a list of the Caen City Herbarium, mentions *Theobroma sativa,* as a Sagot collection from French Guiana without further comment on the author or synonym; it probably refers to *Cacao sativa* Aubl.

1904: Huber, a botanist at the Goeldi Museum, Belém do Pará, inaugurates a new epoch by publishing direct observations on the botany, ecology, and location of species of *Theobroma.* Huber found spontaneous and subspontaneous trees of *T. cacao* in several places of Amazonia and believes that it may really be indigenous in the forests of the Alto Purús Rio, Río Ucayali, and other places down to Santarém and Obidos.

1906: Huber extends his explanations on the indigenism of *T. cacao* on the alluvian soils of the Rio Alto Purús, in the inundatable forests around the mouth of Rio Acre, and along the rivers Ucayali, Japurá, Juruá, and Madeira. Among observations on other species (*T. microcarpum, T. speciosum, T. obovatum* (as *T. sylvestre*), *T. subincanum,* and *T. bicolor*) he shortly describes a new species from Peru, *Theobroma sinuosum* Pavon.

1906: Huber publishes a variety *coriaceum* of *T. speciosum* found in Brazil. At the same time, he mentions having found *T. cacao* growing wild in a forest near the Canchahuaya Lake.

1908: Chevalier, in his extensive studies on cacao crops in western Africa, besides detailed descriptions of the cocoa tree and its growth and ecology in Africa, mentions its variations and describes a new species, *Theobroma sphaerocarpa,* distinguished by its globose, almost smooth fruit 9 to 11 cm. in diameter, which has been cultivated for a long time on the island of São Tomé.

1911: Hart, in the introduction of his book on cacao, gives an excellent account of the varieties of the cultivated cacao, discussing the external features of the chief different types and the qualities of their crops:

"The species known as *Theobroma cacao,* covers innumerable varieties or forms, differing in shape of pods, in size and vitality of trees, in bearing capacity, and in colour, shape and quality of the bean.

The many names under which varieties of this tree (*Theobroma cacao*) are known, do not constitute species, but must be merely considered as varieties of one species. These varieties probably owe their origin to seed variation and cross-breeding, together with the local influence of soil and climate, but it would serve no useful purpose to record the names by which they are known, as these differ in each district, in each plantation, and in each country where they are grown" (p. 2).

"We have therefore a classification under *Theobroma cacao* carrying fourteen types under three classes, but it must be understood that these are separated by no definite margin, and that intermediate forms will be found on estates showing every conceivable form of variation" (p. 3).

Hart's classification here amplifies his initial one of 1892, mainly by broadening the concept of Criollo, in which class he includes types known under this name outside Trinidad a long time before.

THEOBROMA CACAO

Class I. Criollo

Trinidad Criollo.

(1) Var. *a*. Amarillo = Yellow, thin-skinned, bottle-necked.
(2) Var. *b*. Colorado = Red, thin-skinned, bottle-necked.

Venezuelan Criollo.

(3) Var. *a*. Amarillo = Yellow, thick-skinned, high-shouldered, sometimes pointed.
(4) Var. *b*. Colorado = Red, thick-skinned, high-shouldered, sometimes pointed.

Nicaraguan Criollo.

(5) Var. *a*. Amarillo—Yellow
(6) Var. *b*. Colorado—Red

} Thick-skinned, high-shouldered, and very large beans with light-coloured interior.

Class II. Forastero

(7) Var. *a*. Cundeamor verugoso Amarillo = Yellow-warted.
(8) Var. *b*. Cundeamor verugoso Colorado = Red-warted.
(9) Var. *c*. Ordinary, or typical Amarillo = Yellow Forastero.
(10) Var. *d*. Ordinary, or typical Colorado = Red Forastero.
(11) Var. *e*. Amelonado Amarillo = Yellow, melon shaped.
(12) Var. *f*. Amelonado Colorado = Red, melon shaped.

Class III. Calabacillo

(13) Var. *a*. Amarillo = Yellow
(14) Var. *b*. Colorado = Red

} Calabacillo, flat-beaned, smooth, thin- or thick-skinned, and small pods.

THEOBROMA PENTAGONA

(15) Theobroma pentagona = Alligator cacao. Has yellow, much-warted pods, with five distinctly raised ribs, and large beans, having white or light-coloured interior.

Hart characterizes the Criollo varieties by their light-colored seeds, the high quality of the cured product, and the less vigorous growth. The Forastero has light to dark purple seeds in large rough-ridged pods; it is rather variable and is a strong grower. Calabacillo is an inferior but stronger growing tree, having ovoid pods with thin, solid, dark-colored seeds. "*T. pentagona* has the largest seeds of any known species." "In general, however, it is hard to say where one form begins and another ends." In fact in most countries, cacao "consists of a heterogeneous mixture of cross-bred varieties of one species (*T. Cacao*) though of late years it is thought possible that the common species may have become hybridized with *T. pentagona.*"

1914 and 1932: Van Hall publishes his well-known book on cacao which since then has been a textbook and main source of information for cacao growers and agronomists. In his botanical chapter he presents some nonoriginal information on the noncultivated Theobromas. He gives excellent comparative descriptions and evaluations of the most important variations and forms of cultivated cacao. He follows Morris in recognizing two groups: 1. Criollo; 2. Forastero. He describes seven types or subvarieties of the first: the Venezuelan, the Ceylonese, the Javan, the Samoan, the Madagascarian, the Nicaraguan, and the Surinam Criollos. The subvarieties of Forastero described are Angoleta, Cundeamor, Amelonado, and Calabacillo. *Theobroma sphaerocarpa* Chev. is considered a mere form of Calabacillo. In 1932, van Hall introduces a new name *T. aspera*, transferred from *Herrania.*

1914: Pittier publishes two new species of *Theobroma* from Panama: *T. bernouillii* [1] discovered by him in the forests of the Colon province, and *T. purpureum* which belongs to *Herrania.*

1915: Cook, after a thorough morphological field study of *T. bicolor* and *T. cacao*, especially of the branching system and the flower and inflorescence structure, decides that they belong to different genera, and publishes a new monotypic genus *Tribroma* with one species, *T. bicolor;* it mainly differs by its clusters of three branches and the woody pericarp in contrast to the 5-branching clusters and fleshy pericarp of *T. cacao.* Although all observations by Cook are very sound, he does not compare *T. bicolor* with other species of *Theobroma* besides *cacao.*

1916: Cook publishes in detail and with illustrations the results of his studies on growth and dimorphism of branches and leaves of *T. bicolor* and *T. cacao.* He explains the sympodial structure of the *Theobroma* stem, the verticillate primary branching, the formation and succession of upright lateral shoots, which continuing the main stem, bring the clusters into a lateral position and the alternate

[1] Originally so misspelled, although the correct name would have been "*bernoullii.*"

branching of lateral branches. Cook describes the two types of leaves: the long petiolate symmetrical leaves of the seedlings and upright shoots and the bilateral, asymmetrical, dorsiventral, short-petiolate leaves of the lateral branches. The structure of inflorescences and flowers also are studied.

1918: Stahel publishes a precise, illustrated, morphological study of the structure of the inflorescences of *T. cacao* and *T. bicolor*. These inflorescences are always formed in the axil of the subtending bract of a lateral, non- or short-developing bud. The inflorescence in *T. cacao* consists of a cincinnous main axis with many short internodes and a few dichasial final branchlets. In *T. bicolor*, the main cincinnous axis has a few, long internodes, and the lateral branching is dichasial. The peduncles have a bilateral, the pedicels a radial structure.

1921: Benoist publishes a new species of *Theobroma* from French Guiana found by himself, *T. velutinum*. It is characterized by large leaves, velutinous beneath, and by ellipsoid, 5-ridged, velutinous pods.

1923: Standley recognizes three spontaneous species for the Mexican flora: *T. cacao*, *T. angustifolium*, and *T. bicolor*, and gives interesting historical, geographical, and economic data.

1925: Ducke publishes firsthand new botanical and ecological data on several Brazilian species.

1925: Pittier presents his interesting new theory that all existing forms of cultivated cacao are the result of hybridization between two initial species: 1) *Theobroma cacao* L., with elongate, claviform, rugose, 10-ridged pods, containing large, ovoid, white or slightly yellowish seeds, and 2) *T. leiocarpum* Bernoulli, with more or less rounded, smooth, slightly 5-ridged pods, with flattened, more or less triangular and dark purplish seeds. The first type is the one commonly known as "Cacao dulce" or "Cacao criollo," the second is commonly known as Calabacillo or Trinitario and in Guatemala as "Cumacaco." *T. sphaerocarpum* Chev. from São Tomé is a hybrid, retrogressive to *T. leiocarpum*. The two typical forms are united through an unlimited number of intermediate hybrid forms the characteristics of which are very variable; he says that the present nomenclature of varieties should be abandoned.

1925: Chevalier, in his "Observations" to the preceding work of Pittier, accepts basically Pittier's theory, and says that *T. sphaerocarpa* would be the extreme form of the series with smooth fruits and that *T. leiocarpa* is a hybrid between *T. cacao* and *T. sphaerocarpa*.

1926: Pittier answers Chevalier saying that he has never found *T. sphaerocarpum* in Central America, but that he has found growing wild in Costa Rica and Panama forms almost identical to *T. leiocarpum* Bernoulli. He recognizes that the forms with small, round pods often found in the region of Barlovento (Venezuela) are very close to *T.*

sphaerocarpum. Both original species are still found in pure, typical form and it can be said that in most plantations, next to the "primitive species" a number of hybrids are found. "We have still in Venezuela cacao plantations with absolute domination of the Criollo type, as, for instance, it happens at Caruao and Chuao." There can be observed over great extensions of land, tree after tree with elongated, claviform, pointed fruits, which may be reddish or yellow, with rounded seeds and almost white and insipid cotyledons. Pittier adds that at the time Linné described *T. cacao*, the Criollo was the dominant form in cultivation.

1930: Myers reports about his exploration of the upper Mamaboen Creek, a tributary of the Coppename River, where wild cacao was discovered by Stahel ten years earlier. This place is located in the middle of the Surinam rain forests, 40–50 kms. away from the last small Indian village. Abundant trees of cacao in a wild state were found in the lower tree-layer of the forest, under conditions of dense shade and high humidity; most of the cacao trees were found on the flooded margins of the river; few were found on higher ground. The trees were 10 to 25 feet high, and abundantly fruiting; the ripe pods were bright, light yellow in color, and almost smooth (with little indication of longitudinal ribs) and with 40 to 50 seeds with deep violet cotyledons. Myers adds that the fruits were of the Amelonado-Forastero type. He also comments on information about wild trees in other parts of Surinam, British Guiana, Brazil, and elsewhere.

1930: Pittier publishes an abridged key to classify the known species of *Theobroma*, including *Herrania*. Following Schumann in Die Natürlichen Pflanzenfamilien he divides it into three sections, the first being *Herrania*. The other two sections, defined by diantheriferous (Sect. *Eutheobroma*) and triantheriferous stamens (Sect. *Bubroma*), comprise 13 species, which are distributed in subsections corresponding to the Bernoulli sections. In *Eutheobroma* he includes subsect. *Cacao* with *T. cacao*, *T. leiocarpum*, and *T. pentagonum* and subsect. *Rhytidocarpus* with *T. bicolor* and *T. Bernouillii*. In *Bubroma* there are subsect. *Telmatocarpus* with only *T. microcarpum*, subsect. *Oreanthes* with *T. spruceanum*, *T. speciosum*, and *T. simiarum* and subsect. *Glossopetalum* with *T. angustifolium*, *T. grandiflorum*, *T. subincanum*, and *T. sylvestre*. The characters given in the key are few and not always the most typical or correct, some of the species being wrongly placed (*T. Bernouillii*, *T. simiarum*). The binomials *T. glaucum*, *T. martii* and *T. album* are considered dubious. Pittier refers to having received from Cook photographs of two forms of cacao cultivated in Peru with small fruits which might be different species; one has almost spherical, rugose pods called locally "cacao chuncho." Pittier says that, with the exception of *T. leiocarpum* and *T. cacao*

(respectively Calabacillo and Criollo), there do not exist stable forms of cultivated cacao. Forastero from Trinidad stands between these original species and can be considered as the result of their crossing. The Trinidad Forastero seems to be quite different from Venezuelan and Central American Forastero and probably from the Old World Forastero. He also says that it does not make sense to talk about the origin of Forastero, because its forms appear wherever the parental species are present and successive crossings produce constant variations. Commenting on the finding of Myers in Surinam, Pittier says that the wild cacao of the Mamaboen valley belongs to *T. leiocarpum.* The same opinion is expressed in connection with Schomburgk's spontaneous cacao found in the Río Branco valley and numerous references about wild cacao throughout the Venezuelan Guayana. The cacao with tapering, pointed, ridged and rugose pods with white cotyledons (*T. cacao*) has really never been found indigenous to the east of the Panama isthmus. Pittier found it at the isthmus but says that the origin of this species is to be sought towards the north, in the Soconuzco, Chiapas, and Tabasco regions, where the Criollo type finds the best conditions for its development. Conversely, the plantations of Calabacillo do not go much further west than Costa Rica where it was recently introduced. Here are to be found the westernmost stations of *T. leiocarpum*, although the type came from plantations in Guatemala.

1931: Mildbraed publishes a new species *T. tessmannii*, found by Tessmann in eastern Peru. He relates it to *T. ferrugineum* Bernoulli, from which it differs especially by the long, soft tomentum of the leaves beneath.

1932: Cheesman, who had been conducting research on cacao corps for many years, presents a significant account of the economic botany of *Theobroma.* He believes that it is unlikely that any of the now uncultivated species has any direct economic significance. He speaks about the cultivated species, those of section *Cacao*, as interfertile species (*T. cacao, T. leiocarpum, T. pentagonum*). Cheesman says that "the taxonomic status of the group of forms at present included under the collective term *T. cacao* can only be determined by prolonged research, including genetic, and possibly also cytological studies." Cheesman agrees with Pittier in considering that more than one species contributed to build the "cacao complex," adding that this idea provides the most helpful way of regarding the extraordinary variation exhibited by the crop. His discussion on the history, characters, and merits of the varieties is illuminating in many respects, especially when trying to understand their possible origin. In practice, he follows, with slight modification, van Hall's classifica-

tion which he says "is a compromise between a natural and an artificial system."

1932: Pittier insists in his viewpoints on the origin of the cultivated cacao. Finding that *T. cacao* L. is not well typified by a known variety, Pittier decides to abandon this name and to substitute for it *T. sapidum*, but no specific description is given and a type specimen is not indicated. The Calabacillo seems to have a stronger fertilizing power than the Criollo which explains why few trees of the first suffice to alter the plantations of the second.

1933: Ciferri makes a very detailed, critical study of the cultivated cacaos of Santo Domingo giving a thorough classification with definition, descriptions, and illustrations of their numerous types. Morphological, taxonomic, historical, and economic comments are given. Ciferri follows the principles of Pittier in accepting the theory that the majority of the cultivated cacaos are hybrids of two initial types, but he considers these two types varieties instead of species. Ciferri gives the system formal nomenclatural status by publishing the following new varieties: *T. cacao* L. *emend.* var. *typica* Ciferri; *T. cacao* L. *emend.* var. *leiocarpa* (Bernoulli) Ciferri, and *T. cacao* var. *typica* × *T. cacao* var. *leiocarpa* = Forasteros. "I cacao denominati globalmente "Forasteros" sarabbero dunque, secondo l'idea di Pittier, che moi adottiano in pleno, i meticci tra le due varietá sunnominate del *T. cacao.*" Ciferri's work is a significant contribution to the knowledge of cacao varieties and their distribution.

1935: Cheesman describes the branching system and dimorphism in cacao, and studies different ways of vegetative propagation.

1936: Campos Porto publishes information on the species of *Theobroma* cultivated at the botanical garden of Rio de Janeiro, with a photograph of the inflorescences of *T. speciosum;* the other species referred to are *T. cacao, T. bicolor, T. grandiflorum, T. subincanum,* and *T. microcarpum.*

1937: Standley lists and describes five species of *Theobroma* in his Flora of Costa Rica plus a *Herrania* as *T. purpureum.* He considers *T. simiarum, T. angustifolium, T. bicolor,* and *T. cacao* to be wild in the forests and *T. leiocarpum* as probably wild.

1937: Pérez Arbélaez publishes a manual for the cacao growers of Venezuela including a botanical introduction with descriptions of and information on Venezuelan cultivars; he also gives interesting historical data.

1938: Pound finds interesting varieties of cacao in his explorations in South America, especially in the upper Amazon basin.

1938: Bondar publishes a documented book on the cultivation of cacao in Bahia. He gives comments and a key to the known species of *Theobroma.* He considers that the varieties cultivated in Bahia for

many years belong to *T. leiocarpum;* a great uniformity in the product exists, but he believes that recent introductions of Criollo may well stop this uniformity. He also describes and illustrates several forms of Forasteros known in the region.

1939: Diels publishes a new species, *T. calodesmis*, found by Hertha Schultze-Rhonhof in the rain forests of eastern Ecuador, which he relates to *T. speciosum* and *T. bernouillii.*

1939: Cope's investigations in Trinidad on agents of pollination using thrips (*Frankliniella parvula* Hood), red ants (*Wasmannia auropunctata* Rog.), and aphids (*Toxoptera aurantii* B. de Fousc.), suggests that red ants and thrips are the responsible agents of pollination in a cacao population at River Estate.

1940: E. W. Emmart publishes the Badianus Manuscript, the earliest book ever written on Mexican medicinal plants, the work of two Aztec Indians, Martinus de la Cruz who composed the work in Aztec, and Juannes Badianus who translated the text into Latin. On plate 68, illustrating six plants, plant no. 2 represents "Tlapalcacauatl," colored cacao, i.e., "tlapal" = colored, "cacauatl" = cacao, according to Emmart (p. 273), who adds, "This picture is the earliest illustration of the cacao, *Theobroma cacao* L., the source of chocolate." This interesting, primitive drawing clearly illustrates the Criollo variety.

1940: Ducke summarizes his experience of many years in Brazilian cacaos with a new and detailed key to the Brazilian species. He brings new data into consideration in his classification, as for example fruit characters that were unknown before. He gives photographic illustrations and new information, based on direct field observations, about morphological, phenological, and ecological features of the species treated, which are *T. cacao, speciosum, spruceanum, microcarpum, obovatum, subincanum,* and *grandiflorum.* He also includes in *Theobroma* the genus *Herrania* with one species, *T. Mariae.* Concerning *T. cacao*, Ducke recognizes it as indigenous throughout the central and western Amazonia. Ducke considers *T. leiocarpum* Bernoulli a mere form of *T. cacao* and makes the new nomenclatural combination: *T. cacao* L. forma *leiocarpum.*

1942: Schery publishes a new species, *T. asclepiadiflorum*, based on specimens from Panama.

1944: Cuatrecasas publishes a new species with yellow flowers, *T. cirmolinae*, found by the author in the rain forests of the western slopes of the western Andes in Colombia.

1944: Cheesman makes a thorough examination of the taxonomic situation in cacao, the most important conclusion being that the whole assemblage of wild, semiwild, and cultivated cacao constitutes "one interbreeding population." He still supports the main division of

cacao into two groups of varieties, Criollo and Forastero. He proposes the new theory that the Criollo, which may occur wild in some regions from southern Colombia to southern Mexico, may have originated at the headwaters of the Amazon. He divides this group into Central American and South American Criollos. The Forasteros are divided into Amazonian Forasteros, which can be found wild in Amazonia and which are widespread in cultivation, and the Trinitarios, possibly originating from the mingling of South American Criollo and Amazonian Forastero stocks. *Theobroma pentagonum* is a simple form of *T. cacao,* probably a segregate of the large cross-fertilized population. The same opinion is expressed with regard to *T. leiocarpum,* which, according to Cheesman, does not belong to Amelonado; it is an aberrant form of the Criollo, for which reason the binomial falls into the strict synonymy of *T. cacao.* The data assembled and arguments of Cheesman are a very valuable contribution.

1946: Chevalier publishes a monographic revision of *Theobroma.* He recognizes 13 species (excluding *Herrania*) arranged according to the five sections of Bernoulli. He includes in the first section (*Cacao*) only *T. cacao,* in section II, *Oreanthes: T. guianensis* and *T. spruceana;* in section III, *Rhytidocarpus: T. bicolor, T. glauca,* and *T. Bernouillii;* in section IV, *Telmatocarpus* only *T. microcarpa* and in section V, *Glossopetalum: T. sylvestris, T. obovata, T. ferruginea, T. grandiflora, T. angustifolia,* and *T. simiarum.* In the key (Tableau Analytique), the species are differently arranged; they are divided in the two sections of Schumann: *Eutheobroma* with four species (*T. cacao, T. bicolor, T. Bernouillii,* and *T. glauca*), and *Bubroma* with the other nine species. The characters given in the key are not always well chosen, and some species are misplaced in the sections (as, e.g., *T. glauca* and *Bernouillii*). The nomenclature and typification of the species are not always correct; the concepts of *T. speciosa* Willd. ex Spreng., *T. guianensis* (Aubl.) Gmel., *T. velutina* Benoist, *T. sylvestris* Mart., *T. sylvestris* (Aubl.) Don., *T. obovata* Klotzsch ex Bernoulli, *T. ferruginea* Bernoulli, *T. sinuosum* Pavón and others are actually not clarified. Some confusion is also brought with the new names *T. sagittata* Pavón, *T. hastata,* and *T. undulata.* I have identified *T. sagittata* Pavón as *Herrania nitida* and suppose that *T. hastata* Cheval. is a *lapsus calami* for the former and *T. undulata* Cheval. a *lapsus calami* for *T. sinuosum.*

Special treatment is devoted to *T. cacao,* with which Chevalier had long and sound experience. He considers all cultivated cacaos as belonging to a single species, *T. cacao* L., in which four different races or "species jordaniennes" can be recognized. These races, which cross among themselves "à l'infini," can be only distinguished by their

fruits and seeds. These are lacking in herbaria, and therefore the races must be studied in the field. Four of the races or Jordanian species of Chevalier correspond to formerly described species (*T. sativa*, *T. leiocarpa*, *T. pentagona*, and *T. sphaerocarpa*) but he adds a fifth based only on foliage, *T. sagittata*, which, as I have pointed out, is not a *Theobroma*. Chevalier's classification for the "formes jordaniennes" of *T. cacao* L. follows:

Leaves obovate-oblong, acuminate.
Fruits ovoid-oblong 5–10 ridged, ± rugose-bullate, long-attenuate into a point . . . . . *T. sativa*
Fresh seeds yellowish white . . . . . var. *leucosperma*
Fresh seeds dark violet . . . . . var. *melanosperma*
Fruits ovoid, rounded at apex, smooth or with 5–10 shallow furrows . *T. leiocarpa*
Fruits globose, more or less smooth, rounded or depressed at apex . *T. sphaerocarpa*
Fruits ovoid-oblong narrowed to the apex, with 5 very prominent ridges. *T. pentagona*
Leaves narrowly oblong, or oblong-acuminate, more or less undulate . *T. sagittata*

Chevalier goes on to describe the three first "races," and declares that he had insufficient information on the other two. Chevalier uses for what he calls races, Jordanian species, or Jordanian forms, the same binomial denomination as for species, for instance, *T. cacao* L. forma *T. sativa* which should be *T. cacao* L. forma *cacao* according to the present rules of nomenclature. It seems right to consider the original species described by Linnaeus as belonging to the Criollo form, but nothing is clarified by Chevalier using the binomial *T. sativa*, because this name was based on *T. cacao* L. Chevalier considers his *T. sativa* originally from Central America. To the "Jordanian form" *T. leiocarpa* Bernoulli, Chevalier refers the "Cacao creoulo" of São Tomé, the Cumacaco, Calabacillo, and Trinitario, and he supposes it originated in Guiana and Brazil. Concerning the Jordanon *T. sphaerocarpa* Chevalier, described on São Tomé (Africa) plants, very similar specimens have been found in Venezuela (var. *sambito*), in the high Amazonian forests, and at the Rio Marañón. The Jordanon *T. pentagona* has never been found wild; it seems to be originally from Central America. The experience and opinions of Chevalier have to be taken into account when considering the classification and origin of cultivated cacaos.

1946: Cuatrecasas publishes *T. capilliferum* discovered on the Pacific coast of Colombia.

1947: Llano Gómez publishes information about the cultivated cacao in Colombia, with several plates in color representing the principal types.

1948: Rombouts discusses *Theobroma Saltzmaniana* Bernoulli, showing that it might be based on a flower with defective or abnormal

petals and therefore cannot be distinguished from other forms of *T. cacao.*

1949: Standley and Steyermark consider five species of *Theobroma* in their Flora of Guatemala, recognizing *T. pentagonum* and *T. leiocarpum* as different from *T. cacao* following Bernoulli. *T. angustifolium* is given as cultivated and *T. bicolor* as uncertainly native.

1949: Cuatrecasas and León describe a new species, *T. mammosum,* collected by León as a rarity on the Atlantic coast of Costa Rica.

1950: Holdridge publishes some new information on Mexican and Central American species of *Theobroma,* with a key to nine species and one *Herrania.* He suggests that *T. pentagonum* might be the original type and source of the cultivated cacao in Mexico and Central America and that the Criollo types were the product of interbreeding of *T. pentagonum* with the South American *T. leiocarpum.*

1950–1953: Cuatrecasas publishes *T. stipulatum* and *T. nemorale* from the rain forests of the Pacific coast of Colombia and *T. gileri* from the Pacific range of Ecuador.

1951: Freytag publishes a revision of *Guazuma,* which helps in the study of its relationships of *Theobroma.* The genus is reduced to four species.

1951: Addison and Miranda Tavares explain the results of their six-year work in trying to produce hybrids from different *Theobroma* species. They crossed *T. cacao* with all the Amazonian species of *Theobroma,* without success, and proceeded then to cross the other Amazonian species. In 1946, from 719 pollinations of *T. speciosum* on *T. cacao,* they obtained 29 fruits and 979 seeds, which were mostly abnormal and did not germinate. Same results were attained by a few pollinations with *Herrania mariae.* Among 798 cases of pollination of *T. microcarpum* on *T. cacao* 11 fruits and 26 seeds were produced, from which only three seedlings were produced which grew no more than 10 cm. Similar negative results were produced from *T. cacao* × *obovatum* and *T. bicolor* × *cacao.* Some particular trees of *T. cacao* were more receptive than others; one of them gave fruits when submitted to pollination from all other species. When *T. cacao* was used as pollinator on *T. microcarpum, T. speciosum,* and *H. mariae,* no fruits or seeds were obtained. In 1947, another series of cross-pollinations were made on *T. cacao* with similar results, although a few more or less viable hybrids were produced, e.g., *T. cacao* × *microcarpum* gave 28% fruits, but these decayed after developing one month.

Better results were attained by Addison and Miranda in crossing *T. grandiflorum* and *T. obovatum;* many hybrid seedlings were produced and several developed into perfect trees (in 1½ years); the leaves, fruits, and flowers of the hybrids showed intermediate char-

acters, and the pollen grains were normal and fertile. Well-developed hybrids between *T. grandiflorum* and *T. subincanum*, *T. obovatum* and *subincanum*, and *T. speciosum* and *T. sylvestre* (= *spruceanum*) were also produced. In 1948, some fruits were obtained by crossing *T. cacao* with *T. grandiflorum*, but these gave very few seeds, from which only few plants developed up to 15 cm.

Addison and Miranda also made grafting experiments with good results using *T. grandiflorum*, *T. obovatum* and *T. subincanum*. *T. bicolor*, *T. speciosum* and *T. sylvestre* (*spruceanum*) proved to be another successful grafting group.

During their experiments, Addison & Miranda had the opportunity of making interesting morphological and physiological observations. The seeds of *Theobroma* usually germinate within 15 days. *Theobroma subincanum*, *obovatum*, *grandiflorum*, *microcarpum*, and *H. mariae* were found to have hypogeous germination, whereas *T. cacao*, *sylvestre* (*spruceanum*), *bicolor*, and *speciosum* have it epigeous. The very young leaves are green in *T. speciosum*, *sylvestre*, *bicolor*, and *microcarpum*, but they may be green or red in the other species.

1952–1953: The Anglo-Colombian Cacao-Collecting Expedition publishes reports on its explorations in the search for wild and cultivated species of *Theobroma* and *Herrania* in Colombia. The expedition took place from June 1952 to October 1953, with the participation of the British botanists and specialists F. W. Cope, D. J. Taylor, R. E. D. Baker, P. C. Holliday, and B. G. Bartley. The Colombian botanists who joined the expedition were H. Garcia Barriga, Canuto Cardona, R. Romero Castañeda, and Alvaro Fernandez P. The main areas explored were: (1) parts of the rivers Caquetá, Apaporis, Vaupés, Negro (Guainía), Inírida, and their tributaries in the provinces of Amazonas and Vaupés, from 1°30′ S. to 3° N. and from 67° W. to 71° W.; (2) parts of the rivers Putumayo, Caquetá, and Caguán in the provinces of Caquetá and Putumayo, from 0°20′ S. to 2° N. and from 74° W. to 77° W.; (3) parts of the trans-Andean provinces of Valle del Cauca and El Chocó, from 3° N. to 6° N. and between 76° W. and 78° W.; (4) scattered areas in the provinces of Antioquia, Norte de Santander, Magdalena, Santander, and Huila.

The expedition made 191 botanical collections, of which 63 were of living material sent to Trinidad. The well-preserved specimens have been extremely useful for the study of the species and their geographical distribution. Twelve indigenous species of *Theobroma* were collected (*T. calodesmis*, *microcarpum*, *subincanum*, *grandiflorum*, *obovatum*, *capilliferum*, *gileri*, *nemorale*, *cirmolinae*, *simiarum*, *stipulatum*, and *chocoense*). *T. bicolor*, always found planted, and *T. cacao* were also collected. In a very few areas (Río Caguán, Río San Miguel) spontaneous trees of cacao were found inside the forest but under

circumstances that make it impossible to say with complete certainty that these trees were spontaneous. In general the subspontaneous and planted cacaos found in the southeastern region of Colombia were of the very uniform Amelonado type. The information and materials (living and preserved) gathered by this expedition are a very important contribution to the knowledge of *Theobroma.*

1954: Ducke makes a revision of his previous synopsis of the Brazilian species, incorporating new morphological data into an accurate, precise, well-balanced key. He introduces the character of the ramification being 5-whorled and 3-whorled in separating *T. cacao* from the other seven Brazilian species (*T. bicolor, T. speciosum, T. spruceanum, T. microcarpum, T. obovatum, T. subincanum,* and *T. grandiflorum*). Ducke considers each fertile stamen as the union of two or three (stamens geminous and trigeminous), and as Addison, Molina, and Pires had already observed before, characterizes *T. spruceanum* as having geminous stamens. Ducke still retains *Herrania* in *Theobroma,* with two Brazilian species, *T. Mariae* and *T. Camargoanum* (Schultes) Ducke. He summarizes the ecology and distribution of the genus in Brazil, calling it a typical Amazonian genus; he writes that it is not absent in any place in Amazonia where rain forest exists.

1956: Cuatrecasas recognizes seven species of *Theobroma* for the Flora of Peru: *T. calodesmis, T. grandiflorum* (planted), *T. obovatum, T. speciosum, T. subincanum, T. bicolor,* and *T. cacao* subsp. *leiocarpum,* which is found spontaneous in the rain forests of Peru.

1958: Schultes publishes the results of his discoveries and research on *Herrania.* His synopsis comprises 17 species, eight of them new. One species spreads northwards to Costa Rica, and the others are limited to the humid tropics of South America. This monograph shows the consistent unity of the group *Herrania* and the consistency of the characters that may be used to separate it from *Theobroma* and other related genera.

1958: Mora Urpi found a much greater variability in *T. cacao* throughout Mexico and Central America than in South America. In Central America and southern Mexico there can be found today practically all the known forms of cacao, for which reason Mora believes that Central America has been the center of domestication of the cultivated cacao; historical data also support this theory. He considers cacao as having been probably introduced in South America in pre-Colombian times. The geographical distribution of the Criollo type would also prove this theory. The author agrees with Holdridge in considering the *pentagonum* form as playing an important role in the origin of the cultivated hybrid complex; he considers *pentagonum* native in Central America and the original and most ancient form

of *T. cacao*, from which, through mutation, introgressive hybridization, and geographical isolation, the present population arose (p. 34).

1959: Soria confirms the observations of Mora about the great variation in the characteristics of shells and seeds of *Theobroma cacao* in plantations in Nicaragua. Trying to establish the correlation between pod shape and color of the seeds, he found that dark-colored seeds occurred in a large percentage of Criollo type pods, and white seeds were often found in pods of the Forastero and Calabacillo types. This agrees with the previous observation by Mora of dark seeds in the *T. pentagonum* pod-type. These observations, according to Soria, show that it is probable that the genetic factors controlling these characters are independent of each other. Soria sees as reasonable Holdridge's theory that Criollo cacao is a result of crosses between *T. pentagonum* and *T. leiocarpum*. But he adds "The possibility cannot be overlooked, however, that the Criollos originated as mutations in populations on the periphery of the area of distribution of the species, the mutations afterwards being fixed and maintained through geographic isolation and selection. In this case, *pentagona* could be a product of mutations in Criollo cacaos." Soria emphasizes that *pentagonum* can be fertilized very easily in either direction by other types of *T. cacao*. Mora observed such hybrids as often having conspicuous characteristics of *pentagonum*. "All these observations lead to the conclusion that *pentagona* is nothing more than one of the extremes in the variability of the complex of types forming the species *T. cacao*."

1960: At the River Estate Experiment Station of the Imperial College of Tropical Agriculture in Trinidad, 13 species of *Theobroma* were planted for research and observation. Cope and Bartley suggest the possible interrelationships of species of *Theobroma*, distributing them in two groups: 1) with epigeal germination and growth continuing from below jorquette, comprising *T. cacao* with 3–5-branched jorquette and *T. bicolor*, *speciosum* and *calodesmis* with 3-branched jorquette; 2) hypogeal germination and growth continuing from above jorquette in *T. microcarpum*, *grandiflorum*, *subincanum*, *obovatum*, *angustifolium*, *mammosum*, *simiarum*, *cirmolinae*, and *nemorale*. This is the first attempt to classify the genus on the basis of germination and branching.

1960: Cristóbal publishes an excellent monograph on *Ayenia* with important information concerning the relationships with other genera of Sterculiaceae.

1960: León, in Hardy's Cacao Manual, summarizes the taxonomy of *Theobroma*, recognizing 19 species and considering as doubtful *T. kalagua*, *tessmannii*, *ferruginea*, and *glauca*. He gives abridged descriptions and distribution for *T. cacao*, *bicolor*, *bernouillii*, *capillifera*,

calodesmis, asclepiadiflorum, microcarpa, gileri, guianensis (= *speciosa sensu* Chevalier), *spruceana, angustifolia, cirmolinae, grandiflora, mammosa, obovata, simiarum, stipulata, sylvestris* (= *subincana sensu* Chevalier), and *nemoralis*. The fruits of 17 species are illustrated. In the classification he follows more or less Chevalier; under *T. cacao* he distinguishes three subspecies: *sativa* (Lam.), *leiocarpa* Bern. and *pentagona* (Bern.); the listed cultivars are classified according to van Hall.

1961: Soria reports on cacao in Mexico, having visited extensive plantations in Tabasco. Before 1900, the variety cultivated in Mexico was almost exclusively Criollo, but at present that is disappearing, hardier and more productive varieties being substituted. He observes great variability in the pod form in plantations of old Criollo, which always have white seeds. Great variation is also seen at present in the widespread hybrid populations that resemble the Trinitario of South America, although the Mexican types lack the red pigmentation of the shells usually exhibited by Trinitario. (They are mostly whitish green or slightly reddish.)

Morphology

STEM AND BRANCHING (Fig. 1).—There is a dimorphism in the vegetative organs of *Theobroma*. The main stem and the adventitious orthotropic shoots have a radial structure, and the normal, plagiotropic branches are monopodial and dorsiventral. The trunk is sympodial.

The seedlings have an erect stem with regular, long-petiolate leaves arranged in phyllotaxy cycles of 5/13, 5/8, or 3/8 (Cook, Baker). After reaching a height of a few feet the vegetative end of the stem stops growing and by the way of a cluster of secondary buds it forks into 3 to 5 spreading branches arranged in a terminal whorl called a "jorquette" or "fan." These branches are plagiotropic and dorsiventral, with alternate, distichous, short-petiolate leaves with a phyllotaxy of 1/2. Further growth of the stem may now take place by two different ways: 1. One of the dormant buds axillary to the branches of the jorquette, and therefore adjacent to the central, inert, apex of the stem, develops into a new vertical shoot with the same structure as the main stem and looking like its continuation. It grows to a limited extent, ending also with a whorl of 3 to 5 branches; from above this second whorl or jorquette a third shoot is developed in the same way, forming a third internode of the stem, and so on. By this way a sympodial main trunk is built, with alternating internodes and nodes with regularly centered verticils of branches. Since new terminal shoots are produced above the jorquette next to the

apex we can call this pseudapical growth. 2. No buds at all develop above the first whorl of branches but an adventitious lateral one below it grows into a vigorous upright shoot with a structure similar to that of the main stem. Although lateral, it forces the node of the jorquette to one side, and takes progressively the central position of the stem, of which it will appear to be the continuation. After reaching some length it forks, ending in a jorquette; a new adventitious shoot is formed below that jorquette and so successively a sympodial trunk is built, with alternating internodes and irregular nodes. In this case the trunk is usually not truly straight and the whorls of branches, in spite of the fact that these tend to take a circular position around the stem, are always more inclined to one side, often making a lateral bunch; the closer to the jorquette the lateral adventitious shoots originate, the less irregular is the appearance of the sympodium resulting. We can call this subterminal growth.

The dimorphism of the stems is transmitted by the buds. Those of the seedlings and upright (orthotropic) shoots produce only, again, orthotropic shoots (chupons) bearing long-petiolate leaves and producing only the plagiotropic, dorsiventral branches of one terminal jorquette. The buds of the lateral, plagiotropic branches produce only other plagiotropic branches. Only exceptionally due to special physiological conditions or following mechanical injuries (e.g., trimming), do plagiotropic branches originate upright shoots (chupons). More exceptionally the extraordinary formation of alternate plagiotropic branches has been observed on upright stems which have failed to form a jorquette (Baker 1961, p. 9), but this has to be considered an abnormal case due to unknown special conditions of some cultivated trees.

The lateral, plagiotropic branches are monopodial and branch by axillary buds; frequently the growth of a lateral branch bends the young joint of the primary branch forcing this into an angle, thus simulating a dichotomous fork; branches may appear several times forked and are then called "dichotomous" branches.

The stem and branching dimorphism is important in the practice of propagation and cultivation of *Theobroma* trees, because only the trees produced by cuttings of orthotropic stems (chupons) are upright and regular; conversely, those from plagiotropic (dorsiventral) lateral branches, branch bilaterally (dorsiventrally) and tend to slant or to bow (incline), being thus weaker. In cultivated cocoa the formation of adventitious upright shoots (chupons) on branches and at the base of the trees is frequently observed; they may be used in practice to regenerate old trees by pruning, and as cuttings for propagation. But the production of chupons is always too small to serve for ex-

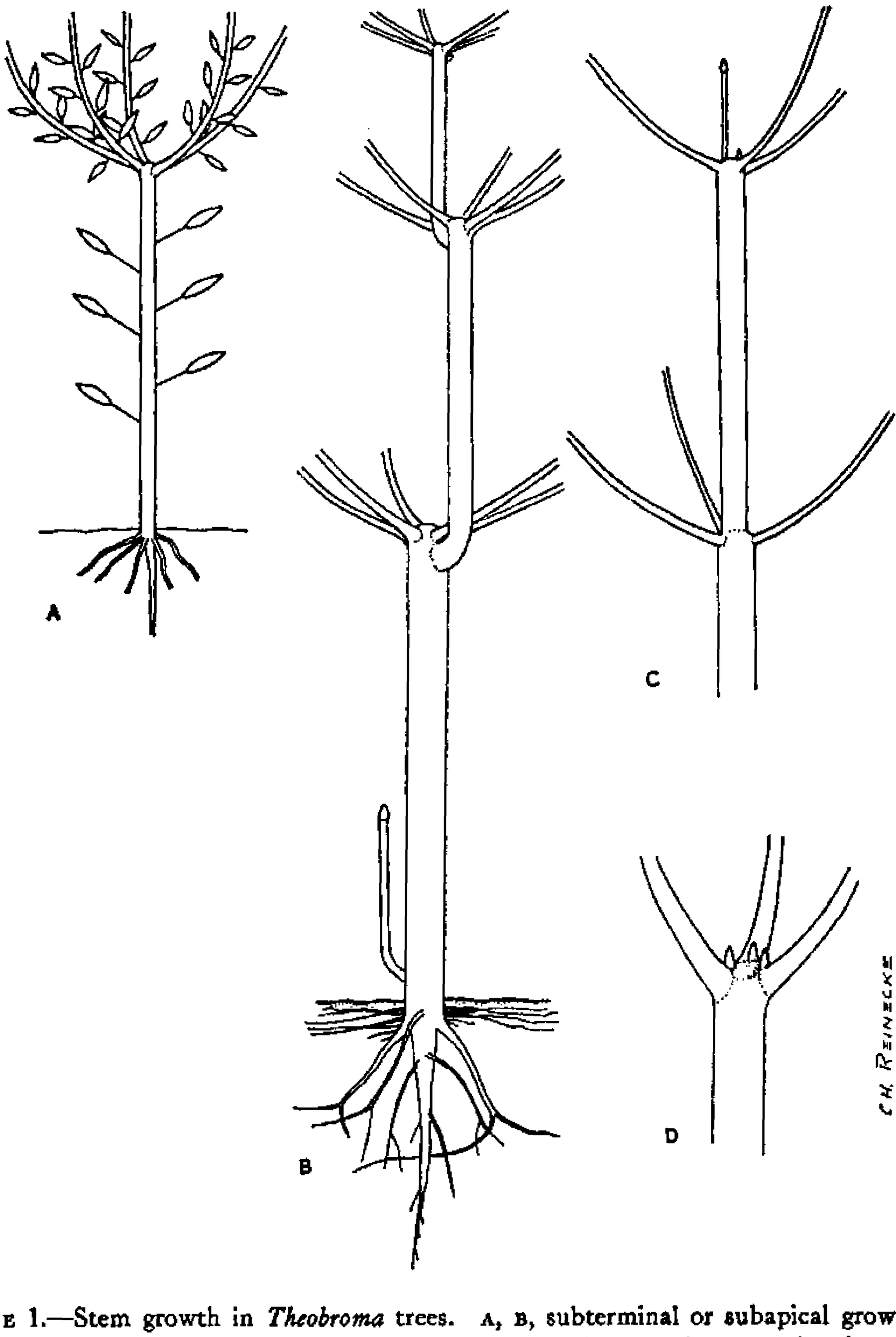


FIGURE 1.—Stem growth in *Theobroma* trees. A, B, subterminal or subapical growth: A, adult seedling of *T. cacao* with its primary stem (bearing long-petiolated, radially arranged leaves) topped by a whorl of dorsiventral, leafy branches; B, formation of the sympodial trunk in *T. cacao* by way of upright adventitious shoots from buds borne below the terminal verticil (or jorquette). C, D, pseudoterminal growth: C, formation of the sympodial trunk by developing one of the axillary buds of the terminal whorl of branches (e.g., sect. *Glossopetalum*); D, apex of stem topped by a whorl of 3 branches each with an axillary bud, of which only one will develop (growth above jorquette).

tensive propagation. The two different kinds of stem growth have taxonomic implications.

LEAVES.—There is a dimorphism of leaves correlated with the dimorphic stems. The leaves are arranged in several phyllotaxic cycles (5/13, 5/8, 3/8 have been recorded) around the radial, orthotropic stems or shoots, and are distichally alternate (1/2 phyllotaxy) on plagiotropic (lateral) branches.

The first leaves (on orthotropic stems) are long-petiolate and symmetrical. The petiole is elongate and thickened at both ends, forming a long, cylindrical pulvinus below the lamina and a more tubercular, shorter one at the base; this normal type of petiole facilitates all kinds of orientation to the blade.

The leaves of plagiotropic branches (the normal ones of the mature tree) are short-petiolate and asymmetrical. The petiole is with very few exceptions reduced to the thickened part of the cushions. The blade has more or less markedly unequal halves, especially at the base, which may be extremely asymmetrical.

The blades are simple and pinnatinerved, thick-coriaceous or chartaceous, with a strong midrib and several alternate, spreading-ascending, prominent secondary nerves; there are elevated tertiary nerves. Lesser ones form a small usually conspicuous reticulum. Often the lowest pair of secondary nerves is somewhat more separated from the next pair than the others, and may give some impression of a trinerved base; sometimes there are one or two stronger developed tertiary nerves, giving some appearance of a 5-nerved or 7-nerved base, but usually the main costa is much stronger than the secondary nerves and these are thicker than the tertiary, so that the mainly pinnate arrangement is always clear. In some cases, as in the primary leaves of *T. bicolor*, the lateral lower nerves are more clearly arranged so as to show a 5–7-nerved base, and some botanists describe them as palmatinerved.

The shape of the blades is often ovate, obovate-elliptic-oblong, or lanceolate, and usually acuminate at apex and obtuse or rounded at base, but there is a great deal of variation from one species to another. The margin is basically entire, but sometimes slightly sinuate or broadly dentate in adult leaves; the primary leaves may be coarsely dentate in the upper half. Indument is present except in a few species; most species have a more or less dense tomentum on the underside, which may be composed of one, two, or three different kinds or sizes of stellate hairs. This tomentum may cover the whole lower surface of the leaves entirely or may cover the areoles between the reticulum leaving all or part of the venation glabrous. The different kinds of hairs and their distribution supply good taxonomic characters.

INFLORESCENCE (Fig. 2).—The inflorescence is of the definite type. In some cases it may be a well-branched dichasium as in *T. bicolor*, but generally, the dichasium is totally or partly reduced to a monochasium

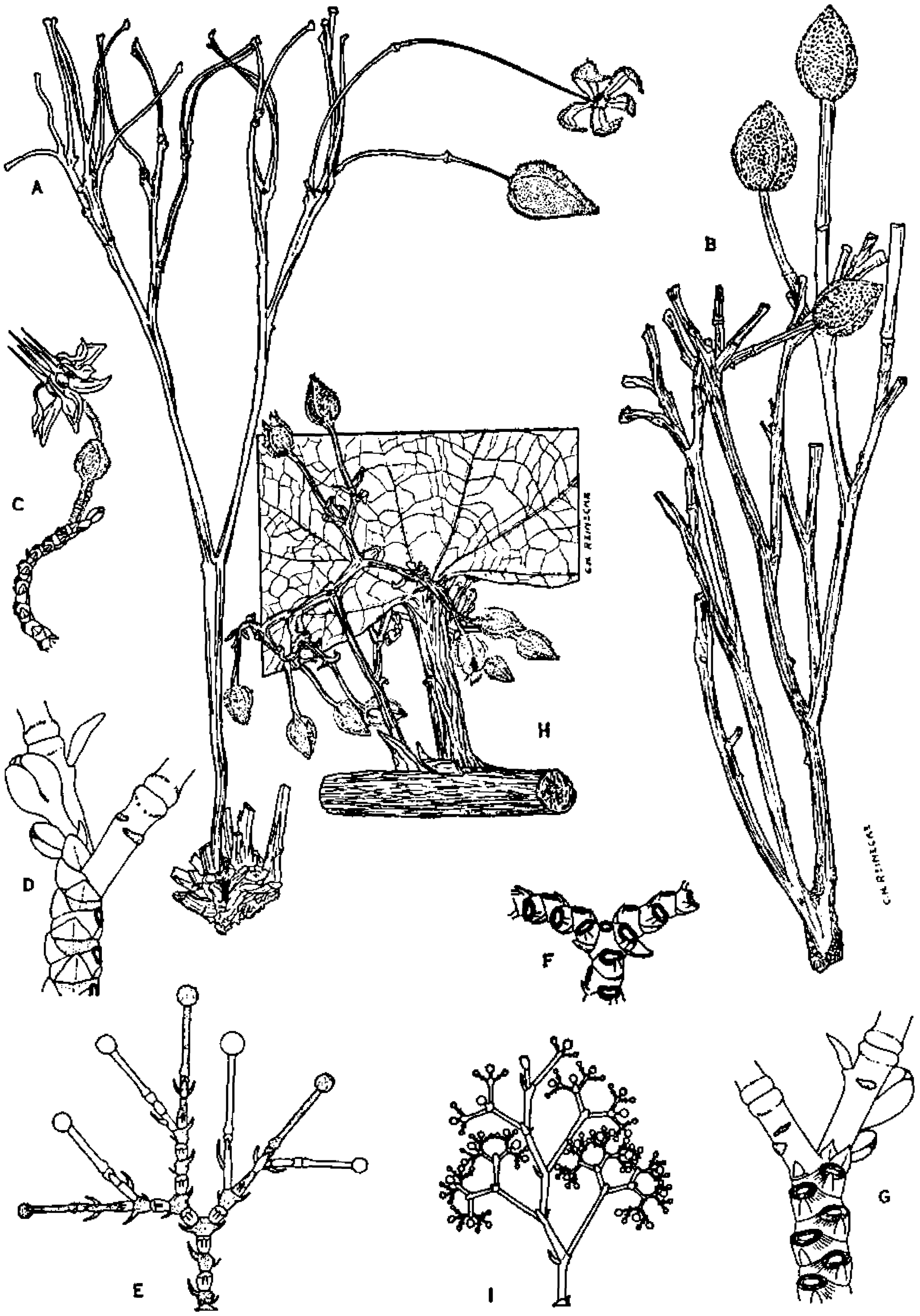
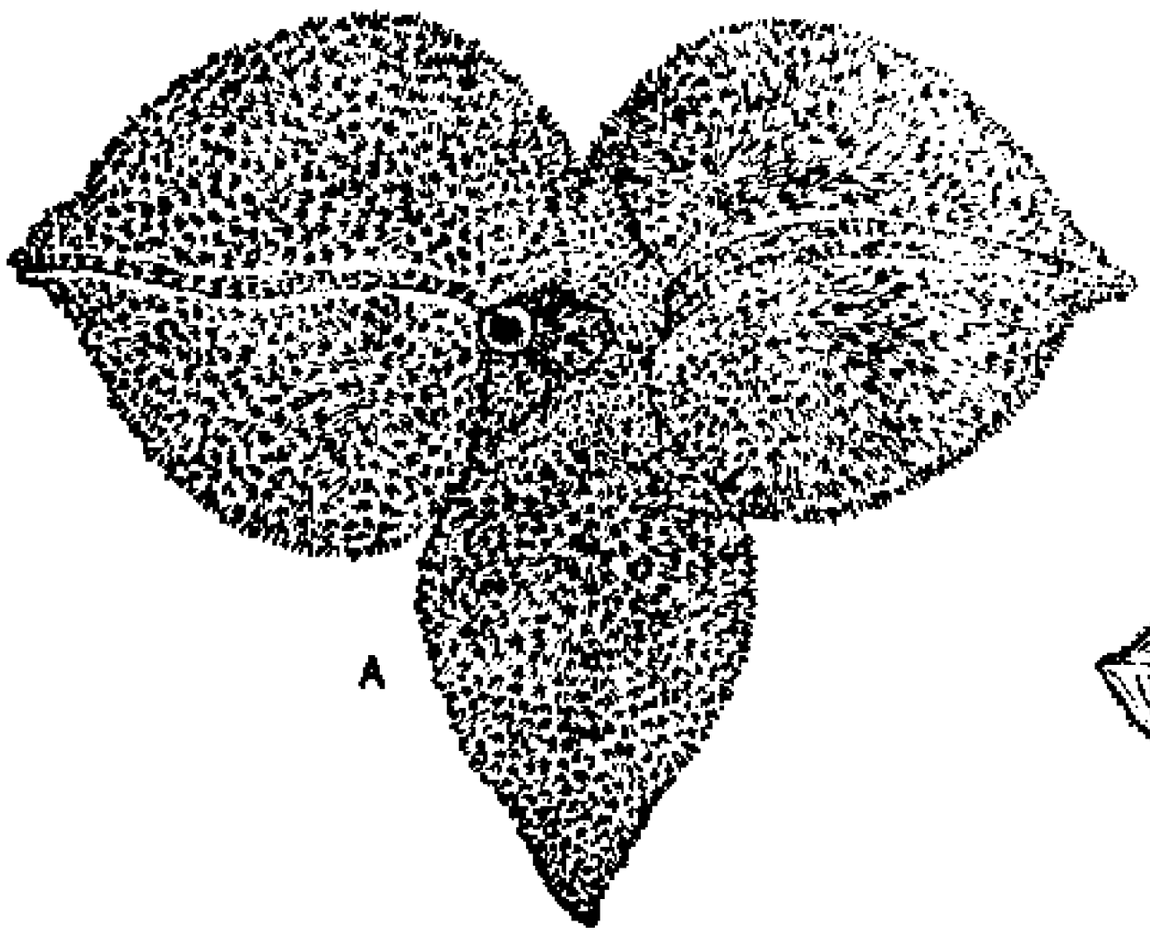
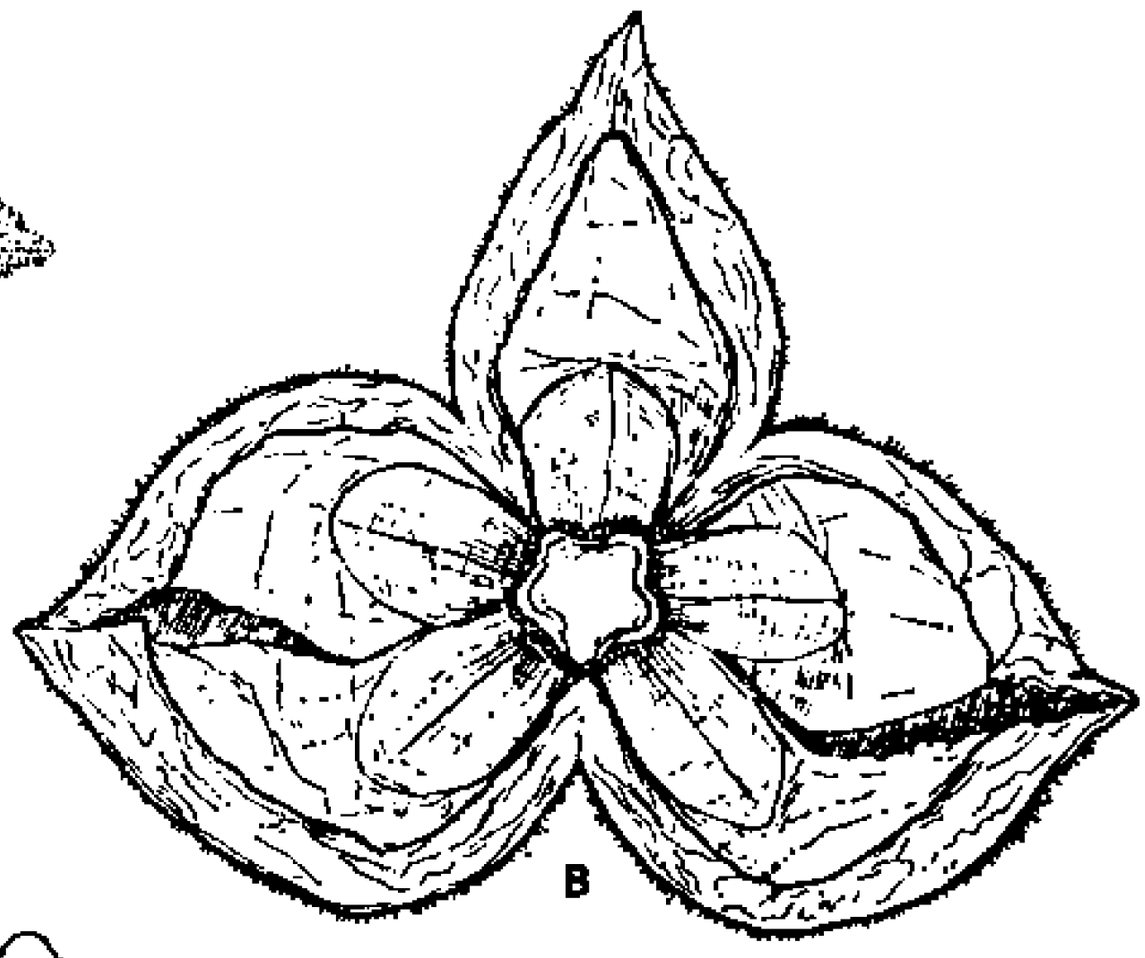
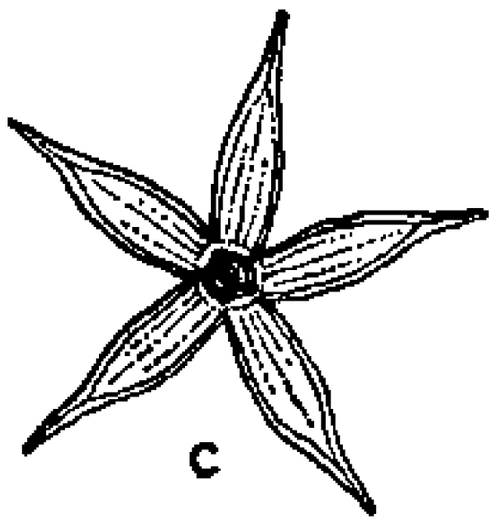
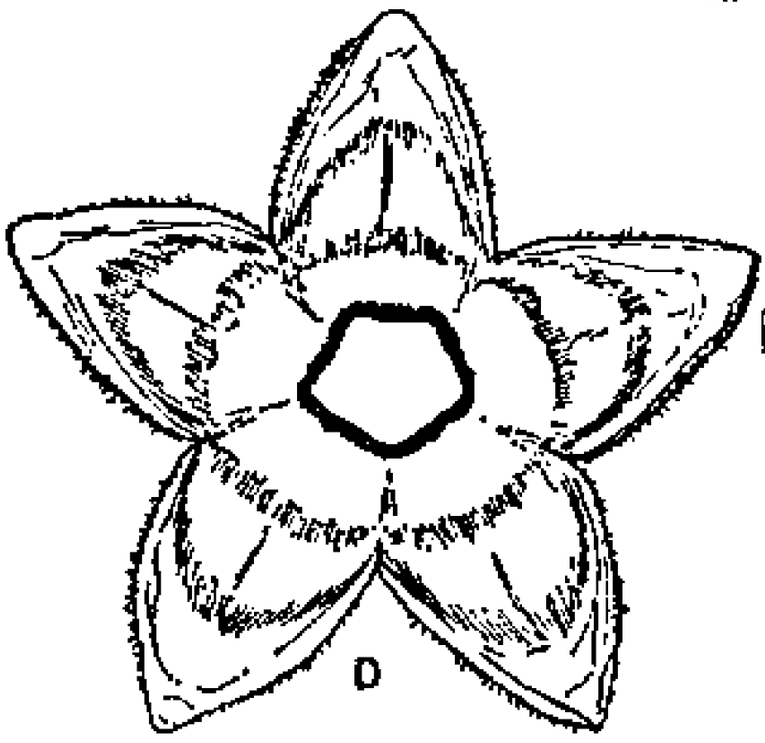


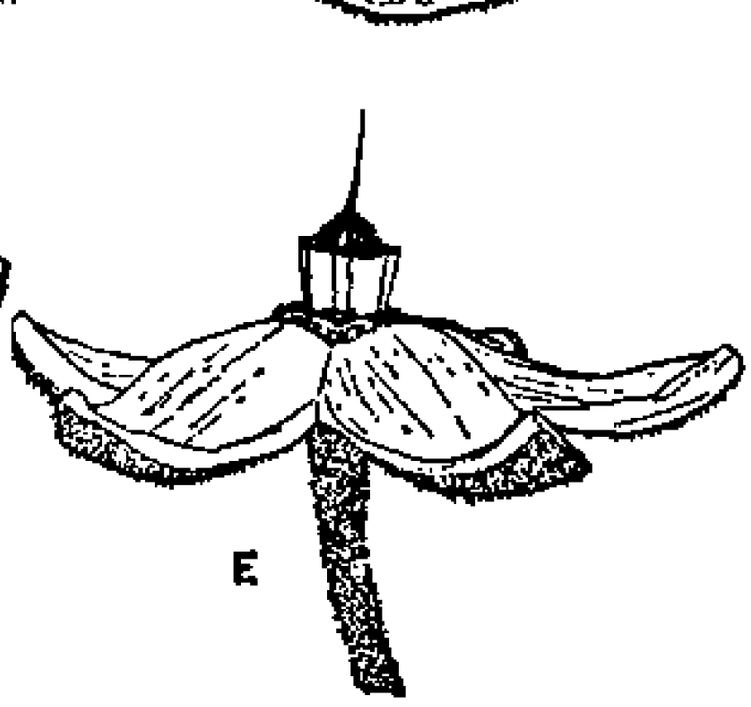
FIGURE 2.—Inflorescence in *Theobroma:* A, caulinar inflorescence of *T. bernouillii* subsp. *capilliferum* (Cuatr. 16160). B, caulinar inflorescence in *T. glaucum* (Cope & Hol. 118). C, diagrammatic terminal inflorescence branch in *T. cacao*. D, detail of sympodia. branch of inflorescence in *T. cacao*, diagrammatic, after Stahel. E, inflorescence of *T. cacao*, diagrammatic, after Stahel. F, G, detail of inflorescence in *T. cacao*, diagrammatic, after Stahel. H, inflorescence of *T. bicolor* (Klug 2021). I, diagrammatic inflorescence of *T. bicolor* after Stahel.

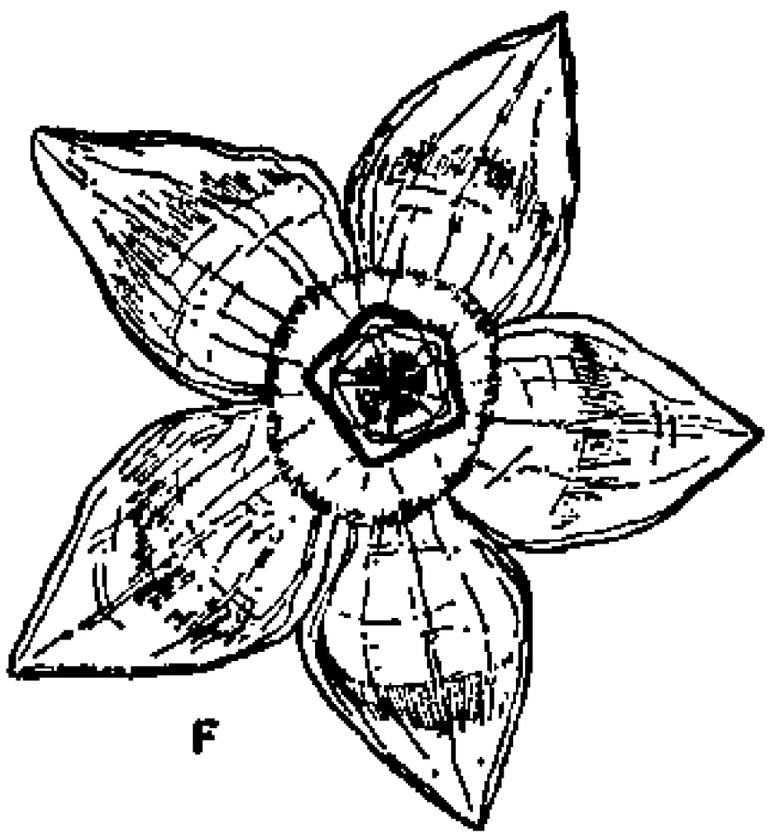


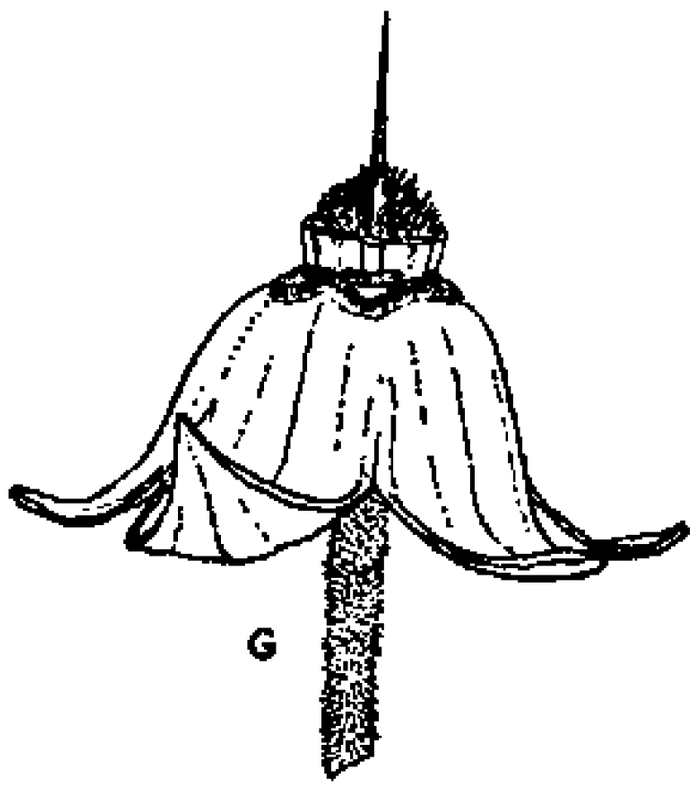


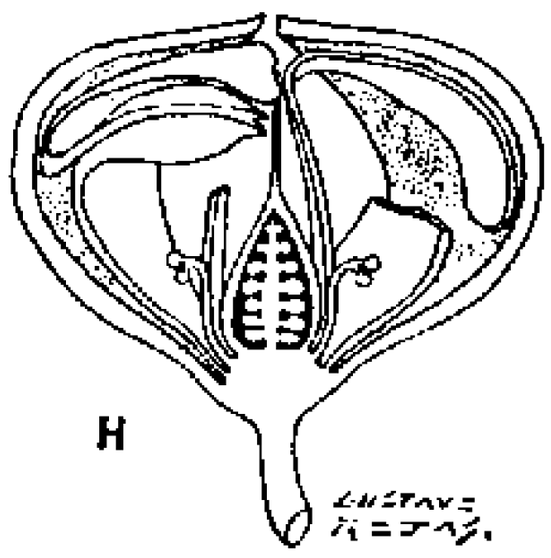


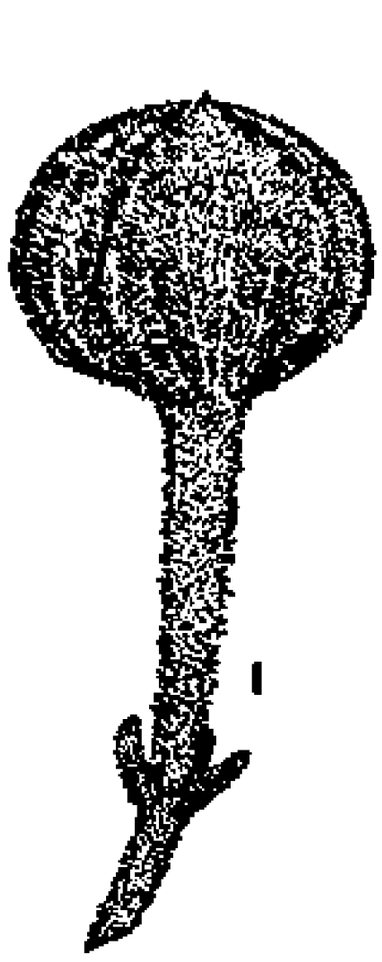


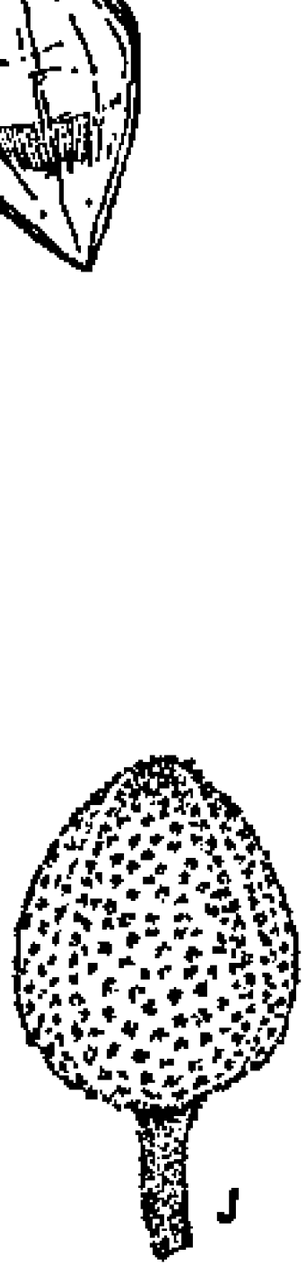


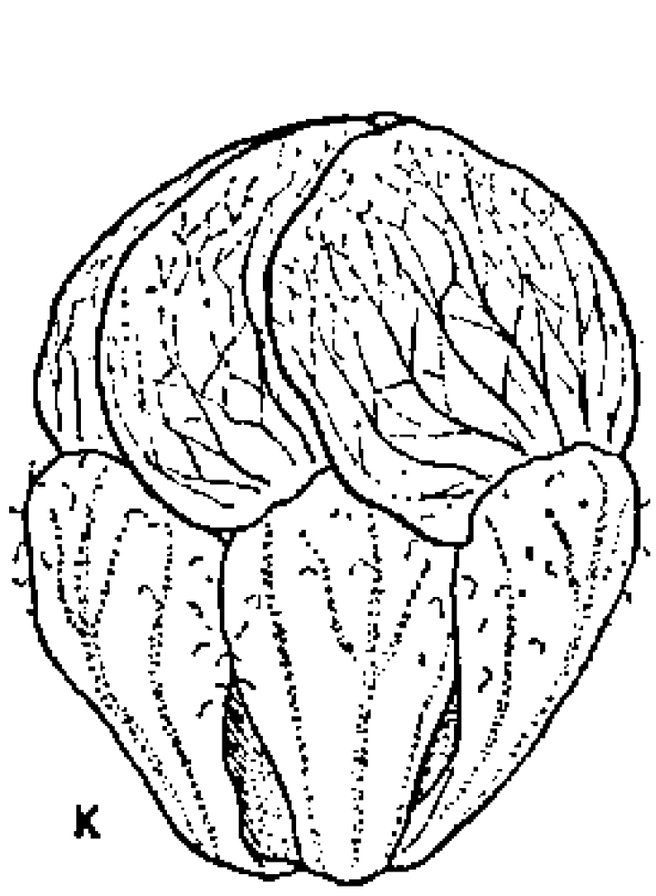


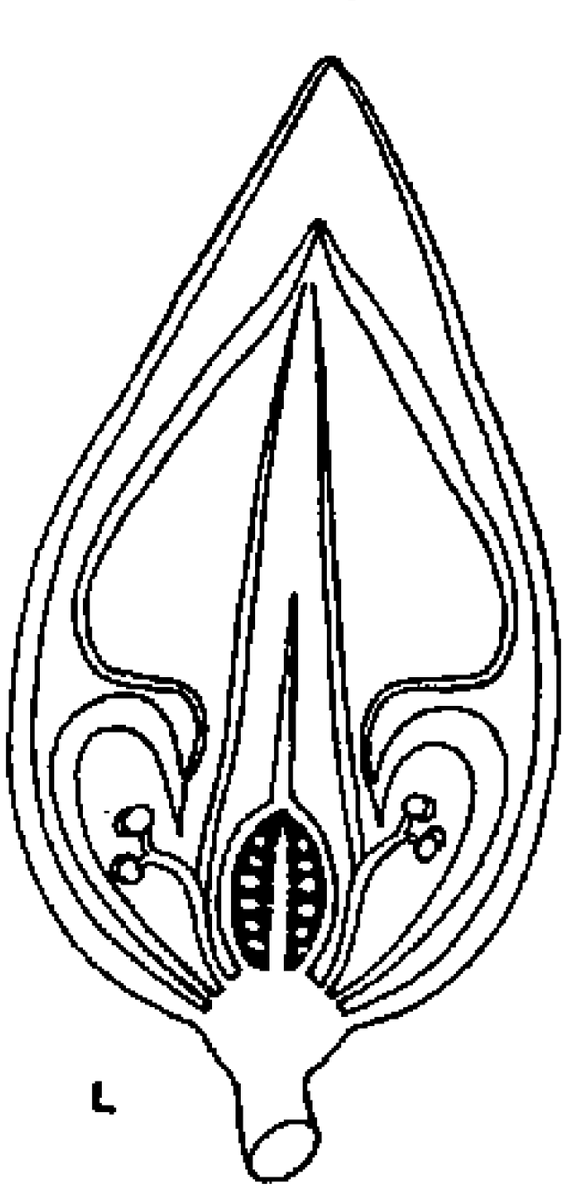












[FIGURE 3]

of the cincinnate type. Frequently the branches are very short, forming nodose, articulated sympodia, in which the internodes are hardly noticeable and the bracts appear almost imbricate. Usually the bracts are alternate and the fertile terminal branchlets or peduncles end with 3 bracteoles and one pedicel, the 3 bracteoles corresponding to a theoretical terminal dichasium which develops only the central flower. According to Stahel the peduncles have bilateral, the pedicels radial structure.

The inflorescences may be axillary, in young branchlets, but more often are originated on short, woody branchlets on the trunk and branches; these perennial branchlets form irregular tubercles, sometimes very protuberant, which may form woody branchlets up to several centimeters in length, producing flowering cymes at their ends. The flowers are always pedicellate, the pedicels being relatively long, longer than the reduced branchlets of the cymes.

Calyx (Figs. 3, 4).—The five sepals are valvate and may be almost free and spreading at anthesis or united from one fourth to one half or more of their length; the lower united part is cupular, the free parts are patulous-reflexed at anthesis but finally the whole calyx becomes reflexed, exposing the inner surface. In some instances, the sepals unite 2 by 2 simulating a calyx of 3 lobes, two of them twice as broad as the third. In the section *Andropetalum* the sepals usually are united by three and two and together form a two-lobate cup. The calyx is persistent and its remains may often be seen below premature fruits.

In most cases the sepals are tomentose outside with abundant stellate, ochraceous or ferrugineous hairs, but they may also be puberulous or glabrous, as in species or forms of the sections *Telmatocarpus* and *Theobroma*. In the latter multicellular, glandular, stipitate trichomes are present. The upper or inner surface of sepals is often glabrous or may be more or less pubescent. The inner margin always has a

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Figure 3.—Calyx and aestivation in *Theobroma:* A, B, calyx of *T. grandiflorum* (Cuatr. 25801) with sepals united by pairs appearing to be trimerous. C, calyx of *T. cacao* (Cuatr. 26004), the sepals spreading, very shortly united at base. D, E, calyx of *T. nemorale* with semispreading and semireflexed sepals, united more than ¼. F, G, calyx of *T. chocoense*, with reflexed sepals unequally united in ⅛–¼ their length; the basal glandular papillas very conspicuous. H, diagrammatic long. section of bud in *T. cirmolinae* showing the relative position of flower parts in section *Glossopetalum;* at the left side the folded petal (the alternating staminode cut away), at right the staminode (the alternating petal cut away). I, globular bud of *T. chocoense* with valvate aestivation, pedicel, bracteoles and peduncle apparent (× 2). J, ovoid, elongated bud of *T. velutinum* (× 2). K, petals in bud showing the contorted aestivation in *T. velutinum* (Benoist 161), × 5. L, diagrammatic long. section of bud in *T. cacao* showing the relative position of flower parts in sections *Oreanthes*, *Theobroma*, and *Rhytidocarpus*.

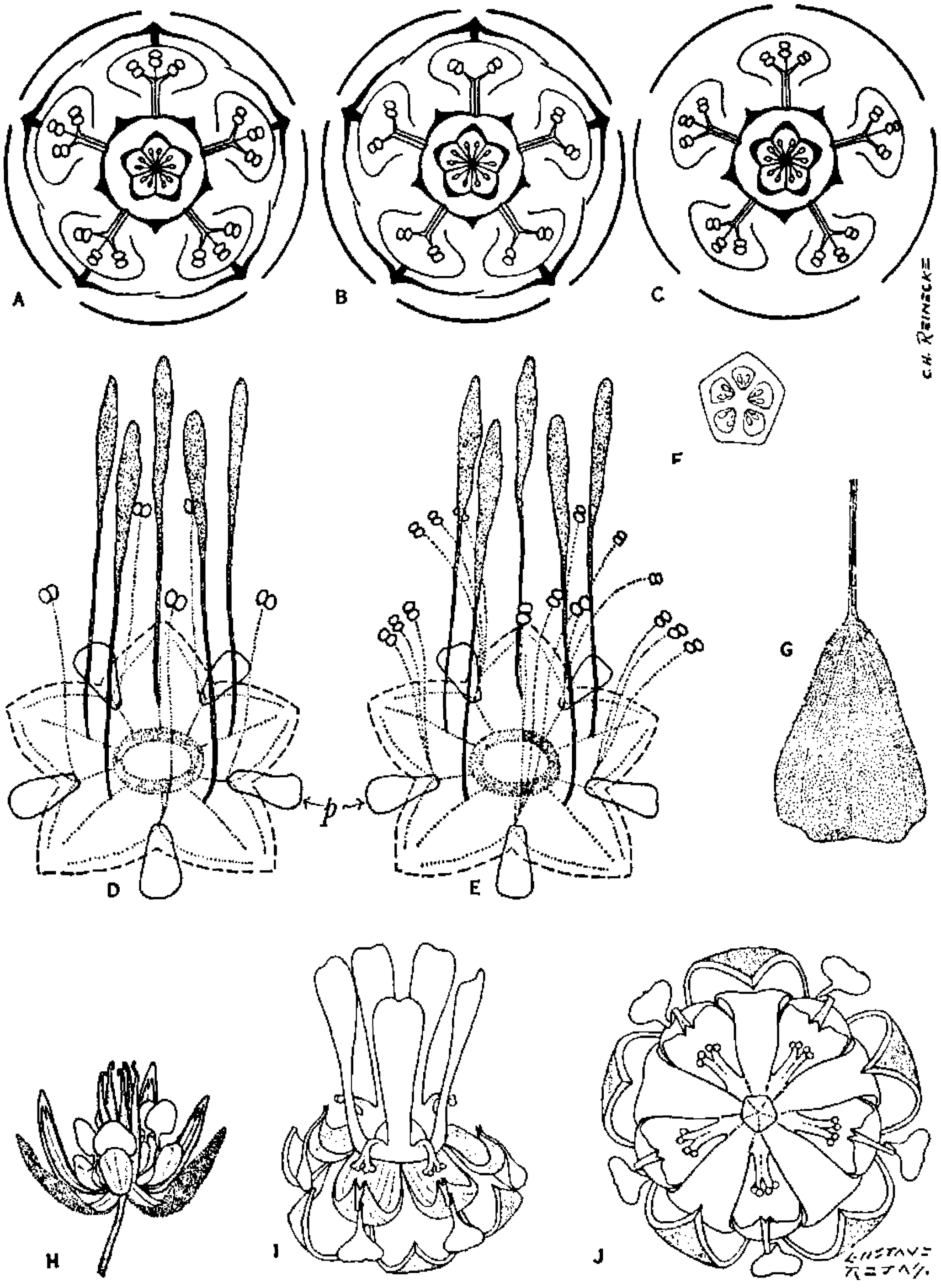

FIGURE 4.—A–C, three types of floral diagrams in *Theobroma:* A, sections *Glossopetalum* and *Oreanthes* (part); B, sections *Theobroma, Rhytidocarpus* and *Oreanthes* (part); C, section *Telmatocarpus.* D, basic diagrammatic representation of vascular bundles in the flower of the Byttnerineae; the marginal vessels (bundles) derive from the vascular branches directed to the petals; the fertile stamens are epipetal, the staminodes episepal; *p*, vascularization of petal in continuous line, after Gazet du Chatelier slightly modified. E, vascular bundles in flower of *Theobroma* (sect. *Glossopetalum*); bundles in stamens branching shortly above the base; adapted from Gazet du Chatelier. F, section of an ovary in *Theobroma* (× 20). G, gynoecium in *T. cirmolinae* (× 5). H, flower in anthesis with spreading sepals in *T. sylvestre* (Ducke 7882), × 2. I, flower in

narrow band of extremely minute and dense, whitish, stellate hairs which join the sepals before anthesis. At the base of the sepals, inside, there are commonly glandular, stalked trichomes, which may be very scarce but often are numerous and dense, forming a ring outside the place of petal insertion. These glandular trichomes are lacking in some species or very rare and scattered above on the sepals.

COROLLA (Figs. 3, 4).—The 5 petals are free and uniform; their special feature is that they are strangulated into two very different parts united by a narrow joint. The lower part is cymbiform and erect, rather carnose and rigid, usually 3–7-(or 1)-nerved and has the appearance of a hood rounded at the top; in fact, it represents the claw of the petal, and because of its appearance, it is called the "hood" (*cucullus*). The upper part of the petal (the lamina) is flat, varying in shape from oblong to elliptical or discoid, membranaceous or very thick, yellow, red or purplish. It is almost sessile and directly articulate to the apex of the hood or may be supported by a narrowly laminar pedicel, which is its basal extension; in some species the lamina is lacking or is almost reduced to the pedicellar extension (*T. mammosum*). The petals are dextrorsely contorted in estivation, the laminae being erect when directly articulated to the hood or horizontal and reflexed through the folding of the pedicel. In anthesis the laminae are erect.

ANDROECIUM (Figs. 3, 4).—This is formed by two verticils, which are connate in a tube at the base. The sterile outer whorl has 5 petaloid staminodes, which are subulate, oblong, or obovate. and usually very showy with the same color of the corresponding petal-laminae. They may be erect or reflexed in estivation, and erect, spreading like a star, or reflexed in anthesis; they are thick-membranaceous or carnose and firm, or when subulate or narrowly lanceolate they may have a thick, carnose midrib; they may be glabrous, but more commonly are hairy or covered by minute, muricate trichomes. The inner whorl consists of 5 fertile stamens, with thick filaments which are connate to the tube except for a short (1–3 mm.) free part; the apex is 2- or 3-furcate and each short branch bears an anther. The filaments are spreading and curved and, being opposite the petals, each anther is concealed in the cavity of its corresponding opposite petal-hood. The anthers are 2-celled, and each cell, ellipsoid or almost globose, is unilocular and opens by a longitudinal slit.

The 2- or 3-antheriferous stamens of *Theobroma* have been treated by some botanists as a result of the coalescence of two or three original

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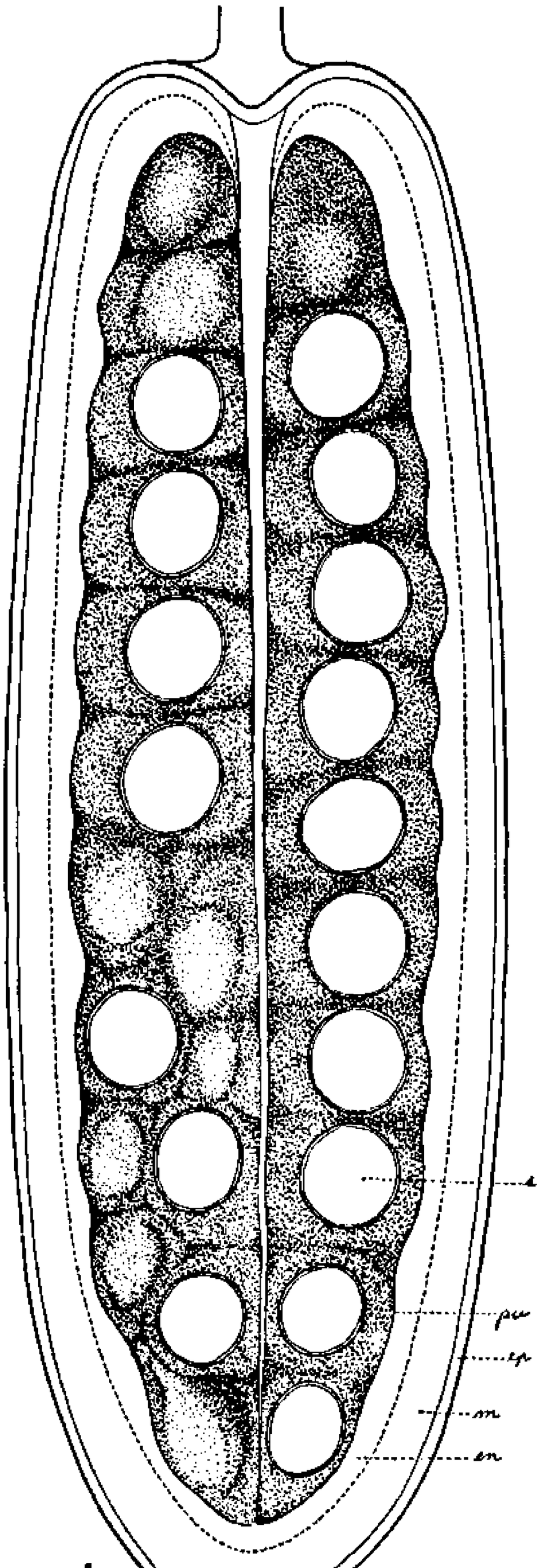
anthesis with reflexed sepals, spreading petals and erect staminodes in *T. cirmolinae* (Cuatr. 15336), × 2. J, flower of *T. cirmolinae* (Cuatr. 15336) initiating anthesis in apical view (× 2).



[FIGURE 5]

stamens. Nevertheless, I consider them to be bifurcate or trifurcate original stamens. The anatomical works of Gazet du Chatelier (1940, p. 278) prove this assertion; at the base of the flower, 5 vascular bundles proceed to the five staminal filaments, these bundles being forked above to serve the two short branches of the filament in *T. cacao*.

GYNOECIUM (Figs. 3, 4).—This is of the coeno-syncarpic type, superior, with carpels opposite to petals. The ovary is 5-celled with axile placentation and many ovules in two rows in each cavity; it is ovoid or ellipsoid, more or less markedly 5-ridged and furrowed, densely stellate-tomentose, or rarely glabrous or covered by stipitate glands.

Stylodes 5, free or more or less adherent to one another, simulating a single style, glabrous, usually about twice as long as the ovary, thin and ending in a punctiform stigmatic apex. The ovules are anatropous with dorsal raphe and two integuments.

FRUIT AND SEED (Figs. 5–7).—The fruit is almost baccate or subdrupaceous and indehiscent, the various types differing in the firmness of the pericarp and in the shape. Almost always there can be distinguished three layers in the pericarp. In the sections *Glossopetalum* and *Andropetalum*, the fruits are externally rigid, hard, the epicarp being woody, about 1 to 2 mm. thick, with an outer tomentose epiderm; the mesocarp is fleshy, differing little in color and firmness from the adjacent endocarp; the inner surface of the latter is a thin but compact membrane; sometimes, the whole endocarp is reduced to this membrane. When the fruit is ripe the carnose inner layers decay or dry, and shrink, but the rigidity of the epicarp maintains absolutely the size and shape of the fruit, keeping the loose seeds inside if they have not been accidentally liberated. In the section *Rhytidocarpus*, the mesocarp is the rigid, woody layer; the epicarp being thinner and carnose, although also with an outer tomentose epiderm; the endocarp is also carnose, and also provided with an inner membrane. In the section *Oreanthes*, typified by *T. speciosum*, the whole pericarp is 5 to 6 mm. thick; the innermost layer, the endocarp, although very thin,

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FIGURE 5.—Fruit sections of *Theobroma* species: A, long. section of fruit of *T. simiarum* (Cuatr. 26515A), × ½. B, transection of pericarp of A, natural size. C, transection of pericarp of *T. grandiflorum*, × 1. D, transection of pericarp of *T. bicolor*, × 1. E, transection of pericarp of *T. gileri*, × 2. F, transection of pericarp of *T. speciosum*, × 1. G, transection of pericarp in *T. cacao* cultivar "cundiamor" (Cuatr. 26492), × 1. H, transection of pericarp in *T. cacao* fma. *pentagonum* (Cuatr. 26540), × 1. I, transection of pericarp in *T. cacao* cultivar "lagarto" (Cuatr. 26004), × 1. J, transection of pericarp in *Herrania cuatrecasana* (Cuatr. 25793), × 2. *ed*, epiderm; *ep*, epicarp; *m*, mesocarp; *en*, endocarp; *pl*, interior pelicule limiting the endocarp inside; *pu*, pulp; *s*, seed.

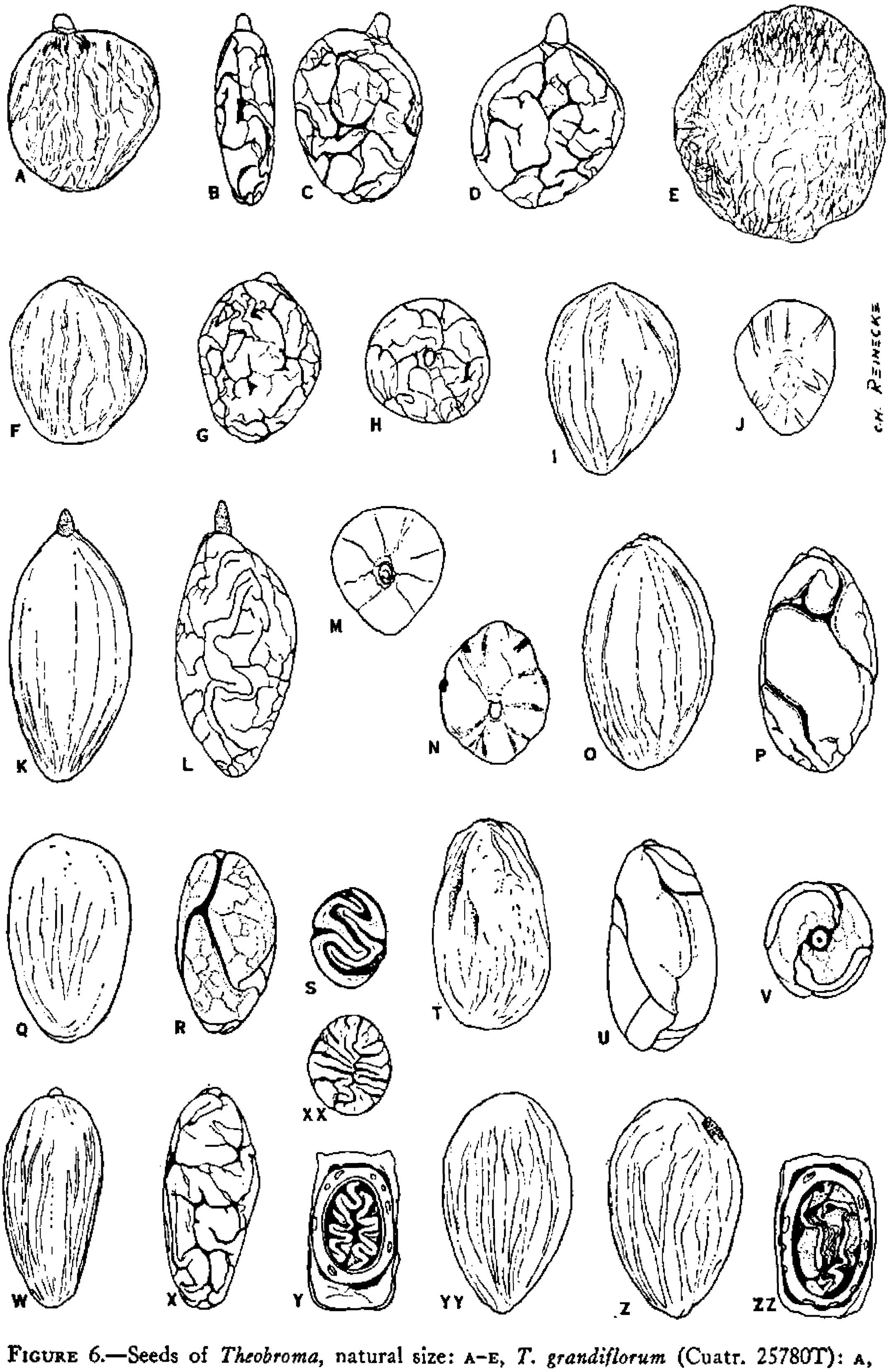

FIGURE 6.—Seeds of *Theobroma*, natural size: A–E, *T. grandiflorum* (Cuatr. 25780T): A, front view of seed stripped from pulp; B, C, D, side and front view of embryo; E, seed surrounded by its pulpy layer. F–H, *T. simiarum* (Cuatr. 26515A): F, seed; G, embryo; H, embryo in apical view. I, J, *T. mammosum* (Cuatr. 25791): seed in lateral and apical

is woody and rigid; the mesocarp is thick and fleshy; the epicarp is also woody but thin and less compact. When the mesocarp dries or decays, the epicarp shrinks slightly, becoming more or less rugose. In the section *Telmatocarpus* the innermost layer, the endocarp, is the most compact and rigid, although thin; the epicarp is coriaceous and thin and the mesocarp is thick and fleshy with strong bundles which build protruding ridges and veins covered by the epicarp. Finally, in section *Theobroma* (Cacao) the fruit is almost baccate because the whole pericarp is carnose; the inner membrane and the outer epiderm may be very firm but the whole pericarp decays easily; it can also dry out, being then coriaceous. Usually the three layers are conspicuous, the epicarp carnose and thick, with glabrous outer epiderm, the vascular mesocarp papyraceous, rigid, thinly woody, and the endocarp carnose, more or less thick, with an inner pellicle; in some forms of cacao the mesocarp may be reduced to a very thin or discontinuous layer or to isolated vascular bundles (fig. 5I); rarely the endocarp is reduced to the inner pellicle (fig. 5H, forma *pentagonum*). Usually, the dorsal vascular bundles of each carpel develop into transverse membranes within the fleshy epicarp connecting with the mesocarpial layer. Gummy sacs are always present in several parts of the pericarp.

The young fruit, as well as the ovary, has five cavities with the incipient seeds arranged in one or two rows in each cavity. At maturity the cell walls vanish and the seeds with their thick outer pulpy layer fill the single cavity, arranged usually in five rows.

The shape and size of the fruit are variable and they are, combined, specific characters except for cultivated cacaos. The fruits range between 6 and 35 cm. long by 5 to 12 cm. broad and may contain, when ripe, from 16 to 60 seeds. They may be ellipsoid, globose, ovoid, oblong, or fusiform, with rounded or attenuate ends, with completely smooth surface like a potato or marked more or less with 5 or 10 ridges, or they may be echinate or verrucose. In all cases they are indehiscent and the liberation of seeds follows the decay of the shell, which in many cases, as in those with hard, woody pericarp, may take so long that the seeds have died. The common natural way of propagation of the seeds is accidental, usually by

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view. K–M, *T. angustifolium* (Cuatr. 25790): K, seed stripped from pulpy layer; L, embryo; M, embryo in apical view. N–P, *T. gileri* (Cuatr. 26167): N, seed in apical view; O, same laterally; P, embryo. Q–S, *T. speciosum:* Q, seed; R, embryo; S, embryo in transection, showing the folding of cotyledons. T–V, *T. bernouillii* subsp. *capilliferum* (Cuatr. 17034): T, seed; U, embryo; V, embryo in apical view. W–XX, *T. cacao* fma. *pentagonum* (Cuatr. 26004): W, seed; X, embryo; XX, transection of embryo. Y, YY, *T. cacao* fma. *pentagonum* (Cuatr. 26540): Y, transection of seed with episperm and pulp; YY, seed. Z, ZZ, *T. cacao* cultivar "cundiamor" (Cuatr. 26492): Z, seed; ZZ, transection of seed with episperm and pulp.

animals (mostly monkeys, but also squirrels, rats, and other animals) which break the pericarp in order to suck the pulp surrounding the seeds, which may be expelled later in other places, thus disseminating the seeds (fig. 5).

The fruits, which are commonly called pods in English, *mazorcas* in Spanish and *cabosses* in French, may stay on the tree or fall down after maturation; in the latter case, they may fall with the peduncle (e.g., *T. bicolor*) or without it (as in *T. grandiflorum*). Precise observations in many species are wanted.

The seeds are ellipsoid, ovoid or amygdaloid, more or less irregularly compressed, complanate, or terete, and range from 15 to 40 mm. long and 10 to 22 mm. broad; the integuments or skin form two strata with an additional outer, thick, gelatinous-pulpy layer surrounding them. The testa is generally thick and subcoriaceous, with an external epiderm covered by a thick cuticle, a thick layer of polyhedric and mucilaginous cells, and an inner layer of sclerosed cells. The inner tegument is a thin membrane of several layers of thin-walled, complanate cells. Inside, the large embryo is composed of two large, thick, strongly folded and corrugate cotyledons and a straight, rather thick, terete radicle, the plumule being scarcely developed. The endosperm at maturity has the shape of a very fine pellicle, containing scattered cells with calcium oxalate, covering the embryo outside and between its foldings. The cotyledons possess an epiderm, often with scattered, stipitate glandular trichomes and a main cellular tissue rich in starch, fat, aleurone, tannoid and alkaloidal substances, among these the important theobromine compounds. In most species the cotyledons are white, but in a few they are violet, reddish, purplish, being stained by tannins (figs. 5, 6). Germination may be either epigeous or hypogeous according to the species (fig. 7).

The pulp surrounding and united to the seeds is white, yellowish, or yellow, and often sweet and aromatic and palatable, but it may be also scentless and tasteless to men; it is, however, always appreciated by animals, which hunt the pods, extract the seeds to suck the pulp, thus disseminating them.

In appropriate conditions the pulp suffers a fermentation process which separates it from the seed; during that fermentation, very well known in the case of *T. cacao*, chemical changes take place inside the embryo developing a special aroma. In the industry of cacao torrefaction completes the desired effects of fermentation.

Premature fruits keep their viability for some time provided they are protected against loss of humidity and stored under suitable temperatures (20–25° C.); when ripe, the seeds become immediately ready for germination; they may germinate inside the pods. The

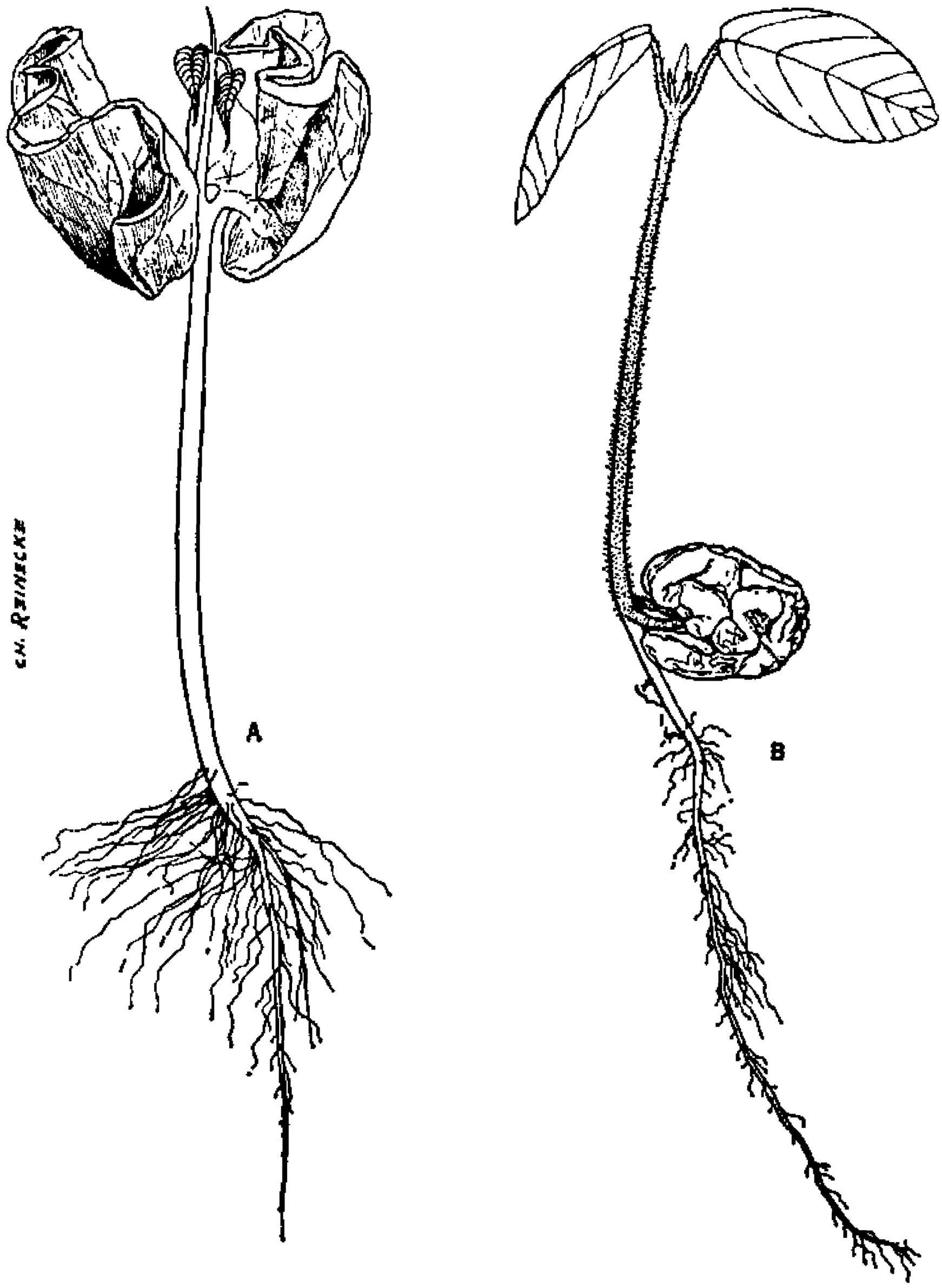


FIGURE 7.—A, Epigeal germination in *Theobroma bernouillii* subsp. *capilliferum* (Cuatr. 17350A). B, Hypogeal germination in *T. grandiflorum* (Cuatr., Cope & Bart. 25780A).

germinating power of *Theobroma* seeds lasts only for a short time, a few weeks; observations on *T. cacao* have shown a maximum extension time of viability to about three months, when carefully preserved in their pods or under special protection. They are extremely sensitive to the degree of humidity, which has to be kept high, and to low temperatures. Recent experiments in Turrialba showed that cacao seeds could not resist low temperatures for even a short time; seeds exposed for 16 minutes at 8° C. lowered the germinating capacity to 6%, and 4 minutes exposure at 2° C. inhibited germination almost completely (Hunter, 1959; Hunter & Boroughs, 1961). This may be the explanation why cacao seeds lose their germinating power

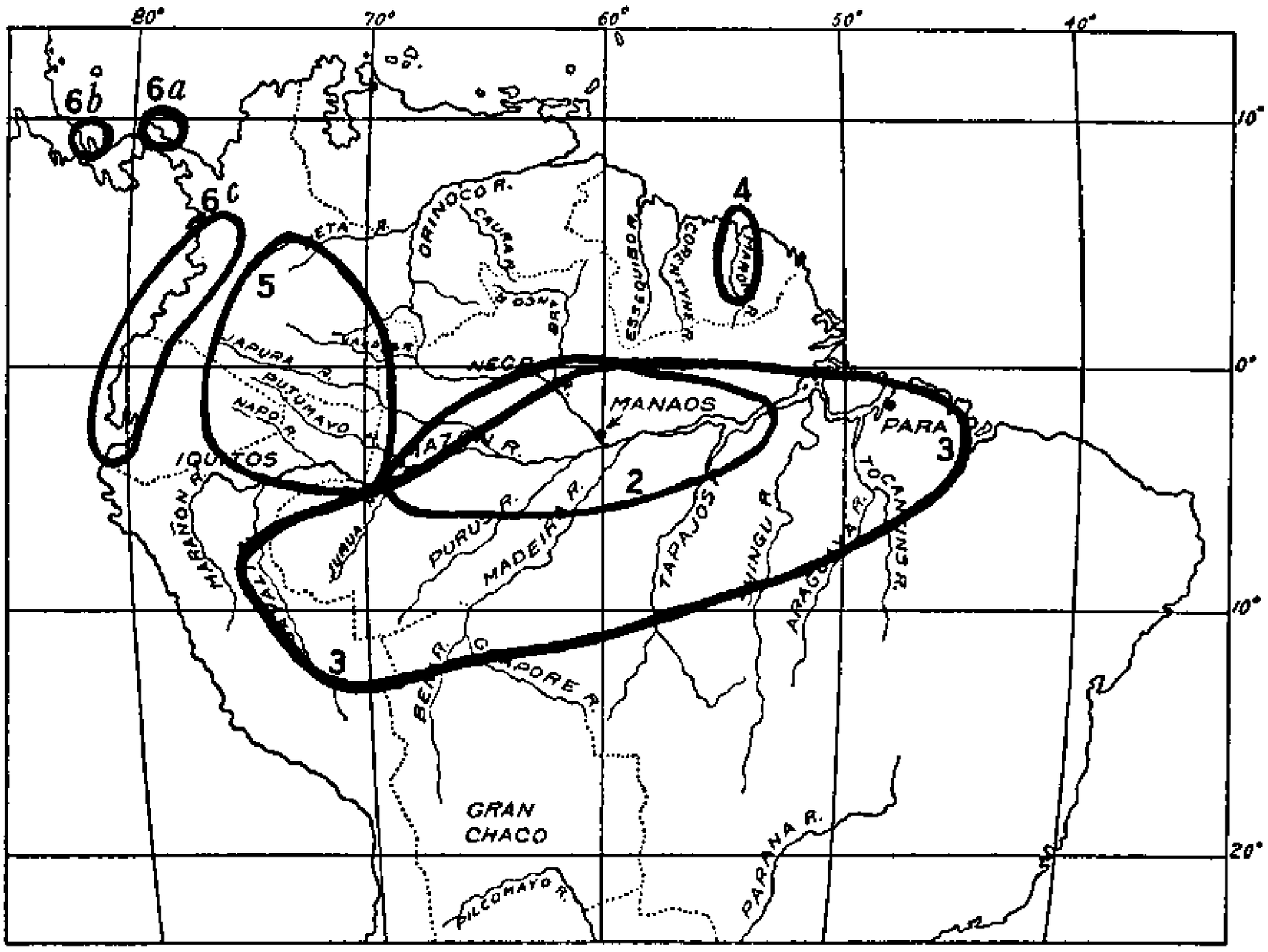
when transported by airplanes at high altitude (Hunter, personal communication).

Ecology

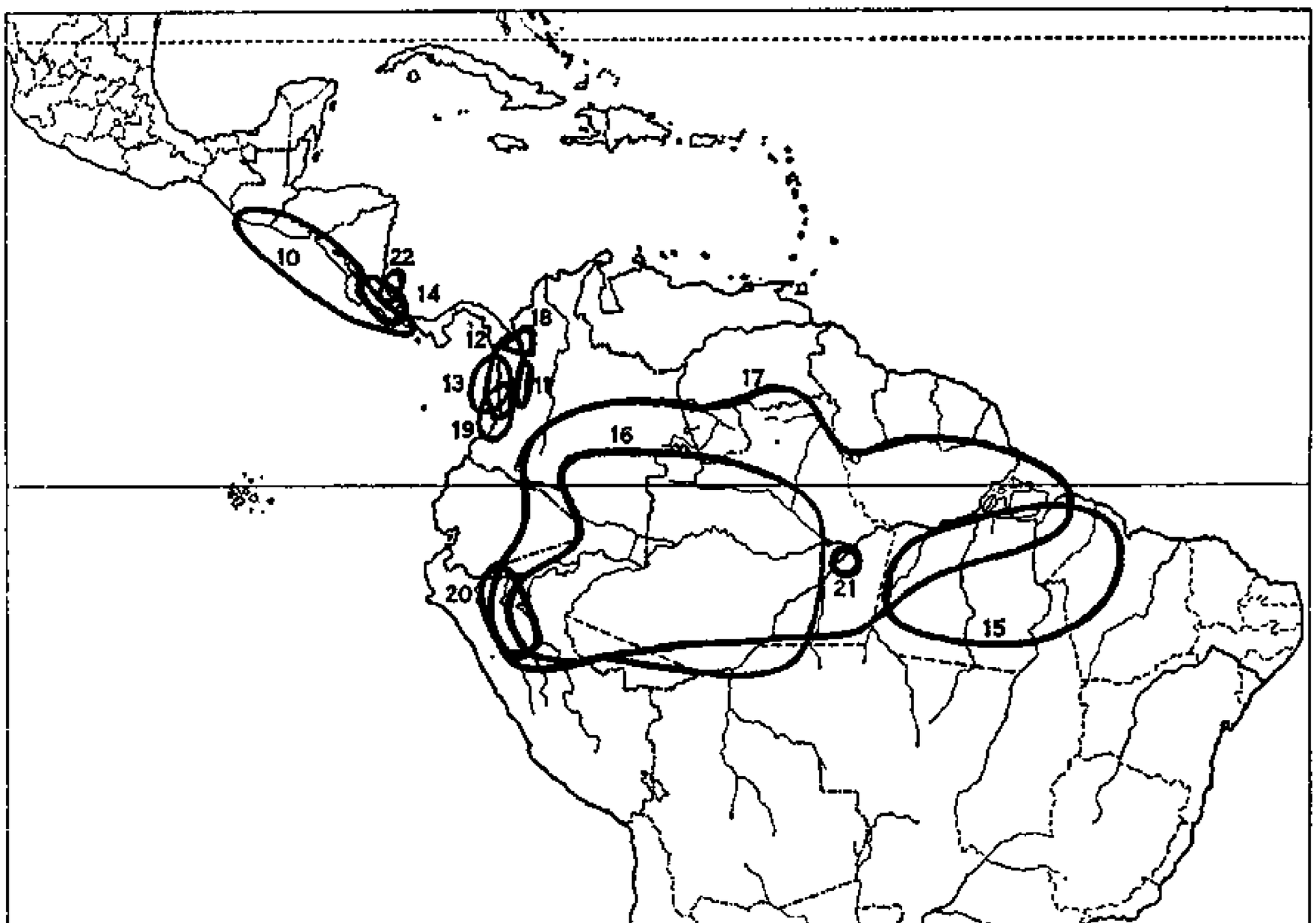
Theobroma is a tropical American genus restricted to the lower tree-story of the evergreen rain forests. The species demand a high degree of mean annual temperature with narrow oscillations, a constant high humidity, and protection (shade) against direct radiation and evaporation. Several species are often found at the edges of rivers or marshes in more or less temporarily flooded areas; others always grow on elevated, drained places. They like relatively rich and neutral soils. These conditions are found only in the warm, wet, forested, equatorial regions between latitudes 18° North and 15° South, with temperatures of 20° to 30° C., with a minimum of 16° and maximum of 40°. A few species grow at higher altitudes up to 1250 meters, being able to withstand minimum temperatures of 14° and even 12° C. Where *Theobroma* is at home, the rainfall is from 2000 mm. to 8000 mm. annually or even higher, and is more or less evenly distributed throughout the year. *Theobroma* does not resist even short dry seasons without the protection of dense shade and local humidity. In cultivation *T. cacao* can endure less humid climates, and more open lighter spots especially when irrigated, and somewhat lower temperatures than the normal optimum. So the area of cultivated cacaos may extend far above 20° North and below 20° South of the Equator. Not only the *Theobroma* trees but also the seeds are highly specialized to the humid equatorial ecological conditions. It is known that the seeds keep for a very short time their capacity for germination, which often takes place inside of the pod; only under high humidity and optimum temperatures can they maintain their viability (see above).

Geographic Distribution

The genus *Theobroma* is a typical neotropical genus, distributed throughout the rain forests of the western hemisphere between latitudes 18° North and 15° South. Some species have a broad range of distribution, like *T. subincanum*, which is spread throughout the Amazon-Orinoco basins, being one of the most ancient of the genus. The elevation of the Andes in the early Tertiary separated populations of *Theobroma* previously widespread before, favoring speciation through isolation. Vicarian species separated by this way are *T. subincanum* (east of the Andes) and *T. hylaeum* (west); *T. microcarpum* (east) and *T. gileri* (west). The complexity of the mountains of the northern part of Colombia through Central America was also an isolating factor which favored speciation in that part of the hemisphere where regional or local endemics are present. Maps 1 and 2 are self-explanatory.



MAP 1.—Geographical areas of *Theobroma* sect. *Oreanthes:* 2, *T. sylvestre;* 3, *T. speciosum;* 4, *T. velutinum;* 5, *T. glaucum; T. bernouillii:* 6*a*, subsp. *bernouillii;* 6*b*, subsp. *asclepiadiflorum;* 6*c*, subsp. *capilliferum.*



MAP 2.—Geographical areas of *Theobroma* sect. *Glossopetalum* (10–21) and sect. *Andropetalum* (22). 10, *T. angustifolium;* 11, *T. cirmolinae;* 12, *T. stipulatum;* 13, *T. chocoense;* 14, *T. simiarum;* 15, *T. grandiflorum;* 16, *T. obovatum;* 17, *T. subincanum;* 18, *T. hylaeum;* 19, *T. nemorale;* 20, *T. sinuosum;* 21, *T. canumanense;* 22, *T. mammosum.*

Pollination

Although transportation of pollen by the wind has had some acceptance, it seems that only pollination by insects has been proved. Works by Harland, Stahel, Posnette, Saunders, Cope, Uzel, Jones, and Pound, have demonstrated that several kinds of flying and crawling insects are involved in pollen transportation, among them thrips, ants, midges, and aphids. Experiments by Cope proved that *Frankliniella parvula* Hood and *Wasmannia auropunctata* Rog. were mostly responsible for pollen transportation in Trinidad. Saunders found in Costa Rica that *Forcipomyia* midges performed pollination in cacao. The aphid *Toxoptera aurantii* Fouse is also recorded as a pollinating agent.

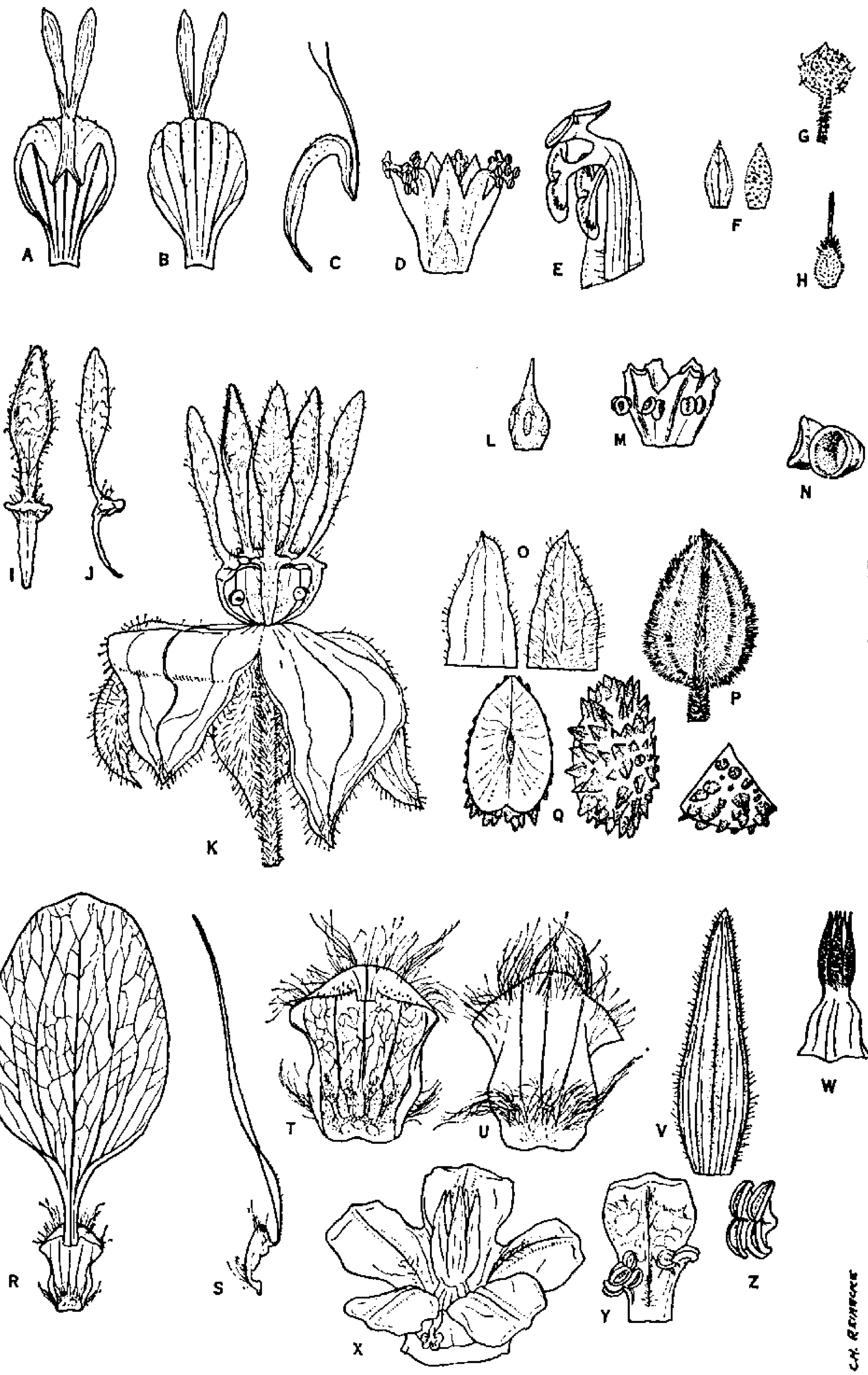
Relationships

The basic features of Theobroma are: Flowers bisexual, pentamerous; sepals valvate; petals strangulated, contorted in bud with cymbiform, cucullate lower half; 5 stamens opposite to petals and 5 evident, alternating staminodes united in a short basal tube; stamens shortly 2–3-branched; anthers 2-celled; ovary superior, 5-celled; ovules many, anatropous with 2 integuments; fruit subdrupaceous or subbaccate; seeds with pulpy envelope; cotyledons folded, corrugate; evergreen trees with dimorphic branching and dimorphic, entire, alternate leaves. This diagnosis places the genus in the family Sterculiaceae (fig. 8).

Theobroma exhibits a unique set of characters which makes it a very "natural" genus. However, some of the outstanding features of its floral structure are also shared by other genera, the most conspicuous being the cucullate or concave lower part of the petals which define the tribe Byttnerieae DC., and determine the close relationships between its members: *Byttneria*, *Ayenia*, *Rulingia*, *Commersonia*, *Theobroma*, *Guazuma*, *Herrania*, *Abroma*, *Glossostemon*, *Scaphopetalum*, and *Leptonychia*. In most of these cases the similarity with *Theobroma* in the flower structure (petals, androecium-tube, staminodia, and position of anthers) is so obvious that it was noticed since early times. The first historical association of *Theobroma* to another genus was by Linnaeus who joined it with *Guazuma* under Polyadelphia Pentandria. Lamarck (1785) was the first to make a family associating *Theobroma* with *Abroma*, *Guazuma*, *Ayenia*, *Byttneria*, and *Kleinhovia*. Jussieu (1789), associated *Theobroma* with *Abroma*, *Guazuma*, *Byttneria*, *Dombeya*, *Assonia*, *Pentapetes*, and *Melhania* in sectio V [bis] of ordo XIV. Kunth (1823) was the first to establish critically the main groups of the Sterculiaceae, one of them the Byttneriaceae verae including *Theobroma*, *Guazuma*, *Abroma*, *Glosso-*

stemon, *Byttneria*, *Ayenia*, and *Commersonia*. This grouping was basically followed by DC. (1824), Endlicher (1840), although he separated the Sterculiaceae from Byttneriaceae, Baillon (1873) in his series Byttneriées, Bentham & Hooker (1862), who enlarged the family to 7 tribes, and Schumann (1890) who enlarged it to 8 tribes. The latter botanist, who made an outstanding contribution to the comparative morphology and taxonomy of the whole family, did not alter the concept of the Byttnerieae DC. as presented by Bentham and Hooker. Recent workers, like Gazet du Chatelier (1940), who made broad comparative anatomical and morphological studies in the Sterculiaceae, found good reasons to keep Schumann's basic taxonomic approach.

Bentham and Hooker divided the tribe artificially in two groups which were named by Schumann Theobrominae and Byttnerinae, with respectively 2–3-antheriferous and 1-antheriferous stamens. On the other hand, the four genera of Byttnerinae differ from *Theobroma* also because *Byttneria* has spirally convolute cotyledons, short, dentiform staminodes and linear, rather thick, petal-laminae; *Ayenia* has very long, linear petal-claws, trilocular anthers, and spirally convolute cotyledons; the Old World *Commersonia* and *Rulingia* have a pitcher-shaped petal base and flat cotyledons. From the other Theobrominae genera, *Theobroma* is distinguished by the special structure of the petals, staminodia, and vegetative system; the Persian genus *Glossostemon* is a shrub with hairy, dentate leaves, ovate-oblong petals, concave at base, and with many short stamens connate to the basal part of the staminodes; the Old World *Leptonychia* differs by its short, squamiform petals, fertile stamens with filaments much longer than the staminodes, and flat cotyledons; the west African shrub *Scaphopetalum* has exappendiculate petal hoods, a campanulate androecium with shortly triangular staminodes and sessile 3-grouped anthers; the tropical American *Guazuma* differs, besides in the fruit, by the long, bifid petal appendages, the spirally convolute cotyledons, and the vegetative structure, the leaves being serrate; *Abroma*, an oriental genus spread from eastern India through the Pacific islands to Australia, is similar to *Theobroma* in the floral arrangement but usually has more developed petal laminae, shorter petaloid staminodes, subsessile anther groups, flat cotyledons, a different vegetative habit, and usually cordate, more or less lobate, hairy leaves. Moreover, all genera mentioned of the Byttnerinae differ from *Theobroma* by their capsular, generally dehiscent fruit. Only *Theobroma* and *Herrania* in the tribe have an indehiscent baccate or subdrupaceous fruit. For this reason, Schumann united them, calling the latter section *Herrania*, an arrangement adopted by other botanists, such as Pittier and Ducke. Nevertheless, Bernoulli, the monographer who



[FIGURE 8]

went deeply into the genus, and Chevalier in his revision consider *Herrania* and *Theobroma* different genera. R. E. Schultes followed the same line in monographing, after long experience, the genus *Herrania* with 17 species. They are undoubtedly two well-defined, independent genera.

Herrania, Abroma, Guazuma, and *Byttneria* surely are the genera closest to *Theobroma.* Chromosome number and palynology help to determine relationships. The chromosome number is identical for *Theobroma* and *Herrania,* $2n = 20$ but it is $2n = 16$ for *Guazuma* and $2n = 14$ in *Byttneria* (Cristóbal); data for *Abroma* not available. The pollen grains are suboblate in *Theobroma,* prolate in *Herrania,* prolate-spherical in *Guazuma,* and oblate in *Abroma.*

Because of the similarity of the fruits and the confusion which had prevailed in the past between *Theobroma* and *Herrania,* their differences are summarized here as follows:

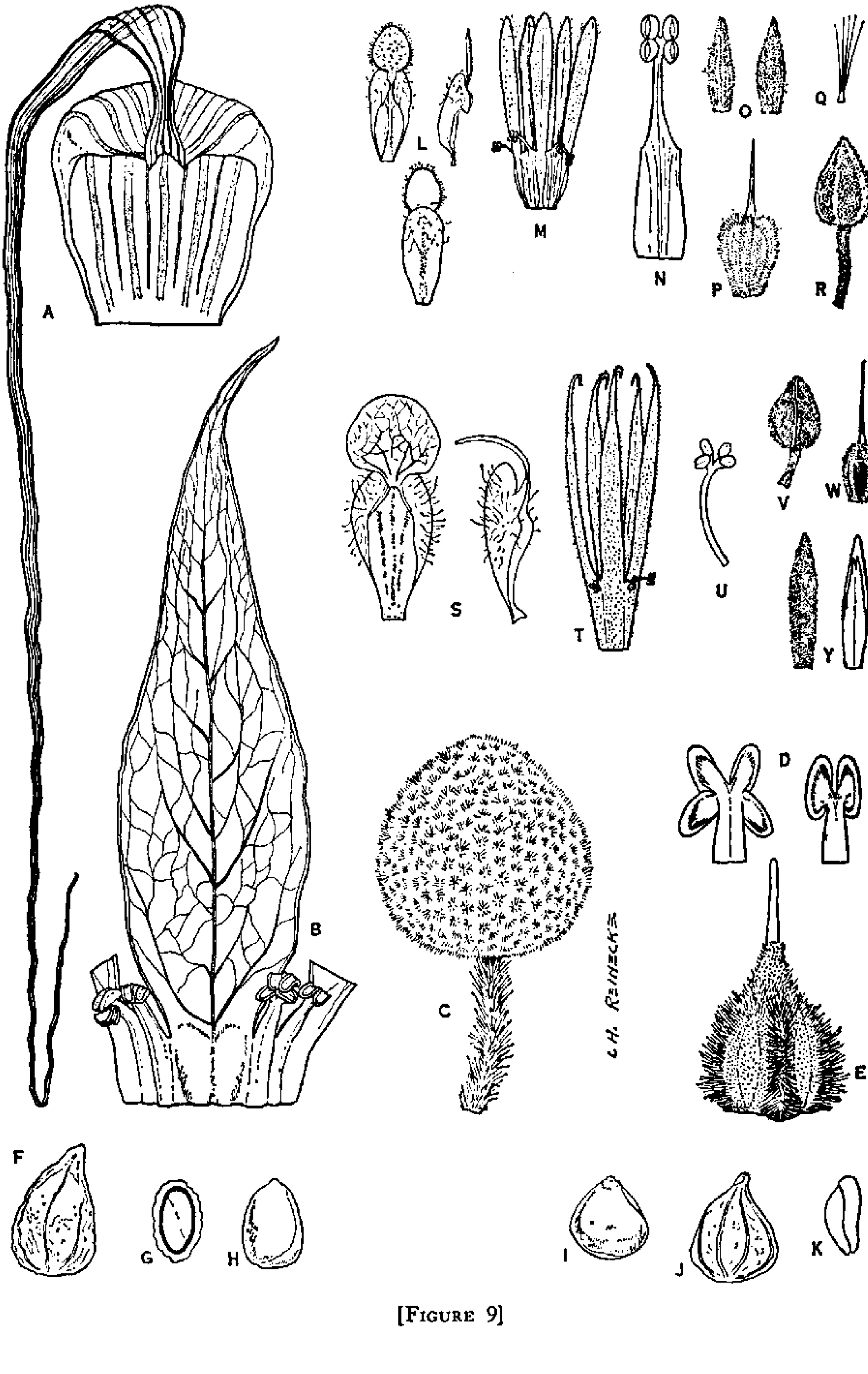
Theobroma. Stem sympodial, with 3–5-verticillate branching; branches dimorphic; branching copious; leaves dimorphic; leaf-blades simple, entire; petal lamina more or less rounded to lanceolate, not more than twice as long as the hood, erect or inflexed and contorted in aestivation; pollen grains suboblate; cotyledons strongly folded and corrugate; fruit usually smooth or rugose, angular, seldom strongly costate; staminal filament symmetrically and shortly 2- or 3-furcate at apex.

Herrania. Stem monopodial, unbranched, with apical growth; leaves uniform, 5–9 digitate, long-petiolate, in a terminal, lax cluster; petal lamina many times longer than the hood, linear, pendulous in anthesis, involute in aestivation; pollen grains prolate; cotyledons thick, flat or very slightly folded; fruit usually strongly costate; staminal filament usually asymmetrically parted in two branches, one 1-antheriferous, the other 2-antheriferous (fig. 9).

Evolution

The question of how the genus *Theobroma* may have originated is a speculative matter on which botanists like Schumann (1886)

FIGURE 8.—Genera related to *Theobroma:* A–H, *Guazuma:* A, articulated and hooded petal with bifid appendix, from inside; B, same from outside; C, same in lateral view, × 5; D, androecium, × 5; E, fertile stamen, × 20; F, sepals, × 2; G, bud; H, gynoecium, × 5 (*G. tomentosa,* Cuatr. 22942). I, J, *Byttneria:* I, articulated petal from inside, × 10; J, same laterally. K, flower, × 10. L, gynoecium, × 10. M, androecium, × 10. N, detail of the anther, × 20. O, sepals, from inside and outside, × 5. P, bud, × 5. Q, carpel of fruit from inside, outside and apical view, × 2 (*B. arguta,* Cuatr. 8226). R–Z, *Abroma:* R, articulated, hooded petal, × 2; S, same in lateral view; T, hood from inside and U, from outside, × 5; V, sepal, × 2; W, pistil, × 5; X, androecium surrounding the gynoecium, × 5; Y, base of staminode with laterally attached stamens, × 5; Z, biantheriferous stamen, × 10 (*Abroma augusta,* Sulit 18880).



[FIGURE 9]

did not want to take a stand. Edlin (1935) who developed a theory on the evolution of the Malvales, considers the family Sterculiaceae limited to the tribe Sterculieae, all other groups forming the family Byttneriaceae; he considers the stamens the result of union. Gazet du Chatelier (1940), after a detailed examination of the Sterculiaceae, came to the conclusion that there was an original unknown type from which were derived two diverging groups (subfamilies or families), the "Eriolaenées" and the "Buettneriées," but he did not go much further in his speculative evolution; the stamens of *Theobroma* are considered as branched by him.

All the genera of the Byttnerieae are similar and probably originated at the same time evolving from an original unknown type; they diversified their flowers and the leaves, probably through mutations aided by geographical and ecological barriers. The parts have evolved independently, e.g., *Rulingia* has undivided fertile stamens, a more ancient character, but pitcherlike petals, a more evolved one. Conversely, *Leptonychia* has simple, more primitive petals but exhibits branched stamens, a more advanced character. *Byttneria* and *Guazuma* have elaborate, advanced petals but less developed staminodes; *Commersonia*, as well as *Abroma* and *Theobroma*, have more advanced petals and staminodes than the other genera. *Scaphopetalum* is an example of a more advanced type due to the loss of the petal lamina and reduction of the staminodes. Even if we can attribute primitiveness or the contrary to some characters, it is not possible to draw a lineal series of genera according to antiquity. Nevertheless, I would venture to say that *Theobroma* and *Herrania* belong to the most modern in the Byttnerieae because of the structure of the fruit, with thick and partly or totally carnose pericarp and delicate, short-lived seeds. These may be characters acquired in the process of evolution and kept by their adaptation to the extremely hot and humid ecological conditions of the tropical American forests. It also seems to me that *Herrania* is a more evolved genus in regard to the flower, but not in the simplicity of the monopodial, juvenile-

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FIGURE 9.—A–H, *Herrania pulcherrima* v. *pacifica* (Patiño 23): A, articulated and hooded petal, × 5; B, segment of androecium with a staminode and the adjacent stamens, × 5; C, bud, × 5; D, stamens, × 10; E, gynoecium, × 5; F, seed, × 1; G, transection of seed, × 1; H, embryo, × 1. I–K, *H. cuatrecasana:* I, embryo; J, seed; K, transection of embryo, × 1. L–R, *Theobroma bicolor* (Garcia B. 11178): L, petal from inside, outside and laterally, × 5; M, androecium, × 5; N, fertile stamen and part of staminal tube, × 10; O, sepal from inside and outside, × 2; P, gynoecium, × 5; Q, styles, × 5; R, bud and pedicel, × 2. S–Y, *T. sylvestre* (Ducke 7882): S, petal from inside and laterally, × 5; T, androecium, × 5; U, stamen, × 10; V, bud, × 2; W, gynoecium, × 5; Y, sepal from outside and inside, × 2.

like, unbranched stems, in the digitate, loosely clustered leaves, and inseparable, hypogeous cotyledons, due probably to the stringent ecological conditions of the shadowy underlayer of the humid tropical forest. Aside from *Herrania*, the sections of *Theobroma* (*Glossopetalum*) with pseudoterminal growth, may be more primitive than the ones (*Oreanthes, Rhytidocarpus, Theobroma*) which have lost the axillary buds of the jorquette branches, necessitating lateral shoots to continue growing. The section *Theobroma* may be more evolved than the others on account of the 5-branching system and carnose fruits. The section *Telmatocarpus* may be more advanced in another direction because of the reduction or absence of the petal lamina and the discontinuity of the vascular, woody system in the pericarp, which is only partially woody and more vulnerable. The parallelism in evolution of the sections *Theobroma* and *Telmatocarpus* is seen in the glabrous or almost glabrous leaves, more suited to rain-forest ecology. The section *Rhytidocarpus* may be an ancient type with less showy petals and staminodes, axillary flowers, and a thick-woody pericarp.

No fossils belonging to *Theobroma* have been recorded.

The geographic distribution does not give any solution to these questions of evolution because almost all sections are represented at both sides of the Andes. It seems that the richest region in species is around Panama and Colombia, where species with a very restricted area are found, especially if we consider this region extended to Costa Rica. I feel that *Theobroma* is a genus with a marvelous set of characters controlled perhaps by independent genes, which seemingly can combine independently resulting in many different sets of combinations.

Economic Uses

The seeds of *Theobroma* are rich in starch (15%), protein (15%), and oil (50%), for which reason they are considered a substantial food. Moreover, they have a volatile oil (cacao-essence) which gives an aromatic flavor and 1.5 to 3% of theobromine, an alkaloid known for its stimulant properties. Caffeine is also present in *Theobroma* seeds. Both alkaloids have been found in the seeds and leaves of *T. bicolor, cacao, grandiflorum, microcarpum, obovatum, speciosum, sylvestre,* and *subincanum* (Willaman and Schubert, 1961). The cacao seeds contain also a red pigment, tanine, and small quantities of malic and tartaric acids, asparagine, and coline.

It is not necessary to emphasize the economic importance of the industry in cocoa and chocolate. Most of the wild species of cacao are often used by the natives, who suck the pulp or prepare refreshing drinks with the pulp. The seeds of most species may serve for the preparation of chocolate, but actually only one species has become

commercially important in this respect, *T. cacao*, which is the only one widely cultivated. An important secondary product from cocoa seeds is the cocoa butter extracted by pressure during the process of making chocolate. Cocoa butter is important in cosmetics and pharmaceutical industries. Cacao extracts and theobromine are important in medicine because of their cardiotonic and diuretic properties.

The wood of several *Theobroma* species is important in local construction and because of its toughness and strength is very much used in the manufacture of tools and parts of instruments and machines.

Anatomy of the Wood

CONTRIBUTED BY WILLIAM L. STERN [1]

This study of the wood of *Theobroma* is based largely on microscope slides borrowed from the S. J. Record Memorial Collection of woods at Yale University and from the wood collection of the Imperial Forestry Institute at the University of Oxford in England.[2] It is regrettable that among these slides, only 9 species were present (table 1). However, the description of the wood probably represents a fairly good outline of at least the qualitative aspects of the microscopic structure, and is sufficiently complete to enable comparisons between *Theobroma* and other genera to be made.

It is evident from this brief study that noticeable variation occurs in the wood anatomy of different specimens of the same species. In this regard it is interesting to note that Record and Hess (1943, p. 517) were impressed with the structural variation in rays in different parts of the same specimen in their study of the woods of Sterculiaceae. As a whole, however, the wood of *Theobroma* species does not present any characters of significant anatomical import which would enable us to separate them on anatomical grounds. Chattaway (1937) also found this to be true of the genera she studied in her investigation of the Sterculiaceae (sensu Edlin 1935).

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[2] I would like to thank Dr. Graeme Berlyn of Yale and Dr. L. Chalk of Oxford for their kindness in making slides available for study.

The imperforate tracheary elements are all fiber-tracheids; that is, the bordered pits are smaller in diameter than those found in the walls of vessel elements in the same species. Bordered pits usually show extended inner apertures; these may be crossed or not. The wall thickness varies from thick to thin, sometimes even within the same species (cf. specimens of *T. bicolor*).

Pores are distributed mainly in the solitary configuration on the transverse section (34–86 percent; average 62 percent); radial multiples are next in abundance (8–47 percent; average 33 percent) and pore clusters are least abundant (0–10 percent; average 4.5 percent). In different specimens of the same species, dissimilarities may occur; for example, in *T. obovatum* (*Williams* 161), solitary pores account for 86 percent of the pores per field, whereas in *T. obovatum* (*Williams* 230), they account for only 57 percent of the pores per field. Perforation plates are entirely simple. Vessel element end walls form angles from 45° to 80° with the vertical. Intervascular pitting is alternate. The

TABLE 1.—*Specimens examined in anatomical analyses*

Species of *Theobroma*	Collector and No.	Origin	Herb. voucher	USw No.*	Yw No.	FHOw No.
angustifolium DC.	*Cooper & Slater* 242	Panama	Y		10595	3502
bernouillii Pitt.	*Pittier* 4105	Panama	US	30		
bicolor H. & B.	For. Dept. Br. Hond. H. 2192/29(?)	British Honduras	F			5632
bicolor H. & B.	"Ford-Brazil 397"(?)	Brazil	F		22075	6998
bicolor H. & B.	*Ll. Williams* 2149	Peru	F		17804	7008
bicolor H. & B.	*Ll. Williams* 3346	Peru	F		18176	7007
cacao L.	"L. 3225 (via Hamburg)"	South America				5703
cacao L.	*Vigne* 2433	Ghana	Kumasi; K(?)			6898
grandiflorum (Willd.) Schum.	*Ll. Williams* 2401	Peru	F		17893	7001
microcarpum Mart.	*Krukoff* 6203	Brazil	US		36510	
obovatum Klotzsch ex Bernoulli	*Ll. Williams* 161	Peru	F		71232	7010
obovatum Klotzsch ex Bernoulli	*Ll. Williams* 230	Peru	F		17263	7011
sylvestre Mart.	*Ducke* 103	Brazil	Y		21362	7009
subincanum Mart.	*Ll. Williams*	Peru	F		17578	7000
subincanum Mart.	*Ll. Williams*	Peru	F		18144	6999

* Abbreviations from W. L. Stern & K. L. Chambers. The citation of wood specimens and herbarium vouchers in anatomical research. Taxon. 9: 7–13. 1960.

bordered pits are frequently crowded and their outlines markedly angular. Other times the pits are rounded to elliptical. Vessel–axial parenchyma pitting and vessel–ray parenchyma pitting generally follow the pattern of the intervascular pitting. Occasionally pits may be elongated or slightly irregular. No deposits or tyloses appeared in any vessels.

Both uniseriate and multiseriate vascular rays occur in each of the specimens examined. Multiseriate rays may be up to 20 cells wide (in *T. sylvestre*), but a width of 10 to 15 cells is more common. Uniseriate rays are much lower in height than multiseriate rays; the latter range from 30 to 230 cells high. There is often evidence of dissociation of these broad, high rays into lower, narrower rays by the "intrusive action" of fiber-tracheids while the cells are still in a plastic stage. Many of the multiseriate rays are characterized by the presence of sheath cells, e.g., in *T. obovatum* (*Williams* 161); however, they never form complete sheaths about the rays and are rare in some specimens. Multiseriate rays are heterocellular, with the multiseriate portion comprising procumbent cells, and uniseriate, alate extensions of 1 to several (15+) upright or square cells; uniseriate rays are usually homocellular composed of square or upright cells and sometimes occasional procumbent elements. The ray cells are commonly characterized by deposits of reddish or yellowish, non-staining materials.

Axial parenchyma occurs in two dispositions: apotracheal, as diffuse and/or diffuse-in-aggregates arrangements, and paratracheal, as vasicentric sheaths 1 or 2 cells wide. Sometimes a ladderlike configuration is formed on the transverse section by short bands of axial parenchyma which frequently intercept vascular rays (e.g., in *T. angustifolium*).

Storying of tissues occurs in the wood of *Theobroma*, but in its most highly developed state, it would have to be considered inconspicuous. Where it does appear, it is limited in distribution and confined to the uniseriate rays. In *T. microcarpum* it was also observed in the axial parenchyma.

Crystals occur in the wood of all species examined. Generally they are more frequent and conspicuous in the cells of rays, although they also occur in axial parenchyma cells of some species. In rays, only crystals of rhomboidal nature were observed except in *T. microcarpum* where large druses were present exclusively. Crystals in axial parenchyma cells are mostly rhomboidal, but in some species small druses occur.

Discussion.—The most significant anatomical studies of the wood of Sterculiaceae are those of Chattaway (1932, 1933, 1937). Unfortunately, her work is of limited value as a basis for comparison here,

for she adopted the restricted view of the family proposed by Edlin (1935) and confined herself to the tribe Sterculieae. It should be mentioned that Edlin suggested dividing the Sterculiaceae, as treated by Bentham and Hooker (1862), into two families: Sterculiaceae, to be restricted to the tribe Sterculieae, and Buettneriaceae, to contain all other taxa (including *Theobroma*). Chattaway corroborated Edlin's proposals according to the anatomical findings which resulted from her studies. Nevertheless, it does not seem to me, judging solely from her summary of the characteristic anatomical features of the Sterculiaceae (*sensu stricto*), that the wood anatomy of *Theobroma* (which would be eliminated from Sterculiaceae according to Edlin's concept) would preclude its being allied with the species upon which she reported if we used only anatomical bases. There are only two apparent anatomical differences between *Theobroma* wood and that of Sterculiaceae (*sensu stricto*): Regardless of statements to the contrary (Metcalfe and Chalk 1950, p. 251), the imperforate elements in *Theobroma* wood are not libriform wood fibers, but fiber-tracheids with small bordered pits (*sensu* Bailey 1936). Chattaway describes corresponding cells in Sterculiaceae (*sensu stricto*) as libriform wood fibers. Also, she indicates that the rays in *Theobroma* woods lack sheath cells (Chattaway 1932, 1937), "but are present in the rays of all genera of the Sterculiaceae except *Heritiera*." I cannot agree that *Theobroma* rays are totally devoid of these specialized elements. Although they are of sporadic occurrence, it is relatively easy to demonstrate them among the rays in any given tangential section.

In summary we can say that *Theobroma* woods are characterized by fiber-tracheids with small bordered pits, mostly solitary pores, simple perforation plates, alternate intervascular pitting, both homocellular uniseriate rays and heterocellular multiseriate rays with sheath cells in the same species, both apotracheal and paratracheal axial parenchyma in the same species, and crystalliferous deposits which are most abundant in the cells of ray tissue. Storied structure is present to a limited degree and is confined largely to the uniseriate rays. Although anatomy is variable within specimens of a given species, it is not consistently variable to allow for the division of the genus on anatomical grounds. In my opinion, the wood anatomy of *Theobroma* does not differ significantly from that in Edlin's Sterculiaceae as delineated by Chattaway.

Pollen Morphology of Theobroma and Related Genera

CONTRIBUTED BY G. ERDTMAN [1]

Theobroma L. (fig. 10): Pollen grains 3-colporate, peritreme, suboblate (about 15–22×17.5–25 μ).

[1] Palynological Laboratory of the Swedish Natural Science Research Council, Stockholm.

Species investigated: *T. angustifolium* Moc. & Sessé (*Pittier* s.n.): about ?×23.5 μ; *T. bernouillii* Pitt. (*Pittier* 4105): about ?×22 μ; *T. bicolor* Humb. & Bonpl. (*Klug* 2021): about 16×18 μ; *T. cacao* L. (*Calderon* 107): about 15×17.5 μ; *T. glaucum* Karst. (*Holliday & Cope* T–118): about 22×24.5 μ; *T. grandiflorum* Schum. (*Archer* 7549): about 19×22.5 μ; *T. microcarpum* Mart. (*Archer* 7551): about 16.5×21 μ; *T. speciosum* Willd. var. *coriaceum* Huber (*Rusby* 647): about 22×24.5 μ.

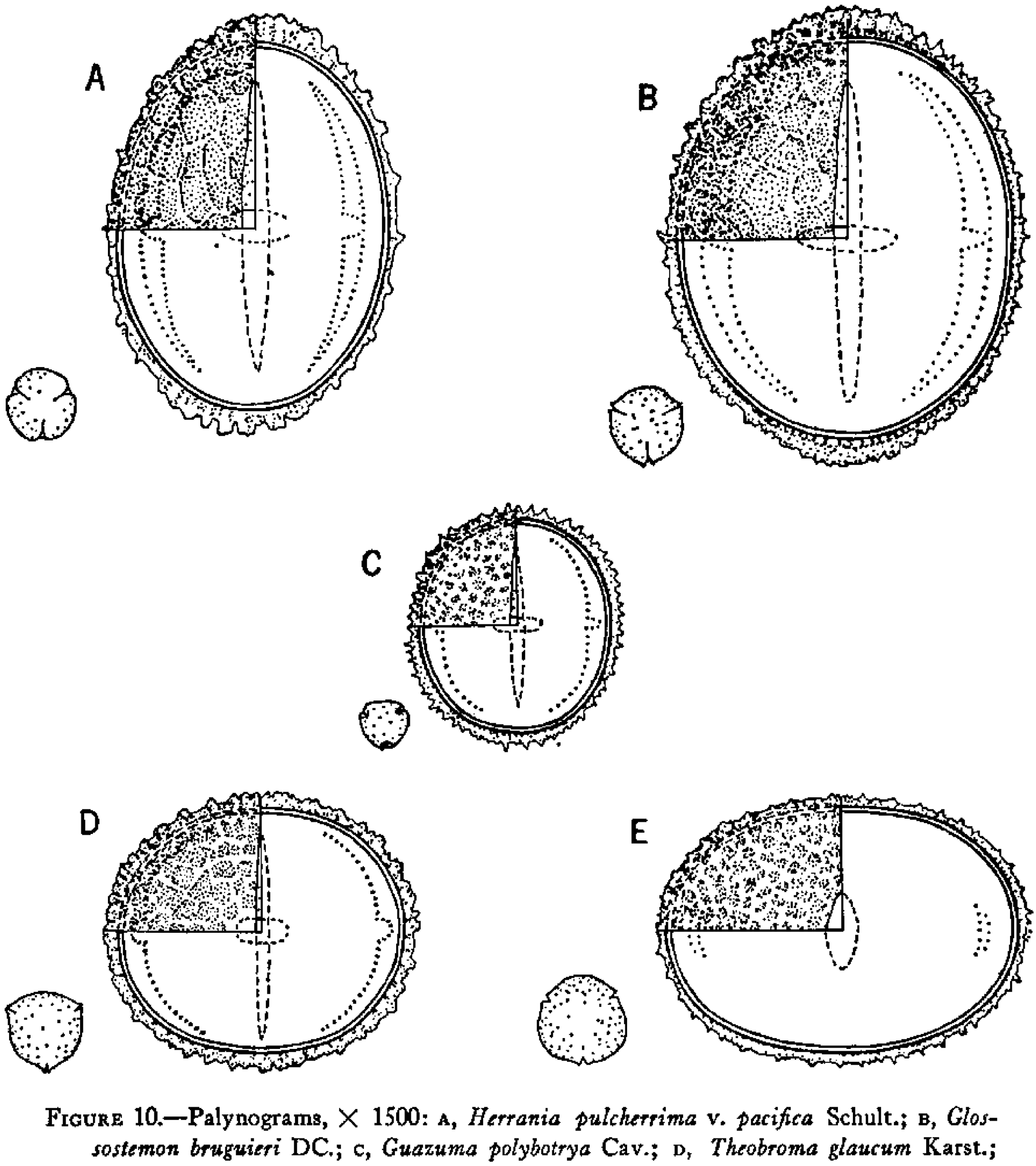

FIGURE 10.—Palynograms, × 1500: A, *Herrania pulcherrima* v. *pacifica* Schult.; B, *Glossostemon bruguieri* DC.; C, *Guazuma polybotrya* Cav.; D, *Theobroma glaucum* Karst.; E, *Abroma augusta* L.; G. Erdtman & A. L. Nilsson, original.

Examples: *T. glaucum* Karst. (*Holliday & Cope* T–118): pollen grains 3-colporate, peritreme (amb circular), oblate spheroidal (about 22×24.5 μ). Apocolpium diameter about 18 μ. Colpi narrow, about 18 μ long. Ora about 3.5 μ broad. Exine about 1.5 μ thick. Sexine as thick as nexine or slightly thicker, tectate. Tegillum distinctly undulating. The waves of the tegillum are smoother than those of, for example, *Herrania pulcherrima* var. *pacifica*, but nevertheless they impart to the pollen surface a reticuloid pattern with muroid ridges (supported by one or two rows of endosexinous bacula) separated by luminoid depressions (diameter up to 3 μ). The tegillar bottom of the latter seems to be supported by stray baculoid rods.

T. microcarpum Mart. (*Archer* 7551): pollen grains 3-colporate (amb circular), suboblate (about 16.5×21 μ). Apocolpium diameter about 13.5 μ. Colpi narrow, about 10 μ long. Ora lalongate (about 1.5×3 μ). Exine about 1.6 μ thick. Sexine thicker than nexine, tectate, undulating (waves not as smooth as in *T. glaucum*). Reticuloid pattern much as in *T. glaucum*, with more or less irregular luminoid areas (longest axis up to about 3.5 μ).

T. speciosum Willd. var. *coriaceum* Huber (*Rusby* 647): pollen grains 3-colporate, oblate spheroidal (about 22×24.5 μ). A single 4-colporate (loxocolpate) pollen grain seen.

Apocolpium diameter about 15 μ. Colpi narrow, about 12 μ long. Ora lalongate (about 3×8 μ).

Exine about 1.5 μ thick or a little less. Sexine thicker than nexine, probably tectate, presenting a reticuloid pattern (OL) with narrow straight muroid and irregularly polygonal luminoid areas (maximum diameter of the latter 1.5 μ). Muroid areas supported by a single row of endosexinous bacula.

The pollen grains of *Herrania* differ from those of *Theobroma*.

Herrania Goud.: pollen grains 3-colporate, peritreme, prolate (about 32–35×23–25 μ).

Species investigated: *H. camargoana* Schult. (*Baker* 39): about 34×25 μ; *H. cuatrecasana* Garcia B. (*Cuatrecasas* 11168): about 35×24 μ; *H. mariae* Schum. (*Ducke* 595 and *Martius* 318 (type)): about 33×25 μ; *H. pulcherrima* var. *pacifica* Schult. (*Patiño* 23): about 32×23 μ.

Example: *H. pulcherrima* var. *pacifica* Schult.: pollen grains 3-colporate, peritreme, prolate (about 32×23 μ).

Apocolpium diameter about 14 μ. Colpi about 25 μ. Ora about 2.25 μ high, slightly lalongate, their horizontal margins incrassate.

Exine about 2 μ thick at poles, 1 μ at center of mesocolpia. Sexine thicker than nexine, tectate. Tegillum undulating, with anastomos-

ing, slightly winding, crestlike and slightly carinate folds imparting a distinct reticuloid LO-pattern to the exine surface. Crests about 1 μ broad at the poles, gradually more narrow (about 0.5 μ or less) in mesocolpia. They are supported by a single row of endosexinous bacula except at the poles, where there are several rows. The luminoid, concave areas between the folds of the tegillum are equally supported by small endosexinous bacula or baculoid rods (largest and longest at the poles). The longest diameter of these areas varies between 2 and 5 μ or more.

The pollen grains in *Glossostemon bruguieri* are somewhat similar to those in *Herrania*.

Glossostemon bruguieri DC. (Iraq, Falluja, *Haines* s.n.): pollen grains 3-colporate, peritreme, subprolate (35×28 μ).

Apocolpium diameter about 8 μ. Colpi about 25 μ, constricted at the equator, ends rounded, margins thickened. Ora lalongate (about 8×1.5 μ).

Exine about 2.1 μ thick at the poles, about 1 μ at the equator. Sexine thicker than nexine, tectate. Tegillum strongly undulating, forming distinct, anastomosing muroid ridges (about 0.5 μ wide) separated by luminoid areas. In the apocolpia and towards the colpi margins the latter are very small (diameter usually not exceeding 0.5 μ); in the mesocolpia they are larger (longest diameter up to 4 μ). The muroid ridges are supported by a single or double row of endosexinous bacula. The tegillar bottom of the luminoid areas is also supported by small bacula. Bacula in apocolpia considerably longer than those in mesocolpia.

The pollen grains in *Abroma* and *Guazuma* are somewhat similar to those in *Theobroma*.

Examples: *Abroma augusta* L. (Assam; herb. Riksmus., Stockholm, marked "no. 370"): pollen grains cf. 3-colporate, peritreme, oblate (21×29 μ).

Apocolpium diameter about 23 μ. Colpi about 5.5×2.5 μ, their margins incrassate. Ora not very distinct.

Exine about 1 μ thick, tectate, very slightly undulating, presenting a reticuloid pattern. Muroid ridges low, about 1 μ wide, supported by a double row of endosexinous bacula and enclosing small rounded luminoid areas 1–2 μ wide. Under each of the latter is one or several endosexinous bacula.

Guazuma polybothra Cav. (Cuba, *Boldo* s.n.; herb. Madrid, marked "no. 94"): pollen grains 3-colporate, peritreme, prolate spheroidal (18.5×16.5 μ).

Apocolpium diameter about 12 μ. Colpi about 12 μ long.

Exine about 1 μ thick, tectate, undulating, with distinct narrow,

carinate muroid folds separated by luminoid, concave areas (diameter less than 1 μ in apocolpia as well as in mesocolpia).

Guazuma ulmifolia Lam. (Mexico, *Pringle* 2570): pollen grains 3-colporate, peritreme, spheroidal (16μ).

Apocolpium diameter about 5 μ. Colpi about 14 μ long, 1 μ wide. Ora lalongate, about 1 μ high and 3.5 μ wide.

Exine about 1 μ thick (of the same thickness in apocolpia as in mesocolpia, probably tectate (tegillum undulating, exhibiting narrow, muroid ridges separated by luminoid areas less than 1 μ in diameter).

Cytology [4]

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CHROMOSOME NUMBERS IN THEOBROMA SPECIES.—The first published count of $2n=20$ for *T. cacao*, the now accepted figure, was made by Davie (1933) from studies of mitosis in root-tips. He noted that "the chromosomes are very small, quite different from Malvaceous chromosomes. A few show median constrictions. Two pairs of satellited chromosomes were seen." In 1935, Davie confirmed the diploid number of 20 from studies of meiosis in pollen mother cells of *T. cacao*.

Confirmation of this number has been made for *T. cacao* by Carletto (1946), Muñoz Ortega (1948), Simmonds (1954) and Cope (unpublished). The first three authors have also shown twenty to be the diploid number in other *Theobroma* species. Carletto counted 20 chromosomes in *T. "leiocarpa," T. speciosum*, and *T. grandiflorum* and Muñoz Ortega in *T. "leiocarpa," T. "pentagona," T. bicolor, T. microcarpum, T. speciosum, T. simiarum, T. capilliferum, T. grandiflorum, T. obovatum, T. angustifolium* and *T. cirmolinae*. Simmonds confirmed $2n=20$ in *T. bicolor* and *T. angustifolium*. According to Muñoz Ortega, the chromosomes throughout the genus show medial, submedial, and terminal centromeres. The chromosomes are uniformly small, with size gradations within each species examined. The largest chromosomes of *T. cacao* are 2 μ in length; the smallest of *T. microcarpum* only 0.5 μ long.

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Pollen Incompatibility [5]

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The incidence of self- and cross-incompatibility, and self- and cross-compatibility in *T. cacao* was first discovered by Pound (1932) when he showed that some trees in Trinidad could not set fruit with their own pollen nor with one another's. These self- and cross-incompatible trees needed pollen from a self-compatible tree in order to set fruit. Posnette (1945) discovered cross-compatibility between self-incompatible types in his studies on cacao trees introduced from the upper Amazon into Trinidad. The existence of self-incompatible and self-compatible cacao trees has now been established in nearly all areas where the species is wild or cultivated.

Cope has shown, in a series of publications, that unlike most other plant species showing incompatibility the site of the incompatibility reaction in cacao is in the embryo-sac, and not in the stigma or in the style. Pollen tubes in incompatible pollinations grow as fast as those in compatible pollinations and deliver their male gametes into the embryo-sacs in perfectly normal fashion. It is only when the male gametes come to lie in contact with their female counterparts that any abnormality appears (fig. 11). According to the genotype of the tree or trees involved in an incompatible pollination, either one quarter, one half, or all encounters between male and female gametes result in failure of the fusion process. When an incompatibly pollinated cacao flower falls from the tree 25%, 50%, or 100% of the ovules in the ovary show nonfusion; in the first two cases the other fertilized ovules in the same ovary show normal fusion between the gametes to give a zygote and a triploid primary endosperm nucleus in each.

The genetic system controlling the nonfusion and fusion of gametes in the embryo-sac of *T. cacao* is now known. Three complementary loci appear to be involved, which have been called A, B, and S. The first two show simple dominance and recessivity; the S locus carries multiple alleles between which dominance and independence relationships exist. The action of the S locus was first postulated by Knight and Rogers (1955), based on results obtained from wholly self-incompatible material. The need for other loci, to act in a complementary

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[5] REFERENCES:

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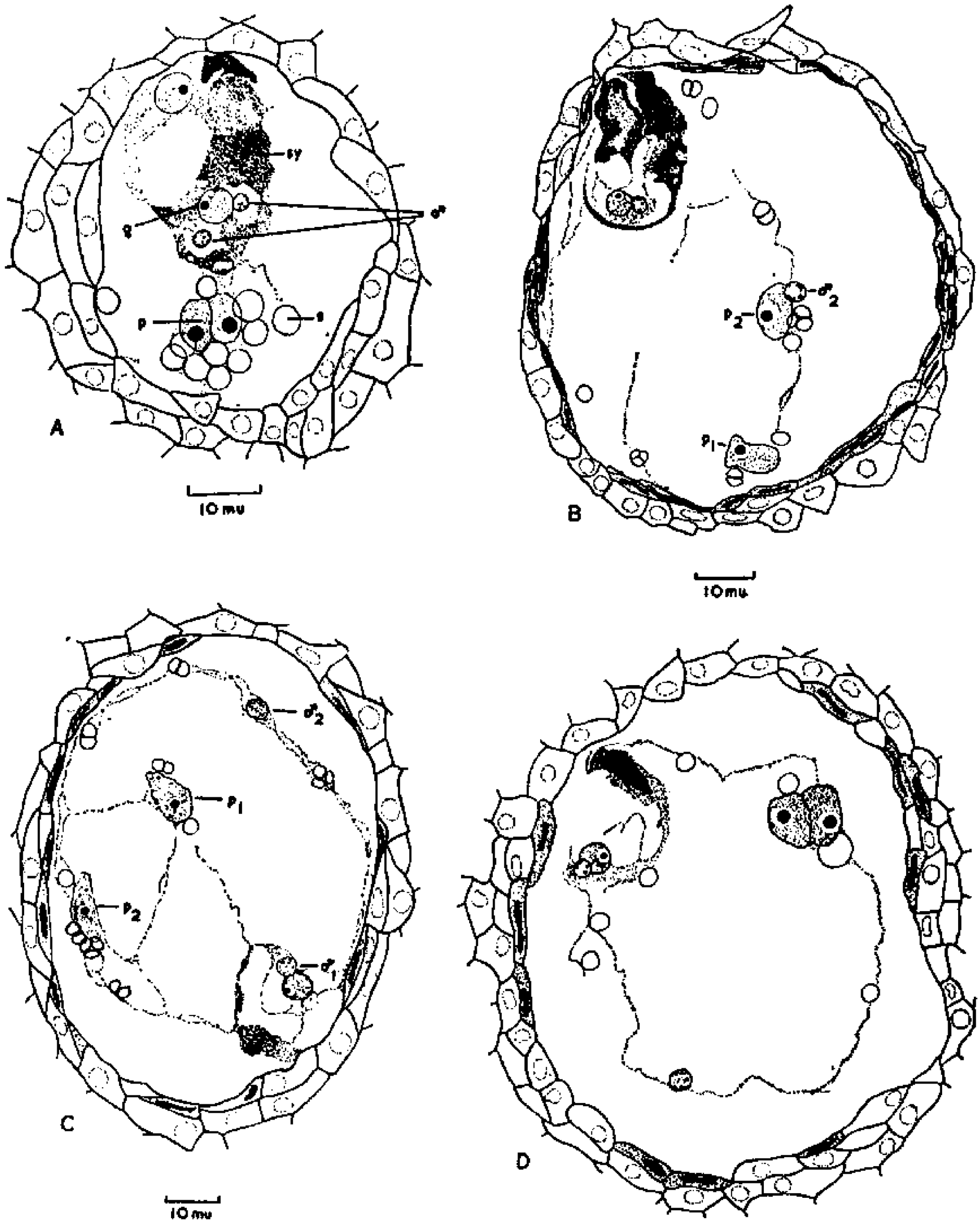


FIGURE 11.—A, Camera lucida drawing of an embryo sac of *Theobroma cacao*, fixed 24 hours after pollination: one male gamete (♂) is in contact with the egg nucleus (♀) and the second is moving towards the polar nuclei, p; the darkly-staining synergid cell (sy) has been penetrated by the pollen tube; and starch grains (s) are abundant. B, camera lucida drawing of an incompatibility fertilized embryo sac of *T. cacao*, 72 hours after pollination: one male nucleus lies in contact with the egg nucleus (top L.H.); and the second male nucleus ($♂_2$) is associated, unfused, with one polar nucleus (p_2), the other polar (p_1) having moved away. C, as in B, except that the second male nucleus ($♂_2$) and the two polar nuclei (p_1 and p_2) are all dissociated ($♂_1$ is the first male gamete lying in contact with the egg nucleus). D, as in B, except that the second male nucleus is separated from the two coherent polar nuclei. F.W. Cope, original.

manner with the S locus, was pointed out by Cope (1958) in order to explain the emergence of self-incompatible progeny from a cross between two true-breeding self-compatible parents.

The A and B loci both act before meiosis. When both are at least heterozygous for the dominant allele, it is believed that a general precursor substance is produced and on this the S locus acts to produce very highly specific incompatibility reactions between gametes carrying the same S allele. The S locus acts both before and after meiosis, the premeiotic action giving the overall sporophytic control of incompatibility and the postmeiotic action leading to a gametophytic reaction between gametes.

If one or more of the A, B, and S loci become homozygous for an inactive allele the self-incompatible condition is lost; the tree is then self-compatible and cross-compatible with any other cacao genotype.

A few examples of genotypes of the two classes of tree are:

Self-incompatible	*Self-compatible*	
$AABBS_{x.y}$	$aaBBS_{x.y}$	$aaBBS_{x.f}$
$AaBbS_{x.y}$	$aabbS_{x.x}$	
$AABbS_{x.x}$	$AABBS_{f.f}$	
$AaBBS_{x.f}$	$aaBbS_{f.f}$	

where S_x and S_y are two active S alleles and S_f is an inactive amorph of the S series.

Self-incompatible genotypes are also cross-incompatible if they have common dominant S alleles; if one has alleles independent in action and one of these is duplicated in the other as a dominant; or if both genotypes, carrying only alleles of independent action, have one allele in common.

Genus Theobroma [6] L.

Theobroma L. [Gen. Pl. 351. 1737; Hort. Cliff. 379. 1737] Sp. Pl. 782. 1753; Gen. Pl. ed. 5, 340. 1754; Benth. & Hook. (1862) 225; Bernoulli (1869) 4; Schumann (1890) 86 *pro parte;* Schumann (1896) *pro parte;* Chevalier (1946) 269.

Cacao [Tourn. Inst. 660, *t. 444*. 1700]. Miller, Gard. Dict. Abr. ed. 4th. 1754.

Tribroma Cook, Journ. Washington Acad. Sci. 5:288. 1915.

TYPE.—*Theobroma cacao* L.

Flowers hermaphroditic, pentamerous, pentacyclic, diplostemonous. Buds globose, ovoid or oblong-ovoid. Sepals 5, valvate in aestivation, almost free and spreading or more or less united in the lower part, cupular, or united by pairs into one single and two double lobes, or rarely in two lobes. Petals 5, dextrorsely contorted in aestivation, each one strangulated in two halves: 1) a lower part corresponding

[6] *Theobroma* is a neuter name and the genus must be neuter by the present International Code of Nomenclature. The feminine endings for the species used by some authors (De Candolle, Bernoulli, Chevalier, etc.) are corrected in this revision into the neuter form except for the original bibliographic references.

to the claw, rigid and strongly veined with the shape of a hood (cucullus); 2) an upper part, a flat blade (lamina), articulated to the inflexed apex of the claw. Androecium in two verticils of five, united in a tube at base: an outer whorl with 5 sterile, petaloid or linear staminodes, opposite to the sepals; an inner whorl with 5 fertile stamens opposite to the petals, the filaments short, minutely 2–3-branched, each branch with an anther. Anthers hidden inside the petal-hoods, bilobate (bithecate), the thecae unilocular and dehiscent by longitudinal clefts. Pollen grains 3-colporate, peritreme, suboblate (about 15–22 x 17.5–25 μ). Gynoecium 5-carpellar, syncarpic, superior, the carpels opposite to petals, the ovary ovoid, pentagonal, 5-celled with axile placentation, the many ovules in two rows in each cell. Stylodes 5, connivent, free or more or less united, filiform. Stigmas apical, short, acute. Ovules anatropous with two integuments and dorsal raphe.

Fruit large, subbaccate or subdrupaceous, indehiscent, ovoid, ellipsoid or oblong, obtuse or acute, smooth or ridged, rugose or tuberculate, the pericarp fleshy or hard and partly woody or coriaceous, the vascular axis thin and vanishing; seeds usually in five rows, each one surrounded by a thick, fibrose, pulpy tissue filling the cavity at maturity, ovoid, ellipsoid, or amygdaloid, the episperm double, thick, subcoriaceous, the outer layer with a trichomatic and gelatinous epiderm developing into a thick, pulpy envelope; embryo straight, the radicle cylindrical, inferior; cotyledons thick, strongly plicate-corrugate; endosperm usually reduced to a filmy membrane covering the cotyledons. Germination epigeous or hypogeous.

Evergreen tree with the apical growth of the stem limited to the production of a terminal whorl of 3–5 spreading branches; sympodial growth of the stem attained by adventitious upright subterminal shoots or by pseudoapical shoots from buds axillary to the apical branching whorl. Primary branching of stem 3- or 5-verticillate, the further branching alternate. Leaves simple, entire, penninerved, persistent, coriaceous, long-petiolate and varied in phyllotaxy on the primary stems, short-petiolate and distichous on the branches.

Inflorescences dichasial or monochasial (cincinate), axillary or on reduced tuberculiform branchlets on trunk and larger branches. Peduncles bracteate, articulate to pedicels.

Pluricellular trichomes in all species, usually as stellate hairs, rarely simple. Globose, stipitate glands present in some species.

Chromosome number: $2n=20$.

Subgeneric classification

The division of the genus *Theobroma* in five sections by Bernoulli is the best to date. He used the characters of the petal-lamina (sessile, stipitate, or lacking), shape of staminodes and their position

in the bud, and the number of anthers. A sound combination of these characters gives five very natural groups. Schumann's (1886, 1890) separation of two sections, *Theobroma* and *Bubroma*, according to their 2-antheriferous or 3-antheriferous stamens, leads to an unnatural grouping because the number of anthers for each stamen may vary in the same section and even in the same species (e.g., *T. glaucum*). For this reason, the combination of Schumann's with Bernoulli's classification made by Pittier (1930) was erroneous, because the section *Oreanthes* cannot be placed in either of Schumann's two groups. Chevalier (1946) used both classifications but without trying to integrate them. Ducke (1954), who published the best elaborated key for 7 Brazilian species, did not pay attention to sections, but he used the 3- or 5-whorled branching as a new character to distinguish the species. Another character, the epigeous or hypogeous germination of the seeds correlated with growth-habit of the tree, was used by Addison and Tavares (1951) for distinguishing species, and by Cope and Bartley (1960) in classifying them.

I have applied to the classification the mode of germination, and the growth and the branching system for all the species, and I have found the sections founded by Bernoulli to be very much reinforced by the addition of these vegetative features, and other floral and fruit characters unknown before. Epigeous germination and subterminal growth apply to all species of the sections *Rhytidocarpus*, *Oreanthes*, and *Theobroma*, whereas the other sections exhibit hypogeous germination and pseudoterminal growing. These vegetative characters prove to be very important and basic, being uniform for each section, but like other characters, even though constant within the section, they are not sufficient to give taxonomic recognition to the two groups separated by those characters. The Bernoulli sections are all of similar rank, independent and probably of parallel origin. Only the new section *Andropetalum*, based in its extraordinarily broad and reflexed staminodes, relatively reduced petal-lamina, and gamosepalous calyx, seems to be closer to *Glossopetalum* than the other sections to each other. The fruit structure, as explained above, is also important in the present classification. The following key will give a clear idea of the characters of each section. Another artificial key is added to facilitate the identification of specimens lacking complete information.

The position of the inflorescences (cauline or axillary), the color, size, and shape of petal-lamina and staminodes, number of anthers, shape of sepals and indument, form and size of fruits, the outline, venation, thickness, and firmness of leaves, and especially the kind of indumentum they bear, as well as the pilosity on different parts of the flowers, inflorescences, and branchlets, and the form and caducousness of stipules are the characters used to distinguish the species.

Key to Sections of Theobroma

1. Cotyledons epigeous at germination; growth of stem by adventitious upright, lateral-subterminal shoots; staminodes in aestivation erect.
   2. Staminodes thick-linear, obtuse; petal-hood 1-nerved; petal-lamina sessile; stamens 2-antheriferous; pericarp thick, ridged and nerved, the mesocarp very hard, woody; primary branches ternate; leaves tomentose beneath . . . . . 1. **Rhytidocarpus**
   (Contains the single species: *T. bicolor*)
   2. Staminodes linear-subulate or lanceolate, acute; petal-hood 3-nerved.
      3. Petal-lamina sessile; stamens 3- or 2-antheriferous; pericarp coriaceous; primary branches ternate; leaves tomentose beneath . . 2. **Oreanthes**
      3. Petal-lamina attenuate-stipitate; stamens 2-antheriferous; pericarp firmly carnose; primary branches quinate; leaves glabrous or puberulous beneath . . . . . 3. **Theobroma**
      (Contains the single species: *T. cacao*)
1. Cotyledons hypogeous at germination; growth of stem pseudoapical; primary branches ternate; stamens 3-antheriferous.
   4. Staminodes flexuose in bud, ovate, subulate-caudate; petal-hood 5-nerved; petal-lamina lacking; pericarp carnose-coriaceous, lignose-ridged and reticulate; leaves glabrous or puberulous . . . . . 4. **Telmatocarpus**
   4. Staminodes reflexed in bud, obovate-oblong, broadly lanceolate or broadly obovate, reflexed or erect in anthesis; petal-hood 7-nerved; pericarp rigid, the epicarp hard, woody; leaves tomentose beneath.
      5. Staminodes oblong-obovate or lanceolate, reflexed or erect at anthesis; petal-lamina broadly developed, flat, stipitate; sepals more or less united and reflexed . . . . . 5. **Glossopetalum**
      5. Staminodes broadly obovate, as broad as long; petal-lamina somewhat reduced, narrow, and plicate; calyx cupular, the sepals united one half or one third their length . . . . . 6. **Andropetalum**
      (Contains the single species: *T. mammosum*)

KEY TO SECTION OREANTHES

1. Leaves stellate-tomentose beneath on the minor reticulate veins, the areoles densely, minutely, stellulate-tomentose.
   2. Filaments 2-antheriferous; inflorescences small, on the leafy branches; flowers rather small (sepals 7–9 x 2–2.5 mm.); fruits globose-elliptical about 10 x 9 cm., glaucous when ripe. Leaves beneath with the quaternary nerves, minor veins, and areoles covered by minute tomentum of minute, thin, white, stellate hairs . . . . . 2. **T. sylvestre**
   2. Filaments 3-antheriferous; inflorescences on the trunk, multiflorous; flowers rather large (sepals 10–12 x 3.5–4 mm.).
      3. Leaves with glabrous primary and secondary nerves beneath or subglabrous with very scattered mediocre stellate hairs and sparse callose spots; fruit globose-ellipsoid, 10 x 8 cm., without ribs, shortly tomentose, yellowish when ripe . . . . . 3. **T. speciosum**
      3. Leaves softly velutinous beneath, the nerves and veins with abundant long, thin, patulous stellate hairs; fruits ellipsoid, densely velutinous, with 5 very prominent ribs . . . . . 4. **T. velutinum**
1. Leaves with glabrous nerves and veins beneath, or subglabrous with very sparse, mediocre stellate hairs, only the areoles covered with compact tomentum of minute, white, stellate hairs.

4. Flowers large: petal-lamina suborbicular 5.5–7 x 5–6.5 mm.; petal-hood 5–6 x 2.5–3 mm.; staminodes lanceolate-subulate 10–12 mm. long; filaments 2–3-antheriferous; sepals 12–13 x 3–4 mm.; petal-hood puberulous; fruit ellipsoid, obtusely pentagonal, attenuate at apex, umbilicate at base, 10–11 x 5–5.5 cm. Leaves coriaceous, broadly ovate or ovate-oblong. **5. T. glaucum**

4. Flowers smaller: petal-lamina suborbicular, orbicular or elliptic, 2.5–4 mm. long; staminodes 6–9 mm. long; filaments 2-antheriferous; sepals 8–10 x 3 mm.; petal-hood hirtellous pubescent; fruit ellipsoid-oblong, obtusely pentagonal, abruptly narrowed at apex, umbilicate at base, constricted or not above the base, 12–25 x 5.2–8 cm. . . . . **6. T. bernouillii**

KEY TO SECTION TELMATOCARPUS

1. Leaves regularly penninerved; inflorescences on trunk and branches; peduncles 5–25 mm. long; pedicels 7–8 mm. long; fruit peduncles 2–3 cm. long; sepals stellate-tomentose; petals pilose above, narrowed in the lower third, the apex blunt or emarginate; staminode-base with very short, thick hairs; ovary ovoid-ellipsoid, tomentose; fruit, when ripe, ovoid, attenuate at apex, slightly 5-costate, alveolate, the epicarp densely appressed tomentose, 7.5–11 x 7–9 cm. . . . . **8. T. gileri**

1. Leaves at base 3-nerved, the two lateral basal nerves ascending at an acute angle, the other 2 or 3 pairs of secondary nerves remotely higher; inflorescences axillary on young branchlets; peduncles 0.5–1 mm. long; pedicels 0.5–1 mm. long; fruiting peduncles 4–8 mm. long and thick; sepals with sparse stellate hairs; petals glabrous, gradually attenuate to the base, the apex acuminate, the acumen acute, 2-dentate; staminode-base with rather thick, long, flexuose hairs; ovary pyriform, glabrous or sparsely granulate, rarely sparsely stellate-pilose; fruit, when ripe, ellipsoid-globose, conspicuously 10-costate, reticulate-alveolate, usually 6.5–7 x 6–6.5 cm. **9. T. microcarpum**

KEY TO SECTION GLOSSOPETALUM

1. Inflorescences born on the trunk and main branches. Flowers large; staminodes obovate-oblong or oblong-spathulate, 9–11 mm. long, erect in anthesis; leaves large (20–54 x 8–30 cm.), coriaceous, obtuse at both ends, strongly nerved and tomentose beneath; stipules coriaceous, persistent; calyx 5-lobate, cupular at base reflexed.
   2. Petal-lamina and staminodes yellow.
      3. Fruit ellipsoid-oblong or ovoid-oblong, attenuate at both ends, umbilicate, obtusely pentagonal, 25–35 x 10–12 cm.; leaves oblong-elliptic or ovate-elliptic, subvelvety beneath with minute, stellate, flexuous, white hairs crowded on the areoles and minor veins, and other equal or slightly larger hairs on the other nerves; stipules oblong-lanceolate, subacute; petal-lamina subdeltoid-spatulate; staminodes oblong-obovate. **11. T. cirmolinae**

      3. Fruit ovoid-ellipsoid or ellipsoid, smooth, rounded at both ends or slightly attenuate at apex, 18–22 x 9–11 cm.; leaves oblong-elliptic or ovate-elliptic, tomentose beneath with minute, stellate, flexuous, white hairs crowded on the areoles and minor veins, and other larger, thicker, ferruginous hairs copious on the other nerves; stipules ovate or ovate-oblong, obtuse; petal-lamina subtriangular-spatulate; staminodes oblong-obovate . . . . . **12. T. stipulatum**

2. Petal-lamina and staminodes red. Fruits smooth (not ridged).
   4. Fruit ellipsoid-oblong, rounded at apex, umbilicate, 16–40 x 6–11 cm.; leaves obovate-oblong, densely covered beneath with minute, stellate, white, intricate hairs on the areoles and minor veins, other mediocre, stellate, ferruginous hairs sparse or copious on nerves, and larger ones with longer rays usually copious on the major nerves; stipules lanceolate; petal-lamina subtrapezoid, attenuate at base; staminodes oblong-obovate . . . . . 14. **T. simiarum**
   4. Fruit ellipsoid-ovoid, rounded at base, obtuse at apex, 19–20 x 10–11.5 cm.; leaves oblong-elliptic or ovate, often rugose, densely covered beneath with minute, stellate, white, intricate hairs on areoles and minor veins, and other larger ferruginous hairs with longer, spreading rays abundant on nerves; stipules ovate, rather obtuse; petal-lamina obovate-deltoid, attenuate at base; staminodes obovate-oblong. 13. **T. chocoense**

1. Inflorescences small, axillary on foliose branches.
   5. Petal-lamina and staminodes yellow; staminodes oblong-obovate, erect. Calyx trilobate, reflexed; leaves thin, subcoriaceous, subobovate-oblong or elliptic-oblong (9–25 x 3–9 cm.), attenuate at both ends, acute, cinereous beneath with minute, stellate, whitish, intricate hairs and larger ones with longer, patulous rays on nerves; stipules membranaceous, subulate, deciduous; petal-lamina subobovate-spatulate, bilobate, emarginate; fruit ellipsoid-elongate, 5-angulate, more or less irregularly tuberculate, 10–18 x 6–9 cm. . . . . 10. **T. angustifolium**
   5. Petal-lamina and staminodes red; staminodes curved, spreading in anthesis.
      6. Young branchlets, petioles, and buds covered with a woolly-floccose, ochraceous or tawny, deciduous tomentum. Adult leaves glaucous or glauco-cinereous, monotrichous beneath, with the principal and tertiary nerves glabrous, glossy, reddish punctate, the areoles and reticulum whitish tomentose by minute stellate hairs.
         7. Flowers large; calyx (14–15 mm. long) 3-lobate; staminodes very acute, lanceolate, spreading (9–13 mm. long); petal-lamina trapezoid-elliptic, thick, dark red; leaves firm-coriaceous; stipules subcoriaceous, persistent; fruits ellipsoid, 16–25 x 10–12 cm., rounded at both ends, smooth . . . . . 15. **T. grandiflorum**
         7. Flowers smaller; calyx (about 7 mm. long) 5-parted; staminodes oblong-elliptic, rounded at apex (6 x 2.8–3 mm.); petal-lamina suborbicular, red, rather thick; leaves thin-chartaceous, very asymmetrical at base; stipules membranaceous, linear-subulate, deciduous; fruit ellipsoid-obovoid, acute, granulate-tuberculate, 5–7 x 3–4 cm. 16. **T. obovatum**
      6. Young branchlets, buds and petioles hirsute, or short-tomentose. Calyx 5-parted.
         8. Young branchlets, buds, and petioles densely hirsute or hirsute-tomentose; leaves beneath tomentose-hirsute (especially in young plants), ferruginous or ochraceous by spreading long-radiate hairs on the nerves and veins, and with minute, white, intricate ones covering the surface.
            9. Pedicels 5–10 mm. long; peduncles 5–10 mm. long; inflorescences loose; sepals about 10 mm. long; petal-lamina and staminodes not ciliate; fruit ellipsoid-pyriform, smooth . . . . 20. **T. sinuosum**

9. Pedicels up to 1 mm. long; peduncles up to 6 mm. long; inflorescences compact, glomerate; sepals about 7 mm. long; petal-lamina and staminodes ciliate; fruit unknown . . . . 21. **T. canumanense**

8. Young branchlets, buds, and petioles densely subappressed-tomentose; leaves cinereous or ferruginous beneath with minute, stellate, whitish, intricate hairs covering the areoles and the smallest reticulum and mediocre, thicker, ferruginous hairs, copious or scattered on the nerves.

10. Bracteoles narrowly linear.

11. Staminodes scarlet, lanceolate, acute or subacute, 6–7.5 x 2 mm.; petal-lamina scarlet, orbicular or subrounded, thick, 2–2.5 x 2.2–3 mm.; ovary glabrous and smooth or very sparsely granular; fruit ellipsoid or oblong-ellipsoid, often slightly attenuate at base, 7.5–11.5 x 5–6.6 cm., the pericarp tomentose, smooth, 3–4 mm. thick when dry . . . . . 17. **T. subincanum**

11. Staminodes brownish red, obovate-oblong, rounded or subspatulate at apex, 5–5.5 x 2–3 mm.; petal-lamina obovate-subrhombic, 4–5 x 4 mm.; ovary densely tomentose; fruit ellipsoid, rounded both ends, 7 x 4 cm. . . . . 18. **T. hylaeum**

10. Bracteoles 3, orbicular, cochlear, embracing the single bud; staminodes brownish red, obovate-oblong, rounded at apex, 6–7.5 x 3.5–4.5 mm.; petal-lamina oblong-elliptic or oblong-obovate, 5–7 x 3–5 mm.; ovary densely tomentose; fruit ellipsoid, rounded at apex, constricted above the base, 8–10 x 4.5–6 cm., the pericarp, when dry, 1–1.8 mm. thick, the epicarp 1 mm. thick, fragile at maturity . . . . . 19. **T. nemorale**

Artificial key to the species

1. Leaves glabrous or puberulous beneath.

2. Leaves firmly coriaceous, regularly penninerved, with 10–14 secondary nerves each side, usually 20–30 x 7–10 cm.; fruits glabrous, ovate-oblong, more or less pentagonal or decagonal, with carnose relatively thick pericarp; stamens 2-antheriferous; staminodes linear-subulate, erect in bud, red; petal-lamina spatulate, stipitate, yellowish; jorquette with 5 branches; growth below jorquette. Flowers on trunk and on branchlets. 7. **T. cacao**

2. Leaves chartaceous with 3–6 pairs of secondary nerves; fruits smaller, ovoid or subglobose, with hard-costate reticulate tomentose pericarp; stamens 3-antheriferous; staminodes subulate-subflagelliform, flexuous in bud; petals lacking laminae or ligular appendages; jorquette with 3 branches; growth above jorquette.

3. Leaves 5–20 x 1.5–8 cm., regularly penninerved with 5 or 6 nerves on each side, puberulous beneath, the midrib tomentulose; peduncle 5–25 mm. long; pedicels 7–8 mm. long; ovary tomentose; fruit ovoid, slightly 5-costate and reticulate, 7.5–11 x 7–9 cm., fruiting peduncle 2–3 cm.; flowers on trunk and on branchlets. Sepals tomentulose. 8. **T. gileri**

3. Leaves 6–16 x 2–7 cm., 3-nerved at base, the two lateral-basal nerves ascending, quite distant from the other 2 or 3 pairs of secondary nerves, glabrous or minutely and sparsely puberulous beneath; peduncle 0.5–1 mm. long; pedicel 0.5–1 mm. long; ovary glabrous or sparsely granulate; fruit ellipsoid or subglobose ellipsoid, strongly

10-costate and reticulate 6.5–7 (–9) x 6–6.5 cm.; fruiting peduncle 4–8 mm. long; flowers only on branchlets . . . 9. **T. microcarpum**

1. Leaves densely stellate-tomentose beneath. Jorquette 3-branched.
   4. Leaves thin, chartaceous, tomentose-cinereous beneath. Flowers on terminal, leafy branchlets.
      5. Leaves ovate or ovate-oblong, subcordate or cordate at base, cinereous or ochraceo-cinereous (more or less silvery) beneath, the hairs uniform, minute, stellate, covering the surface and nerves; stamens 2-antheriferous; petal-lamina subsessile; growth below jorquette. Dichotomous inflorescences on branches; fruit large, ellipsoid with thick-woody, strongly costate-reticulate and lacunose pericarp; flowers small, red dish; staminodes thick-linear, obtuse . . . . . 1. **T. bicolor**
      5. Leaves oblong, elliptic-oblong, lanceolate-oblong, regularly pinnate-nerved, obtuse or cuneate at base, tomentose-cinereous beneath; stamens 3-antheriferous; petal-lamina stipitate; growth above jorquette.
         6. Leaves obovate-elliptic or obovate-oblong, obtuse and very asymmetrical at base with 5–7 nerves each side, 7–35 x 3–13 cm.; homotrichous, covered by minute, dense, white, stellate hairs beneath, except for the glabrous red-punctate main veins; young vegetative parts with a floccose, lanate, ochraceous, deciduous indument; fruit small, ellipsoid-obovoid, tuberculate-warty, 5–7 x 3–4 cm.; calyx 5-lobate. Flowers small; staminodes petaloid, red.
            16. **T. obovatum**
         6. Leaves elliptic-lanceolate or oblanceolate, rather oblong, slightly asymmetrical at base, heterotrichous beneath with dense, white, minute, stellate hairs and longer, patulous or subpatulous, pale ochraceous ones on the main nerves; young vegetative parts minutely tomentose; fruit large; calyx 2- or 3-lobate.
            7. Leaves subobovate-oblong or elliptic-oblong or oblanceolate, acute, 9–25 x 3–9 cm., with 6–8 secondary nerves on each side; petal-lamina and erect staminodes yellow; fruit ellipsoid-oblong, irregularly sulcate tuberculate, 10–18 x 6–9 cm.
               10. **T. angustifolium**
            7. Leaves elliptic-oblong or sublanceolate, 10–25 x 3.5–8.5 cm., with 9–12 secondary nerves each side; petal-lamina small, narrow, red; staminodes red-purplish, very broad, reflexed, covering the stamens and petals; fruit ellipsoid-oblong, constricted above the base and at the top below the apex, 10–20 x 6–8 cm.
               22. **T. mammosum**
   4. Leaves coriaceous, firmer and more markedly nervose-reticulate than in the species above.
      8. Leaves ovate-oblong or elliptic-oblong, long-caudate, with curved, ascending secondary nerves, softly velvety or apparently glabrous and shining beneath; growth below the jorquette; petal-lamina sessile; staminodes lanceolate or subulate, erect in bud.
      9. Leaves more or less bullate, softly velvety beneath, heterotrichous with a layer of dense, minute, white, stellate hairs and longer, thin-rayed, patulous, stellate hairs on the nerves. Flowers purplish red on trunk; fruit ellipsoid with 5 protuberant ribs, 8–9 x 6–6.3 cm.
         4. **T. velutinum**

9. Leaves flat, with practically homotrichous, cinereous or whitish indument beneath, of minute, white, stellate hairs; larger hairs very rare, the major nerves glabrous.
10. Leaves beneath with glabrous major nerves, the quaternary and minor veins stellate-tomentulose, the areoles densely whitish tomentose.
11. Inflorescences small, on leafy branchlets; flowers small, brownish red; stamens 2-antheriferous; fruit ellipsoid-globose, glaucous, 10 x 9 cm. . . . . **2. T. sylvestre**
11. Inflorescences large, on the trunk; flowers purplish red, larger than above; stamens 3-antheriferous fruit globose-ellipsoid, 10 x 8 cm., yellowish . . . . . **3. T. speciosum**
10. Leaves beneath with completely glabrous veins, only the smallest veins of the reticulum subglabrous with scattered mediocre hairs, the areoles with very appressed tomentum of minute, white, stellate hairs, the leaf surface with a glabrous appearance.
12. Flowers 12–13 mm. long; petal-lamina suborbicular 5.5–7 x 5–6.5 mm. long; staminodes lanceolate-subulate, 10–12 mm. long; stamens usually 3-antheriferous, also 2-antheriferous; fruit ellipsoid, obtusely pentagonal, 10–11 x 5–5.5 cm. **5. T. glaucum**
12. Flowers 8–10 mm. long; petal-lamina elliptic, suborbicular or orbicular, 2.5–4 mm. long; staminodes 6–9.5 mm. long; stamens 2-antheriferous; fruit ellipsoid-oblong, more or less pentagonal; 12–25 x 5.2–8 cm. . . . . **6. T. bernouillii**
8. Leaves broad or oblong with regularly spreading, pinnate, secondary nerves, cinereous or ferruginous tomentose beneath, with prominent venation; growth above the jorquette; petal-lamina pedicellate or very reduced; staminodes broadly oblong. Stamens 3-antheriferous.
13. Inflorescences on leafy branches.
14. Leaves beneath monotrichous, glaucous, covered by minute, white, intricate, stellate hairs, the main nerves glabrous with scattered reddish, callous spots; young vegetative parts with ferruginous, floccose-lanate, deciduous indument; calyx trilobate; fruit large, ellipsoid, smooth, 16–25 x 10–12cm.; stipules persistent. Flowers dark red . . . . . **15. T. grandiflorum**
14. Leaves beneath heterotrichous, with minute, white, densely intricate, stellate hairs covering the surface, and larger, thicker, reddish or ochraceous stellate hairs on the veins; calyx 5-lobate; fruits ellipsoid, smooth, 7–11.5 x 4–6.6 cm.; stipules caducous.
15. Young branchlets hirsute or hirsute-tomentose; leaves with long, spreading radiate hairs beneath.
16. Pedicels 5–10 mm. long; peduncles 5–10 mm. long; sepals about 10 mm. long; staminodes and petals not ciliate. **20. T. sinuosum**
16. Pedicels almost lacking (up to 1 mm. long), peduncles up to 6 mm. long; sepals about 7 mm. long; staminodes and petals ciliate . . . . . **21. T. canumanense**
15. Young branchlets and leaves beneath subappressed-tomentose.
17. Bracteoles broadly ovate or orbicular. Staminodes obovate-oblong, rounded at apex; petal-lamina oblong, obovate spatulate; ovary densely tomentose . . . . . **19. T. nemorale**
17. Bracteoles linear.

18. Staminodes scarlet, lanceolate, acute, or subacute; petal-lamina scarlet, orbicular or suborbicular; ovary glabrous or very sparsely granular . . . . . 17. **T. subincanum**
18. Staminodes brownish red, obovate-oblong, rounded or subspatulate at apex; petal-lamina obovate, subrhombic; ovary densely tomentose . . . . . 18. **T. hylaeum**

13. Inflorescences on trunk and branches. Leaves usually large and thick-coriaceous, strongly nervose beneath; stipules persistent.
19. Flowers yellow.
20. Indument of leaves beneath subvelvety, the minute stellate hairs on veins slightly larger than those of the surface; stipules oblong-lanceolate, subacute; fruits ellipsoid-oblong, obtusely pentagonal narrowed at apex, 25–35 x 10–12 cm. . 11. **T. cirmolinae**
20. Indument of the leaves beneath, tomentose, the hairs on the veins ferruginous, larger than those of the surface; stipules ovate, obtuse; fruits ovoid-ellipsoid, rounded at both ends, smooth, 18–22 x 9–11 cm. . . . . 12. **T. stipulatum**
19. Flowers purple-red.
21. Leaves obovate-oblong with three kinds of hairs beneath (minute, mediocre, and longer); stipules lanceolate; fruit ellipsoid-oblong, rounded at apex, 16–40 x 6–11 cm. . . 14. **T. simiarum**
21. Leaves oblong-elliptic or ovate, usually rugose, with two kinds of hairs beneath (minute and larger); stipules ovate, rather obtuse; fruit ellipsoid-ovoid, rounded at base, obtuse at apex, 19–20 x 10–11.5 cm. . . . . 13. **T. chocoense**

Section I. Rhytidocarpus

Theobroma sect. *Rhytidocarpus* Bernoulli, Uebers. Art. Theobroma 9. 1869.
Sect. *Eutheobroma* subsect. *Rhytidocarpus* (Bernoulli) Pittier, Rev. Bot. Appl. **10**(110):779. 1930.

Petal-lamina very shortly stipitate, subsessile. Petal-hood 1-nerved. Staminodes linear-oblong, obtuse, thick, erect in aestivation. Filaments 2-antheriferous. Fruits subglobose-ellipsoid with hard pericarp, strongly costate and reticulate-nerved, minutely tomentose, the mesocarp thick-woody, very hard. Cotyledons epigeous at germination. Leaves beneath, appressed stellate-tomentose. Primary leaves palmatinerved, regular leaves subpalmatinerved, the base 5–7 nerved. Inflorescences axillary or extra-axillary on leafy branches. Sympodial growth of stem by orthotropic, adventitious, lateral-subterminal shoots. Primary branches ternate, deciduous in age, leaving a naked stem; leafy crown lax, flat. Secondary branching dichotomous.

TYPE SPECIES.—*Theobroma bicolor* Humb. & Bonpl.

A single species known.

1. **Theobroma bicolor** Humb. & Bonpl. FIGURES 2, 5, 9, 12, 18, 35; MAP 3
Theobroma bicolor Humb. et Bonpl. Pl. Aequin. 1:104, *pl. 30.* 1806; H. B. K. (1823) 317; Triana & Planch. (1862) 208; Bernoulli (1869) 9, *pl. 4;* Schumann in Mart. (1886) 73; Jumelle (1899) 21, *figs. 10, 11;* Preuss (1901)

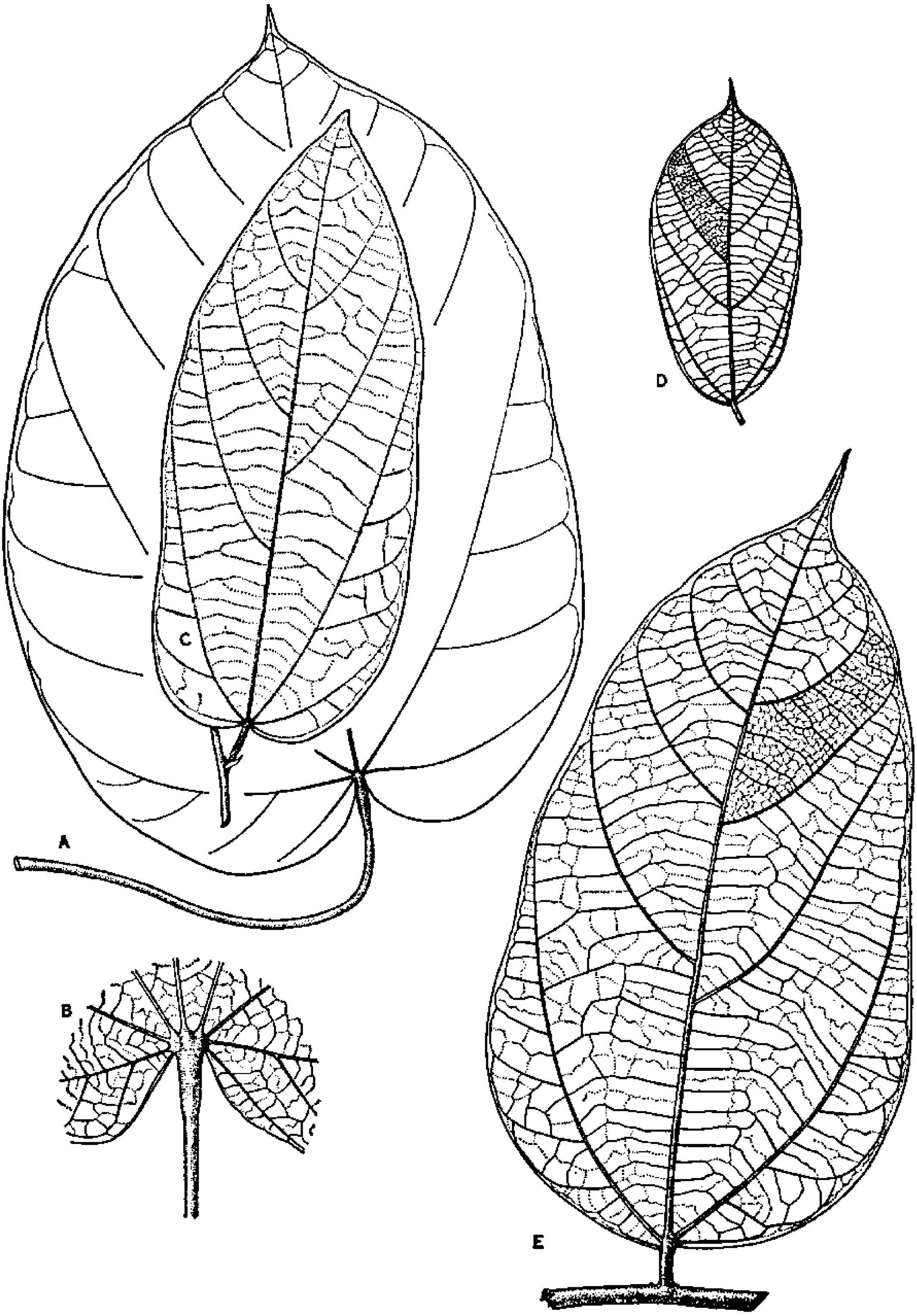


FIGURE 12.—Leaves of *Theobroma*, × ⅛: A, *bicolor*, from orthotropic branches (Dawe 83), from above; B, base of same from underside; C, *bicolor* from plagiotropic (current) branches (Kill. & Smith 30006); D, *speciosum* var. *coriaceum* (Huber 1567); E, *velutinum* (Benoist 516).

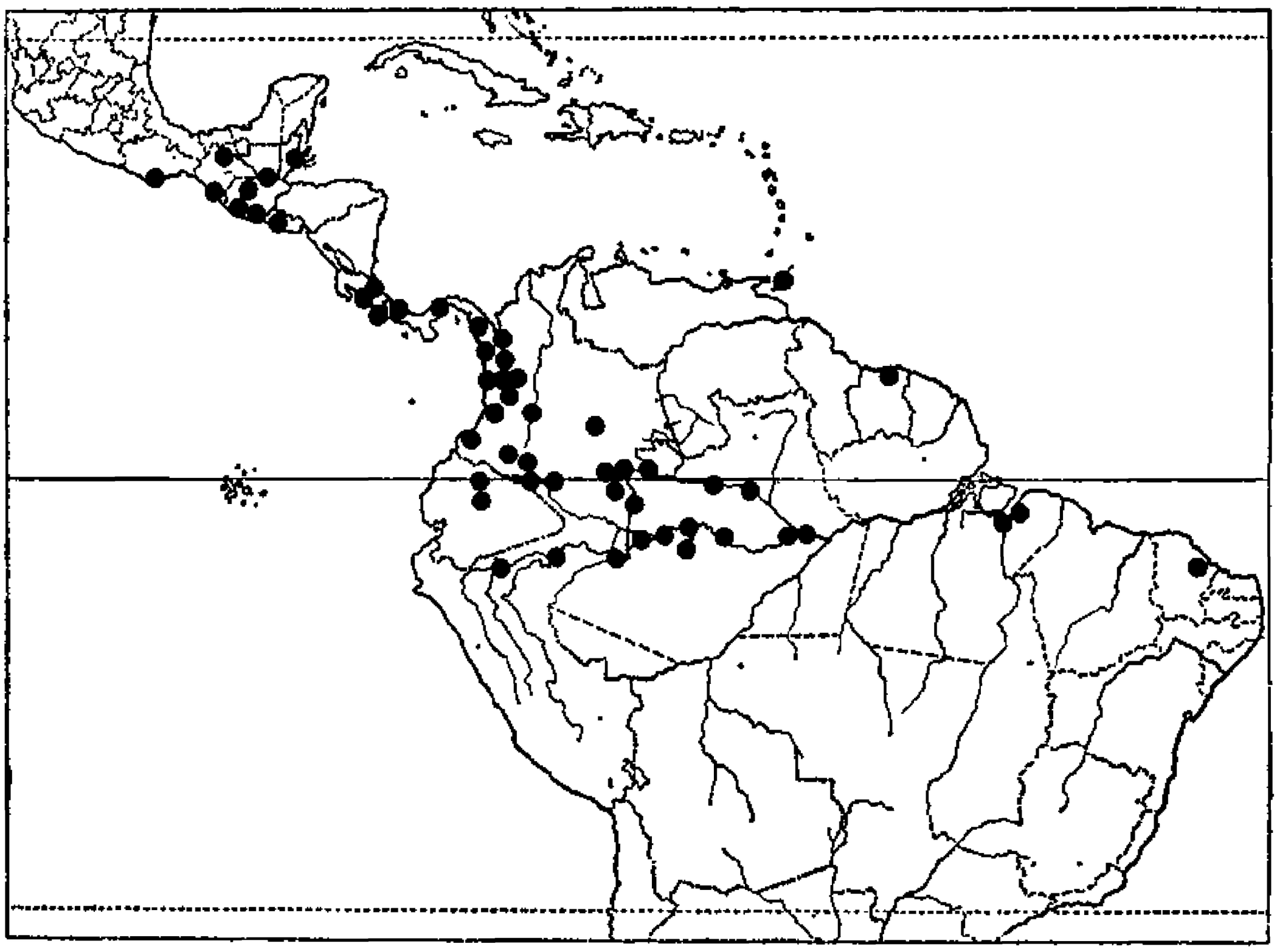
251, 255, *pls. 3, 4;* De Wildeman (1902) 94; Huber (1906a) 274; Standley (1923) 808; Ducke (1925) 132; (1940) 269, *pl. 1, fig. 2;* (1954) 13; Standley (1937) 687; Chevalier (1946) 276; Standl. & Stey. (1949) 422; Holdridge (1950a) 3; Addison & Travares (1951) *pls. 10, 13, fig. 8;* Baker, Cope & al. (1954) *fig. 9;* Cuatrecasas (1956) 652; León (1960) 313, 315 *fig.*

Theobroma ovatifolia Moc. & Sessé ex DC. Prodr. **1**:485. 1824; Icon. Fl. Mex. DC. *pl. 113.*

Cacao bicolor (Humb. & Bonpl.) Poir. in Lam. Encycl. Méth. Suppl. **2**:7. 1811.

Tribroma bicolor (Humb. & Bonpl.) Cook, Journ. Washington Acad. Sci. **5**:288. 1915; Contr. U.S. Nat. Herb. **17**(8), *pls. 46, 47, 48, 49, 50, 52, 54,* 1916.

Theobroma cordata Ruíz & Pavón, Fl. Peruv. Chil. vol. 6, *ined.*



MAP 3.—Geographical distribution of *Theobroma bicolor*, based on specimens mostly from planted trees.

TYPES.—*Humboldt & Bonpland*, Colombia (P). *Mociño & Sessé*, Mexico (of *T. ovatifolia*).

Commonly a small tree 3–8 m. tall, attaining in high forest a height of 25–30 m., with rather narrow crown; sympodial growth by lateral, subterminal, upright shoots; trunk erect with light bark and white wood; primary branches ternate, dichotomous, spreading; young branchlets often horizontal or pendulous, more or less flexuous, subterete, densely and appressed cinereous tomentose with minute

stellate hairs; older branches glabrate, smooth, gray; stipules oblong-lanceolate, 5–8 mm. long, 1.2–2 mm. broad, minutely appressed-tomentose, more or less persistent.

Leaves subpalmatinerved, firmly chartaceous, green above and silvery greenish or silvery cinereous, sometimes pale ochraceous beneath; petiole rather thick, subterete, rigid, minutely appressed-tomentose, 12–25 mm. long, transversely rimose when old; blade oblong-ovate or elliptic-ovate, more or less deeply cordate or emarginate, asymmetrical at base, attenuate, abruptly acuminate at apex, entire or rarely sinuate at the upper margin, 12–34 cm. long, 6–18 cm. broad, the acumen triangular, 6–12 mm. long, glabrous above or with scattered stellate or furcate hairs, green or when dry, pale brownish, the main nerves noticeable, the lesser slightly conspicuous, cinereous beneath, covered with a dense layer of intricate, white, sericeous, stellate hairs, at base 5–7-nerved, the thicker costa and 2 or 3 main nerves on each side strongly prominent, the interior, basal nerves upright, ascending, the 1 or 2 exterior basal pairs arched, spreading, thinner, on the ⅔ upper part with about 4 secondary nerves each side, prominent, ascending, near the margin curved and vanishing, the tertiary transverse nerves prominent, the lesser prominulous veins minutely reticulate; leaves of young upright (orthotropic) shoots larger, symmetrical, long-petiolate, the blades broadly ovate, deeply cordate, more markedly palmatinerved, 30–50 cm. long, 21–36 cm. broad, the petiole 10–38 cm. long, thickened-pulvinate at both ends.

Inflorescences axillary or extra-axillary on leafy, juvenile branchlets, usually 3–6 cm. broad, with very short axis and divaricate, dichasial and cincinnate branching; branchlets and pedicels angulate, densely ochraceous or cinereous tomentose; peduncles very short, supporting an articulate pedicel subtended by a bracteole; pedicels erect, tomentose, 3–6 mm. long; bracteoles lanceolate, subacute, rather thick, more or less curved, densely and minutely tomentose, 1.5–2.5 mm. long, 0.6–1 mm. broad; buds oblong-ovate, subacute, slightly 5-angulate, densely adpressed and minutely cinereous or ochraceous tomentose.

Sepals lanceolate or ovate-lanceolate, acute, shortly connate at base, spreading and more or less curved-inflexed, 5–6 mm. long, 2–2.5 mm. broad, 3-nerved and sparsely pilose inside, glandular at base, subappressed stellate-tomentose and reddish outside, the margin minutely whitish tomentellous.

Petal-hoods 2–2.5 mm. long, 1–1.2 mm. broad, submembranaceous, whitish rosy, or reddish with darker midrib, oblong-obovate-elliptic, rounded-cucullate, emarginate, auriculate and incurved apex, glabrous with a thick trifurcate midrib inside, hirtellous-pubescent with a depressed tomentellous midrib outside; lamina rather carnose, red,

brownish red or purplish, ovate, rounded at apex, abruptly contracted at base in short nail, articulate to the claw, hirtellous pubescent, 1–1.2 mm. long, 0.8–1 mm. broad, the nail 0.2–0.3 mm. long, erect in bud.

Androecium tube 1.5–1.8 mm. long; staminodes 5 mm. long, brownish red, usually lighter red toward the base with whitish margin, carnose, linear-oblong, obtuse or subacute, slightly narrowed at base, copiously covered with minute, thickish, patulous hairs, erect in bud, 3.5–4.5 mm. long, 0.6–0.8 mm. wide; filaments compressed, curved, reflexed, glabrous, about 1–1.5 mm. long, shortly 2-furcate, 2-antheriferous; anther lobes ellipsoid, 0.2–0.3 mm. long; ovary obovate-oblong, sharply 5-costate, greenish white, velutinous-tomentose, 1.8–2 mm. long, 1–4 mm. broad; styles whitish, about 1.7 mm. long, united, rigid.

Fruits subglobose-ellipsoid, oblong-ellipsoid, or ovoid-ellipsoid, 15–20 (10–25) cm. long, 9–12 (–15) cm. broad, green, when ripe yellow or brownish; pericarp hard, strongly 10-costate, the commissural ribs thick and elevated, the 5 alternate similar but diminishing in thickness towards the apex, the deep furrows reticulate (ligno-nerved), deeply lacunose; pericarp composed of three layers: 1) carnose endocarp about 2 mm. thick, 2) woody, very hard, ribbed and nerved mesocarp, 3–6 mm. thick, 3) firm, carnose becoming coriaceous epicarp 1–2 mm. thick with an outer, densely stellate-pilose epiderm, the whole pericarp about 7 mm. thick on the furrows and 14–15 mm. thick on the ribs; pulp surrounding seeds fibrose, yellowish, sweet, scenty; seeds arranged in 5 rows, complanate, ovoid-amygdaliform, 16–30 mm. long, 14–23 mm. wide, 8–13 mm. thick; embryo white; germination epigeous.

Theobroma bicolor is unique in the genus, easy to recognize by its small, lax crown of few whorls of horizontal, dichotomous branches topping a naked stem, and by its leaves, fruits and flowers. The large papery, firm leaves are whitish silvery beneath and those of the upright shoots are larger, palmatinerved, cordate, and very long petiolate. The flowers are small and pale red generally. The large fruits are strongly ribbed and nerved, with a hard, woody, carved shell; they keep the green color until ripening, when they become yellow or brownish, falling from tree.

COMMON NAMES.—In English: Patashte. Mexico: Patashte, patashtle, pataste, petaste, patatle, petaxte, patasht, pataste de sapo, pataste simarron, cacao malacayo, cacao blanco. Guatemala: Patashte, pataxte, patasht, balamati, balam (*Kekchi*), pec (*Pokonchi*). Costa Rica: Pataste, pataiste, skar-ub (*Bribrí*), uerba (*Terraba*), scarbo (*Bribrí*), carvu (*Kabekara*), saparón (*Estrella*), erefa (*Guatuso*). Panamá: Pataste, cu-lu-hu (*Choko*). Colombia: Bacao (general), ca-

cao silvestre, cacao marraco, and marraco (in Caquetá). Ecuador: Patas, cacao blanco. Peru: Macambo, majambo, najambu. Brazil: Cacau do Peru (Belém), cupuassú, cupua-í, cacau bafú, cacao bravo.

The Anglo-Colombian Cocoa Expedition (Baker, 1953) recorded the following names: heé-a (*Maku*), (Piraparaná, Taraira); aõ (*Makuna*) (lower Piraparaná, Popeyacá); la-na-pee-tá-ma-ca-la-chu-na-ni (*Yakuna*) (Miritiparaná); há-ha (*Tanimuka*) (Guacayá); maraca bacao (Chocó).

Uses.—The pulp is frequently eaten or used by natives to prepare refreshments although its flavor is not very attractive. The seeds are used in many places like those of cacao, giving a chocolate of inferior quality; it is also locally used to manufacture pastry and candy. The seeds of *T. bicolor* have been commercially mixed sometimes with those of cacao. They are poor in theobromine but they have a great proportion of a good quality cocoa butter. In Guatemala the seeds are known in commerce as "tiger" "wariba" or "pashte" cacao (Standley).

According to Llano (1947), in Colombia this species has been tried for grafting but the bark heals with difficulty.

The hard shells of the pod are used locally, as containers like those of *mate* or *tutuma* (*Crescentia cujete*). According to Tafalla it is called "cacao de Castilla" in the Ecuadorian region of Uchiza, where the shells of the pods are smoothed to be used as bowls.

Distribution.—*Theobroma bicolor* is widespread in cultivation throughout all humid tropical America, from southern Mexico to Bolivia and Brasil. It is never cultivated extensively, but a few trees can always be seen where cacao is cultivated, and usually also in backyards of tropical farms and in secondary growth. It is frequently found also subspontaneous in more or less open thickets. I have always seen the species in cultivation only. Its true native place is uncertain. Probably it originated in Central America where it is said to be found in primary forests. Miranda (l.c.) writes "se encuentra en acaguales de las selvas altas" in Chiapas; Steyermark found it in dense forests of the region of Ixcan (Huehuetenango) in Guatemala. Another possible original region is the eastern region of Peru and Ecuador. Ynes Mexía recorded it from dense forests in the Napo-Pastaza river basin. Llewellyn Williams found it spontaneous in secondary growths in Loreto. But thus far I have no assurance of a place where it is incontestably native.

MEXICO: Herbarium Sessé et Mociño No. 3620, preserved at the Madrid Botanical Garden "Plantae Novae Hispaniae a Sessé, Mociño, Castillo et Maldonado lectae (1787–1795–1804)-*Theobroma Patastle* Ic. N." (MA, lectotype of *T. ovatifolium;* BM, F, G, isotypes); the MA specimen has foliage, inflorescences and flowers and may be considered the holotype of *Theobroma ovatifolium* Mociño

et Sessé ex DC.; I select it as the lectotype; it is photograph FM No. 48412. The Chicago specimen is a duplicate of this and has only one leaf; the very good British Museum specimen, and two at Geneva are certainly isotypes in spite of not bearing the name of Sessé and Mociño and having "*Theobroma Patastle*, N.E." as only information; some specimens have the indication "Herb. Pavón," having been sent by Pavón from Madrid. The collections with the number 3621 Sessé et Mociño et al. (MA) are paratypes and may be duplicates of 3690, having been numbered recently (in 1935); they include normal foliage and inflorescences and juvenile long-petiolate, broadly cordate leaves (FM photographs 48414 and 48413). The photograph FM 30526 is from plate 485 of the Mociño and Sessé Flora Mexicana, No. 113 in De Candolle's copies.

OAXACA: Pochutla, Capital Rancho Viejo; tree 15 m., flowers purple, "cacao malacayo," Feb. 1941, *Reko* 6068 (F).

CHIAPAS: Acagoyagua, Escuintla, "pataste de sapo," 22 VII 1947, *Matuda* 16733 (F). Ibidem, "pataste simarrón," fruit only, 6–7 x 4 cm., 28 VIII 1947, *Matuda* 16840 (F, MEXU). Esperanza, Escuintla, "pataste," cultivated, 11 VIII 1947, *Matuda* 16690 (BR, F, MICH, MEXU, NY). Palenque, 100–150 m. alt.; tree up to 25 ft. tall; commonly cultivated around Palenque for its fruits; fruits yellow; seed ground and mixed with cornmeal for making "pazoli"; flowering and fruiting in May; said to be common in the forests on the slopes above Chacamax River, V 1937, *Ll. Williams* 9345 (F, Y).

GUATEMALA: Without locality, "cacao," 10 V 1914, *Davidson* s.n. (US). ALTA VERAPAZ: Trece Aguas, cacao plantation at Cacao, "petaste" or "patashte," 9 III 1914, *Cook & Doyle* 50 (US); Trece Aguas, near Finca Sepacuité, "petaxte" IV 1905 (leaf from upright stem of young tree), *Cook* 4 (US). Ibidem, Chirujija Oxee, near Finca Sepacuité, "balamati," 25 V 1902, *Cook & Griggs* 756 (US). Chama, 900 ft. alt.; tree 25 ft., flowers reddish, fruit large, hard shelled, "patashte" cultivated by Indians; used similarly to cacao, rather sweeter in flavor, 15 VI 1920, *H. Johnson* 237 (F, US). Cubilquitz, 350 m. alt., VI 1901, *von Tuerckheim* 7824 (GH, K, NY, US). Vicinity of Sibicte, 370 m. alt., small tree 25 ft. tall, leaves firmly membranaceous, deep green above, gray silvery beneath; flowers with grapy-purple calyx, "balam" (*Kekchi*), "patasht" (Spanish), cultivated, 12 III 1942, *Steyermark* 44941 (F).

HUEHUETENANGO: Sierra de los Cuchumatanes, 150–200 m., between Ixcan and Río Ixcan; tree 30 feet tall, leaves membranaceous, papyraceous, dark green above, silvery green beneath; dense rich forest, 23 VII 1942, *Steyermark* 49317 (F, US). Huehuetenango, 1800 m. alt., seeds in market brought here from the Pacific Coast, *Standley* 82446 (F).

SANTA ROSA: Region of Platanares, between Taxisco and Guazacapán, 220 m. alt.; wet forested quebrada, simple shrub 3–4 m. tall; escaped here, 3 XII 1940, *Standley* 79069 (F).

SUCHITEPEQUEZ: Mazatenango, cultivated, III 1865, *Bernoulli* 94 (F, G, NY). Ibidem, III 1865, *Bernoulli & Cario* 3145 (GOET).

BRITISH HONDURAS: Conservation Forests H. 2192/29 (F, GH, UC). Stann Creek Valley, Big Eddy Valley; tree 13 inch diameter, fruit 8 inch long, "pataste," "mountain cacao," 16 XII 1840, *Gentle* 3464 (F, GH, MICH, MO, NY, U).

EL SALVADOR: Sonsonate, cultivated, "patashte," "pataste," 20 IV 22, *Calderón* 23610 (F, GH, MO, NY, US); ibidem, "pataste," 1922, *Calderón* 627 (GH, NY, US).

COSTA RICA: Peninsula Osa ad Golfo Dulce, circa Puerto Giménez, ad litus; arbor 6–8 m., floribus purpureis, 15 IV 1930, *Cudofontis* 92 (WU). Vicinity of Guapilés (prov. Limón), 300–550 m. alt.; planted tree 25 ft., flowers dull red 12,

13 III 1924, *Standley* 37374 (US). Puerto Giménez de Osa and vicinity, 14 IV 1930, *Brenes* 12333 (Herb. Nac. C.R. 212) (F, NY). Edge of the road to Tuis, 650 m.; tree with spreading branches, "pataste" or "pataiste," XI 1897, *Tonduz* 11304 (F). Tucurrique, grassland at Las Vueltas; tree 40 cm. diam., 15–20 m. high, 635 m. alt., "pataste," "pataiste," III 1899 *Tonduz* 13110 (G, P, US). Hacienda Baltimore (Limón), 10 m. alt., in a small plantation of this species, 8 VII 1949, *Holdridge* s.n. (TURRI). La Lola, planted, 6 XI 1961, *Cuatrecasas & Paredes* 26534 (US).

PANAMA: Bocas del Toro, in Laguna de Chiriquí and its neighborhood, Pope's Island, XI, XII 1885, *Hart* 158 (US). Darién, Headwaters of Río Chica, 500–750 ft.; tree 35 ft.; flowers dark red; cultivated by Choco Indians, "cu-lu-hu," *Allen* 4593 (G, MO, NY). Canal Zone, along Caño Quebrado, 2 XII 1914, *Pittier* 6883 (GH, NY, US).

TRINIDAD: L'Eranche Est, Sangre Grandre, 10 VII 1929, *Boehlmer* 12229 (TRIN). Blue Basin, 2½–3 miles distant, 21 IX 1928, *Lange* 12056 (TRIN). Grounds of I.C.T.A., River Estate Diego Martínez, field 19; fruits 19.3 x 13.3 cm., yellowish at maturity, specimen from seeds brought from Jinogojé, Apaporis, Colombia, 31 VIII 1961, *Cuatrecasas, Cope, & Bartley* 25784T (US); same field; calyx pale red, hoods with darker midrib, petal-lamina very small, brownish red, staminodes brownish red, lighter reddish toward the base, with whitish margin, styles whitish, ovary greenish white, 1 IX 1961, *Cuatrecasas & Cope* 25795 (US). Tree from seeds from La Pedrera, Colombia; fruits 16.2 x 14 cm., 31 VIII 61, *Cuatrecasas, Cope, & Bartley* 25787T (US). Field 2; fruits 15 x 10, 16 x 10.8, 16.5 x 10, 18.2 x 11.2, peduncle 0.7–0.9 cm., 31 VIII 61, *Cuatrecasas, Cope, & Bartley* 25786T (US).

SURINAM: Paramaribo Gardens, cultivated, VI 1910, *Stockdale* s.n. (K, U).

COLOMBIA: Antioquia: Savaletas, 100–500 m., XII, *Lehmann* 7909 (K).

Tolima: Ibagué, II 1916, "cacao silvestre," *Dawe* 83 (US).

Huila: Valle del Magdalena, Garzón, IV 1845, *Goudot* s.n. (G, P).

El Valle: Palmira, Granja Agrícola, 900 m. alt. "bacao," *Duque Jaramillo* 1205 (F). Ibidem, X 1943, *Llano* s.n. (COL, F). Palmira, 925 m., cultivated in grounds of experiment station (said to have been brought from the Chocó); tall, erect tree, leaves hanging vertically, almost white beneath, flowers dark red with maroon staminodes, fruit oblong, green with the furrows strongly rugose, 29 X 1944, *Fosberg* 21310 (NY, UC, US). Palmira; tree 4 m., "bacao," I 1947, *Duque Jaramillo* 4403A (COL). Ibidem; tree 3 m., flowers red, "bacao," 3 XII 1947, *Cardeñosa, Murgueitio, & Barkley* 17C934 (COL, F). Cartago, *Goudot* s.n. (P, WU). Pacific Coast, Río Calima, La Trojita, left side of river, 5–20 m. alt.; tree 3 m., "bacao," 27 II 1944, *Cuatrecasas* 16526A (F, VALLE) (fruit only). Buenaventura (and Tumaco) 0–400 m., fl. perpetual, *Lehmann* 9021 (K, NY).

Chocó: "Nvelle. Grenade, Chocó," "bacao," *Humboldt and Bonpland*, s.n. (P, holotype). *Bonpland*, probably isotype, from Paris (F). Near Istmina, road to Cértegui, in forest, 75 m. alt.; tree 6 m., flowers red, "bacao," 3 VII 1944, *García Barriga* 11178 (COL, US). Chocó (i Barbacoas), 25 m. alt., "bacao," IV 1853, *Triana* 5333 (–3) (BM, COL). Ciudad Mutis, 27 X 1946, *Romero Castañeda* s.n. (COL).

Nariño: Pacific Coast, Amarales, "bacao," 1866, *Triana* s.n. (BM, BR, COL, G, K, NY, WU).

Caquetá: Solano, 3 km. SE of Tres Esquinas, on Río Caquetá, below mouth of Río Orteguaza, wet tropical forest of Amazon basin; tree 8 m. high, 10 cm. DBH; dark brown, smooth, lichen patches, flowers red; watermelonlike fruit 18 cm. long, 10–11 cm. broad, yellow, edible; Indians plant it; secondary lowland forest, river bank; possibly an escape from cultivation; several cultivated trees

seen March 13 walk near Río Caquetá, 2 km. s. of Solano; "cacao marraco," 6 III 1945, *Little & Little* 9598 (NY, US).

PUTUMAYO: Vicinity of Mocoa; small tree 4 m., sterile; apparently cultivated, 17 III 1953, *Holliday & Cope* T 77 (COL, TRIN, US).

VAUPÉS: Río Negro, near San Felipe, Caño Mayabo, river level; tree 4–5 years old, introduced on a house site, 27 X 1952, *Baker* 34 (COL, F, TRIN). Río Inírida, right bank below mouth of Caño Caribe; tree 25 m. high, 1 m. diameter at ground level, growing on slope just above high watermark; overtopping the surrounding forest; not thought to be wild. 23 I 1953, *Bartley & Holliday* T66 (COL, TRIN, US). Río Vaupés, opposite confluence with Río Papurí, Yavaraté, Silesian Mission São Miguel; trees 3–4 years old from seed brought by Indian from the interior of Colombia, 20 II 1952, *Bartley & Holliday* T 47 (COL, TRIN, U, US). Caño Umuña, Río Piraparaná, river level; cultivated tree in Indian garden, 8 IV 1952, *Baker & Cope* 11a (TRIN). Jinogojé, on Río Apaporis, small tree 15 ft. cultivated in Indian garden, 23 VIII 1952, *Baker & Cope* 2 (TRIN). Río Apaporis, Gino-Gojé, between the rivers Piraparaná and Popeyacá, 250 m. alt.; tree 4 m., leaves white below, 3–11 IX 1952 *García Barriga* 14416 (US).

AMAZONAS: Río Caquetá, La Pedrera, river level; tree 30 ft., presumed cultivated, 1 X 1952, *Baker & Cope* 26 (COL, F, TRIN, US). Río Igaraparaná, vicinity of La Chorrera, 180 m. alt.; small tree, cultivated, "marraca," 4–10 VI 1942, *Schultes* 3922 (COL, F).

ECUADOR: *Muller* s.n. (K). Balao; arbor 40 m., in forest, flowers purplish, "cacao blanco," I 1892, *Eggers* 14244 (A, L, LE, M, US). Río Sucumbíos, between Putumayo and Quebrada Teteyé, 260 m., "cacao" (*Kofán*), 29 III 1942, *Schultes* 3471 (NY).

NAPO-PASTAZA: Between Tena and Napo; tree about 15 m. high, petals dark red, staminodia blackish brown, 5 I 1940, *Asplund* 10271 (S). NE of the province, Tiputini-Lagartococha, 20 I–5 II 1953, *Fagerlind & Wibom* 2371 (S). Cantón Napo, near Tena, 400 m. alt., dense forest; tree up to 18 m. high, fruit called "Patas," size of small watermelon, the pulp being eaten and the seeds cooked or raw much appreciated, 2 II–VI 1935, *Mexía* 7214 (F, P, UC, US).

BRAZIL: "Brazil, Dr. Martius," no data (G). Manaquiry forest; 15–30 ft., leaves white beneath, flowers dark purple, *Spruce* s.n. (K).

AMAZONAS: Rio Negro, Barcellos, matta, cult.?, 27 VI 1905, *Ducke* 7202 (BM, MG, US). Ibidem, *Ducke* 7202-B (BM, MG). "Prov. Rio Negro, in sylvis, Martius Obs. 28823, Iter-Brasiliensium 319, *Martius* [862, 863, 864, 865] (M). Rio Negro, Lagos, "cacao bravo," 5 VIII 1874, *Traill* s.n. (GH). Rio Negro, *Schomburgk* 870 p.p. (BM, G, GH, GL, K, OXF, P, US). Saõ Antonio de Içа, capueira, "cupuassú," 3 VIII 1906, *Ducke* 7638 (MG). Municipio São Paulo de Olivença, basin of creek Belem; tree 40 ft. high, trunk 5 inch diam., planted by Indians 26 X–XII 1936, *Krukoff* 9019 (A, BM, F, G, K, LE, MICH, MO, NY, P, US). Manaos, Campos Salles, 15 m., 20 VIII 1928, *Luetzelburg* 23895 (M). Manaos, Agricultural Experiment Station, 25 m. alt.; tree 30-35 ft., fruit oblong on ultimate branches (25 x 10 cm.), cult.?, 13 X 1929, *Killip & Smith* 30006 (GH, NY, US), fruit collection 681 (US). Experimental Garden of Nord Brazil, cultivated and wild in forest, "cacao d'Anta," 20 VIII 1928, *Luetzelburg* 23065 (M). Ega, "colitur circum Indorum villas, Oct. 1830," *Poeppig* 2746 p.p. (WU); "In Bras. tropica fl. Amazonas Oct. 1839," *Poeppig* 2746 pp. (GOET). Ega, *Poeppig* 2746 p.p. (F, LE). Teffé, forest, 29 VI 1906, *Ducke* 7397 (BM, G, MG, US). Fonte Bõa, firm land, medium-sized tree, "cacau bafú," 28 III 1945, *Frões* 20625 (F, IAN, K, NY, US). Rio Juruá, Santa Clara, cultivated, "cupuaçú" Baum, X 1900, *Ule* 5030 (BM, G, HBG). Rio Juruá, Gaviao; flowers purple, "cupua-i," III 1875, *Traill* 60 (K, P). Rio Sapo, 21 II 1874, *Traill* 60 (K). "Ad oram meridionalem

flum. Amazonum ad ostium flum. Solimoes," VI 1851, *Spruce* 1609 (BM, K, M, P, WU).

CEARA: Ceará, VIII–XI 1838, *Gardner* 870 (G).

PARÁ: Belém, Horto do Museu Goeldi, arvore 483; medium size tree, granate flowers, 10 X 1957, *Cavalcante* 310 (MG, US). Belém, cult., *Pires & Black* 746 (IAN). Belém, I.A.N. cult., "cacau do Perú, 6 XI 1952, *Pires* 4340 (IAN, NY).

PERU: "Theobroma cordata del Perú, sp. nov.," *Ruiz & Pavón* (BM). "Peruvia, Herb-Pavón" (G). Perou, *Pavón* 617 (G). 1909–1914 *Weberbauer* 6245.

LORETO: Mishuyacu, near Iquitos, 100 m.; forest, tree 6 m. high, flowers dark violet and rose, clearing, "macambo," V–VI 1930, *Klug* 1523 (F, NY). Florida, Río Putumayo at mouth of Río Zubineta, 200 m.; forest clearing, tree 4 m., flowers garnet, "macambo," III–IV 1931, *Klug* 2021 (A, F, GH, K, MICH, MO, NY, S, US). Paraíso, upper river Itaya, 145 m.; "najambu," 1 X 1929, *Ll. Williams* 3346 (F, US). Amazon River, Caballo-Cocha, 6 VIII 1929, *Ll. Williams* 2149 (F, GH, US). Maynas, *Poeppig* (L), *Poeppig* 18 (BM). Marañón River from Iquitos to the mouth of Río Santiago at Pongo de Manseriche, ca. 77°30′ W., 1924, *Tessmann* 4079 (NY, S).

Section 2. Oreanthes

Theobroma sect. *Oreanthes* Bernoulli, Uebers. Art. Theobroma 7, 1869.

FIGURE 4; MAP 1

Sect. *Bubroma* subsect. *Oreanthes* (Bernoulli) Pittier, Rev. Bot. Appl. **10**(110):779. 1930.

Petal-lamina sessile, large. Petal-hood 3-nerved. Staminodes linear-subulate or lanceolate, erect in estivation. Filaments 3- or 2-antheriferous. Fruit more or less angulate or costate with coriaceous, tomentose pericarp, the endocarp rigid, thin-lignose. Cotyledons epigeous at germination. Leaves densely, minutely, stellate-tomentose beneath inside the reticulum. Inflorescences many-flowered, on the trunk or, in few cases, small and on leafy branches. Sympodial growth of stem by orthotropic, adventitious, lateral-subterminal shoots. Primary branches ternate, deciduous when old, leaving an unusually long, naked stem. Leafy crown loose, flat. Secondary branching dichotomous.

TYPE SPECIES: *Theobroma speciosum* Willd. ex Spreng.

2. Theobroma sylvestre Mart. FIGURES 4, 9, 13, 16, 18; MAP 4; PLATE 1

Theobroma sylvestre Mart. in Buchner, Repert. **35**:24. 1830; Linnaea, Litt. Ber. 32. 1831; Bernoulli (1869) 14, *pl. 7, fig. 1;* Schumann in Mart. (1886) 78 (as *T. silvestre*); Jumelle (1899) 34; De Wildeman (1902) 98.

Theobroma Spruceana Bernoulli, Uebers. Art. Theobroma 9, *pl. 3, fig. 1.* 1869; Ducke (1925) 131; (1940) 270, *pl. 3;* (1954) 13; Chevalier (1946) 276; Addison & Tavares (1951), *pl. 5, fig. 1, pl. 6, fig. A, pl. 12, fig. 4*; León (1960) 318, 319, *fig.*

Theobroma nitida Bernoulli, Uebers. Art. Theobroma 15, *pl. 7, fig. 2.* 1869.

Theobroma Martii Schum. in Mart. Fl. Bras. **12**(3):78. 1886; Jumelle (1899) 35; De Wildeman (1902) 98.

Theobroma speciosum var. *Spruceana* (Bernoulli) Schum. in Mart. Fl. Bras. **12**(3):75. 1886; Jumelle (1899) 32, *fig. 16;* De Wildeman (1902) 95.

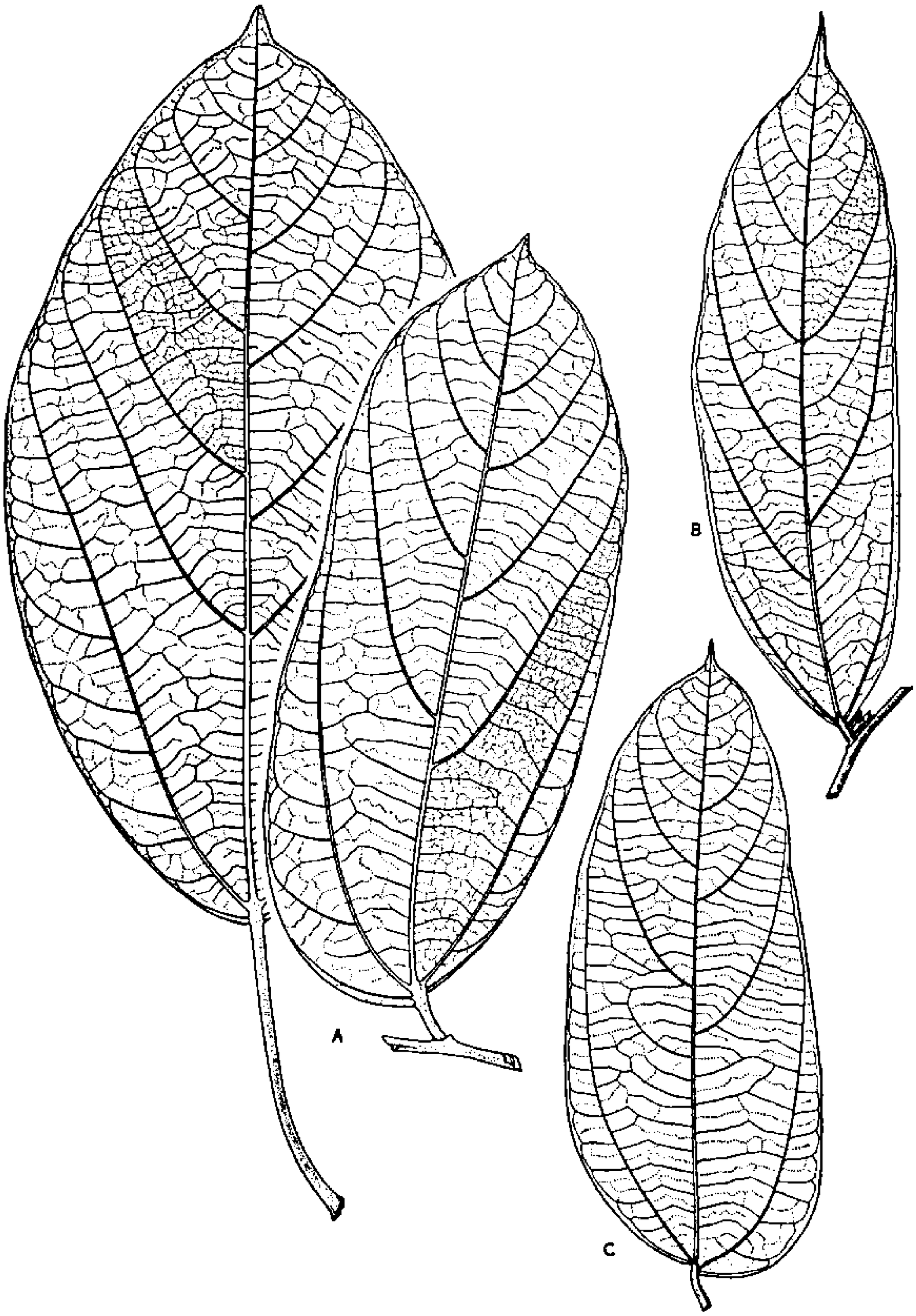
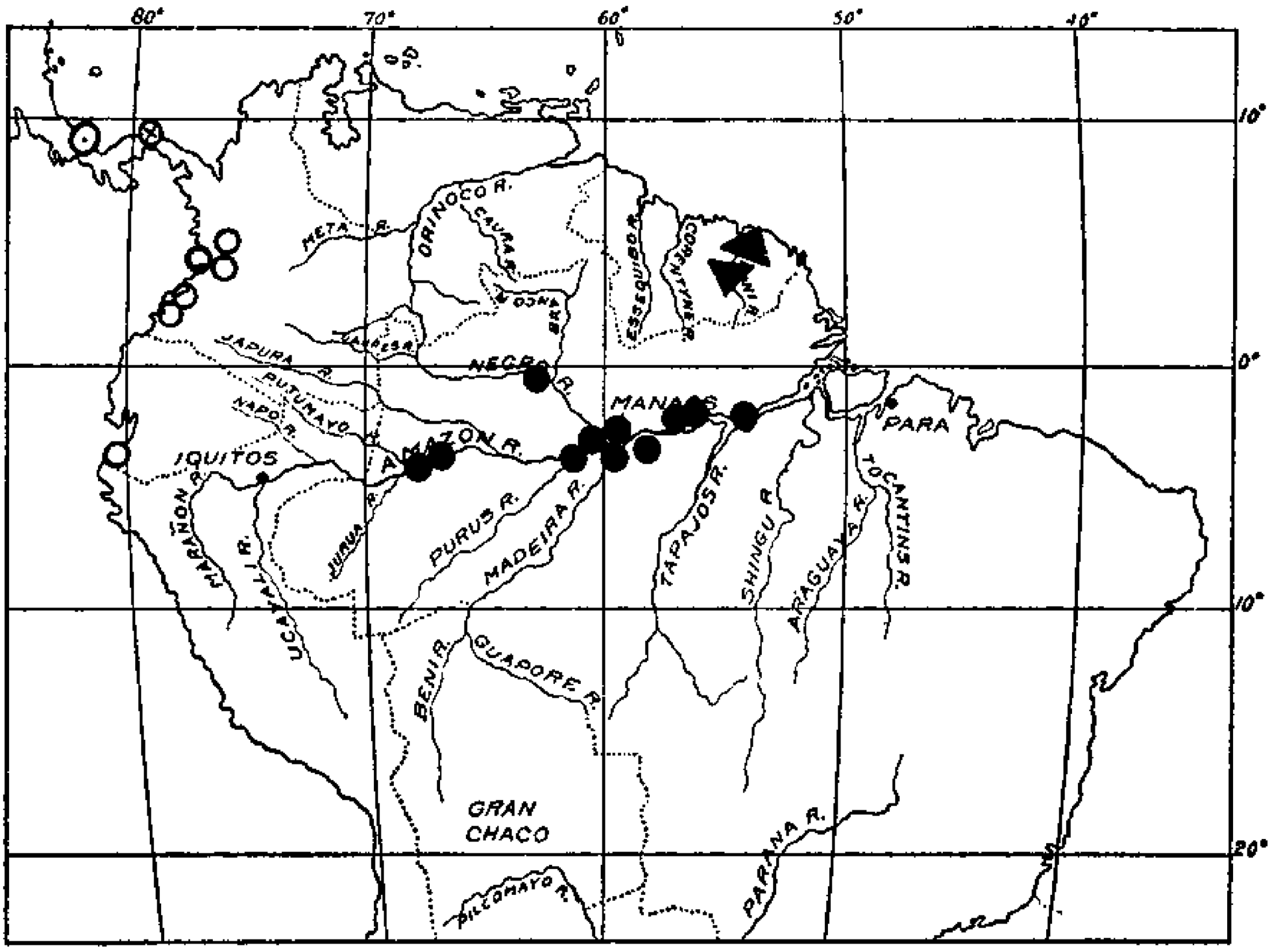


FIGURE 13.—Leaves of *Theobroma*, × ⅓: A, *speciosum*, from orthotropic and plagiotropic branches (US–1031918); B, *sylvestre* (US–1693105); C, *sylvestre* (Martius, type).

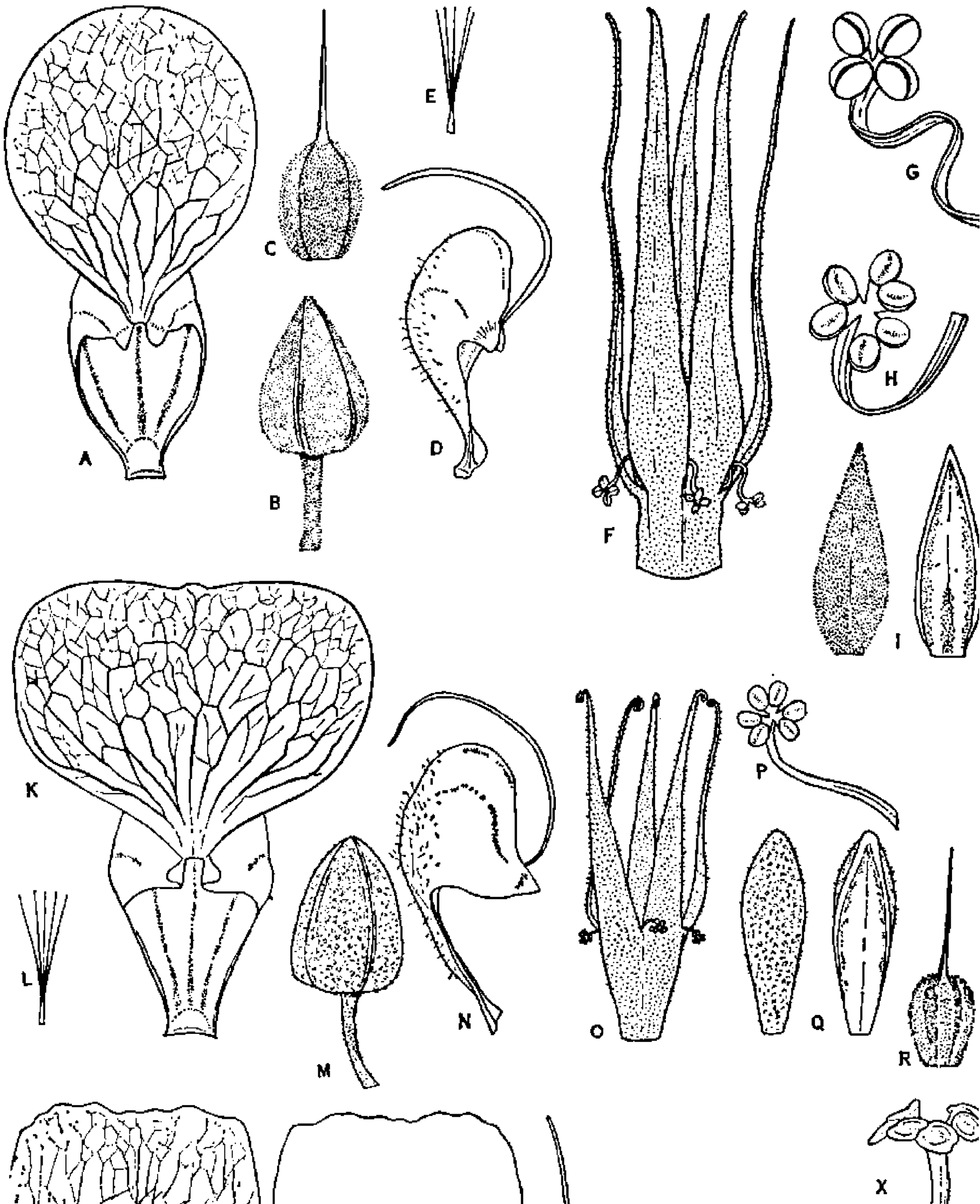


MAP 4.—Distribution of *Theobroma sylvestre*, ●; *T. bernouillii* subsp. *bernouillii* ⊕; *T. bernouillii* subsp. *asclepiadiflorum* ⊙; *T. bernouillii* subsp. *capilliferum* ○; *T. velutinum* ▲.

TYPES.—*Martius*, Brazil, Iter Brasil. 322 (in M, no. 891) (Photo F. M. 19644). *Spruce* 166, Brazil, Pará, Obidos (of *T. Spruceana*). *Martius*, Brazil, Iter Brasil. 322 (in M, no. 890) (Photo F. M. 40709) (of *T. nitida*).

Small- or medium-sized tree up to 12 m. high, sympodial growth by lateral, subterminal upright shoots; primary branching ternate; terminal, leafy and floriferous branches dichotomous, terete, rugulose, dark brownish, the hornotinous ones pulverulent, stellate-tomentellous, soon glabrate or glabrous; stipules small, soon deciduous.

Leaves distichous, firmly coriaceous; petiole short, robust, appressed stellate-tomentose, 5–10 mm. long; blades elliptic-oblong with obtusely cuneate, asymmetrical base, often ovate-oblong or oblong-ovate with rounded, asymmetrical base, attenuate and acutely acuminate at apex, the margin entire or slightly sinuose, 12–30 cm. long, 5–8 (–13) cm. broad, the acumen 1.5–2.5 cm. long, rather lustrous above, pale brownish when dry, glabrous, the costa and secondary nerves subfiliform, prominulous, the other nerves almost unnoticeable, paler beneath with tawny nervation, the costa very prominent, the secondary nerves about 6 pairs, prominent, ascending, decurrent, arching and uniting near the margin, the inferior pair forming a much more acute angle, the transverse tertiary nerves distant 5–10 mm. from



[FIGURE 14]

each other, thin and prominent, the lesser veins forming a minute, prominulous reticulum; midrib, secondary and tertiary nerves glabrous, those of the fourth rank subglabrous, the lesser reticulate veins and the areoles covered by dense, minute, whitish, sericeous tomentum of stellate hairs.

Inflorescences small, axillary or extra-axillary on small branches; panicles short, 1–2 cm. long, branched from base, the branchlets 1–8, fasciculate, crowded, scarcely ramulose, densely stellate-tomentose, bracteolate at joints, bracteoles ovate, or ovate-lanceolate, 1–2 mm. long, stellate-tomentose; pedicels 2–5 mm. long, moderately thin, densely tomentose; sepals shortly united at base, thick, sublanceolate-oblong, subacute, involute at margin, ferruginous, stellate-tomentose outside, glabrous inside except for the minutely stellate-tomentose margin and glandular trichomes at base, curvate and spreading at anthesis, 7–9 mm. long, 2–2.5 mm. broad.

Petal-hood thick-membranaceous, trinerved, pale and reddish striate, rugulose, papillose, sparsely pilose outside, oblong-obovate, cucullate-rounded at apex, 4 mm. long, 2 mm. broad; petal-lamina brownish red or rose, rotundate-subreniform, minutely crenulate, rugose, 2 mm. long, 2.2–2.5 mm. broad, suddenly constricted into a short claw, articulate at base; androecium tube 1.5–2 mm. high; staminodes brownish red or rose, linear-subulate, abruptly narrowed-acuminate at apex, the acumen often curled, densely and minutely pilose-muricate throughout, 5–6 mm. long, 0.7–0.8 mm. wide; filaments 1–1.2 mm. long, glabrous, arched, diantheriferous, the lobes of the anthers ellipsoid, 0.4 mm. long; ovary ovoid-ellipsoid, 5-ridged, ferruginous-tomentose, 1.5–2 mm. long, the apex whitish tomentulose; styles 5, thin, acute, connivent, united only at base.

Fruits elliptic-globose, or subglobose, about 6 x 5.8 cm., rounded at apex, umbilicate at base, the pericarp coriaceous, minutely and densely tomentose, glaucous when ripe, about 5 mm. thick, the inner and outer layer hard, thin, the middle one carnose; seeds ovoid-oblong, 1.4–2.1 cm. long and 0.5 x 0.9 mm. broad; pulp rather sweet, scentless, white; fruiting peduncle about 1.8 cm. long, 7 mm. thick.

At the Botanische Staatssammlung in Munich there are several specimens from Martius' trip to Brazil which bear the annotation

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FIGURE 14.—A–I, *Theobroma glaucum* (Baker & Cope 11 and 18): A, petal from inside × 5; B, bud, × 2; C, pistil, × 5; D, petal laterally, × 5; E, styles, × 5; F, androecium, × 5; G, 2-antheriferous stamen, × 10; H, 3-antheriferous stamen, × 10; I, sepal from outside and inside, × 2. K–R, *T. speciosum* (Archer 7619): K, petal from inside, × 5; L, styles, × 5; M, bud, × 2; N, petal laterally, × 5; O, androecium, × 5; P, stamen, × 10; Q, sepal from outside and inside, × 2; R, pistil, × 5. S–Y, *T. velutinum* (B. W. 1161): S, petal from inside, × 5; T, pistil, × 5; U, petal from outside, × 5; V, petal, laterally, × 5; W, androecium, × 5; X, stamen, × 15; Y, sepal from inside and outside, × 2.

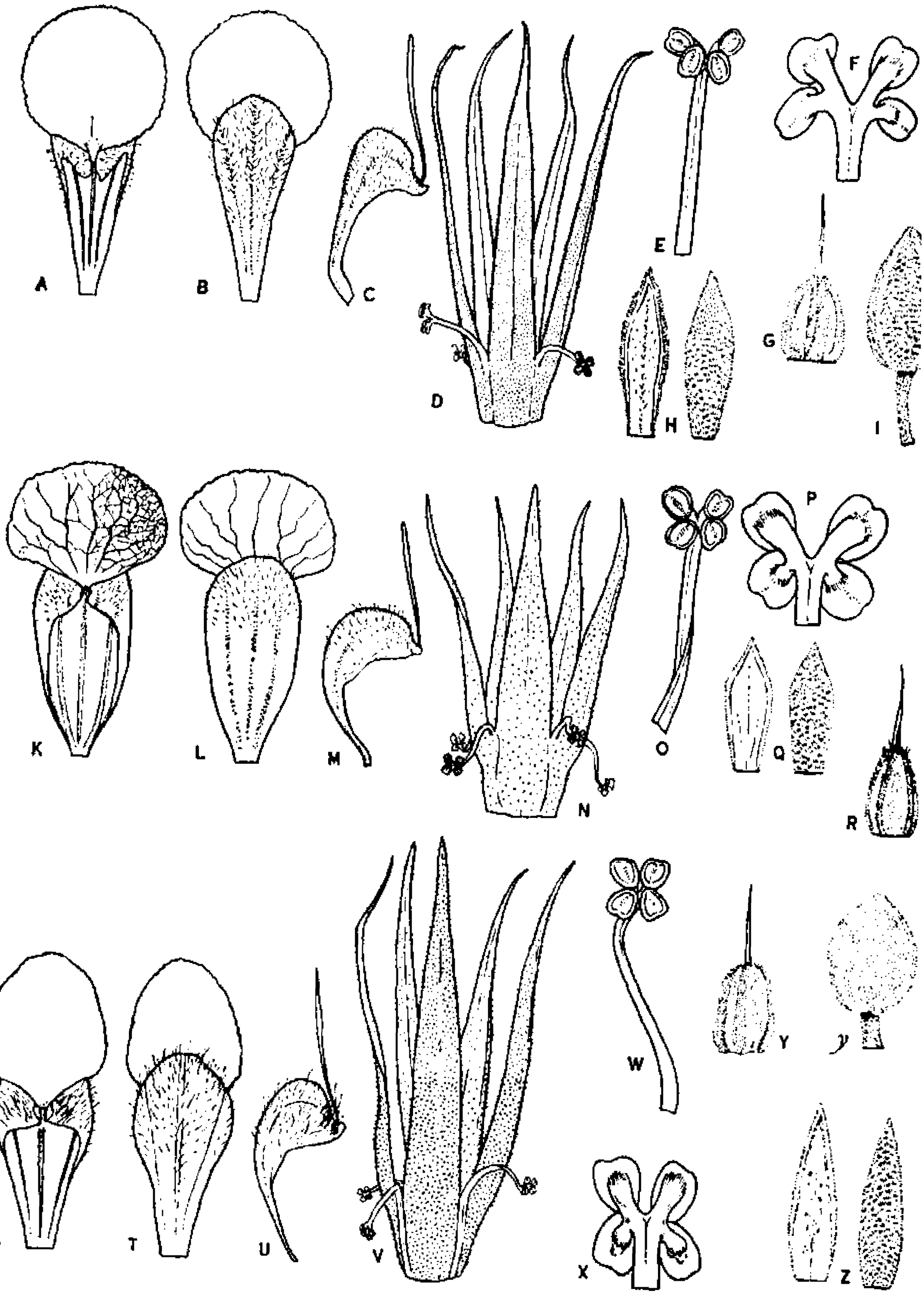
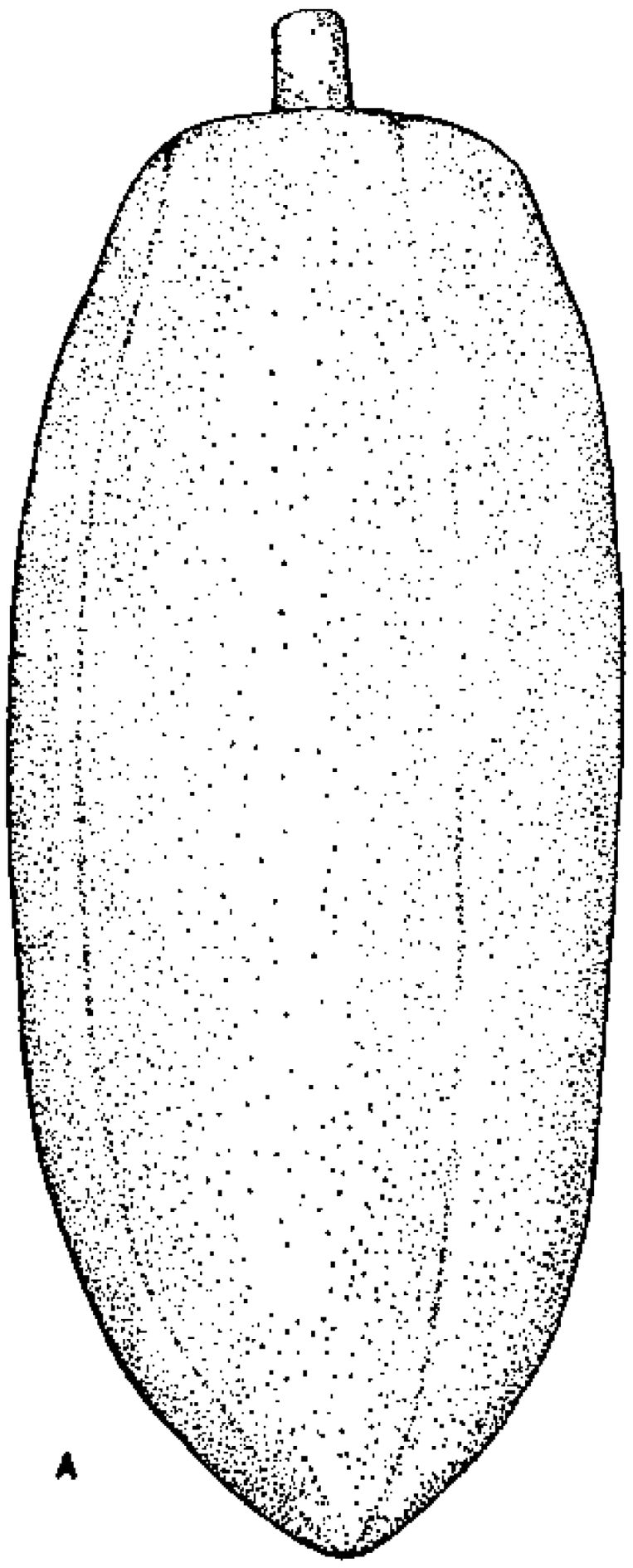
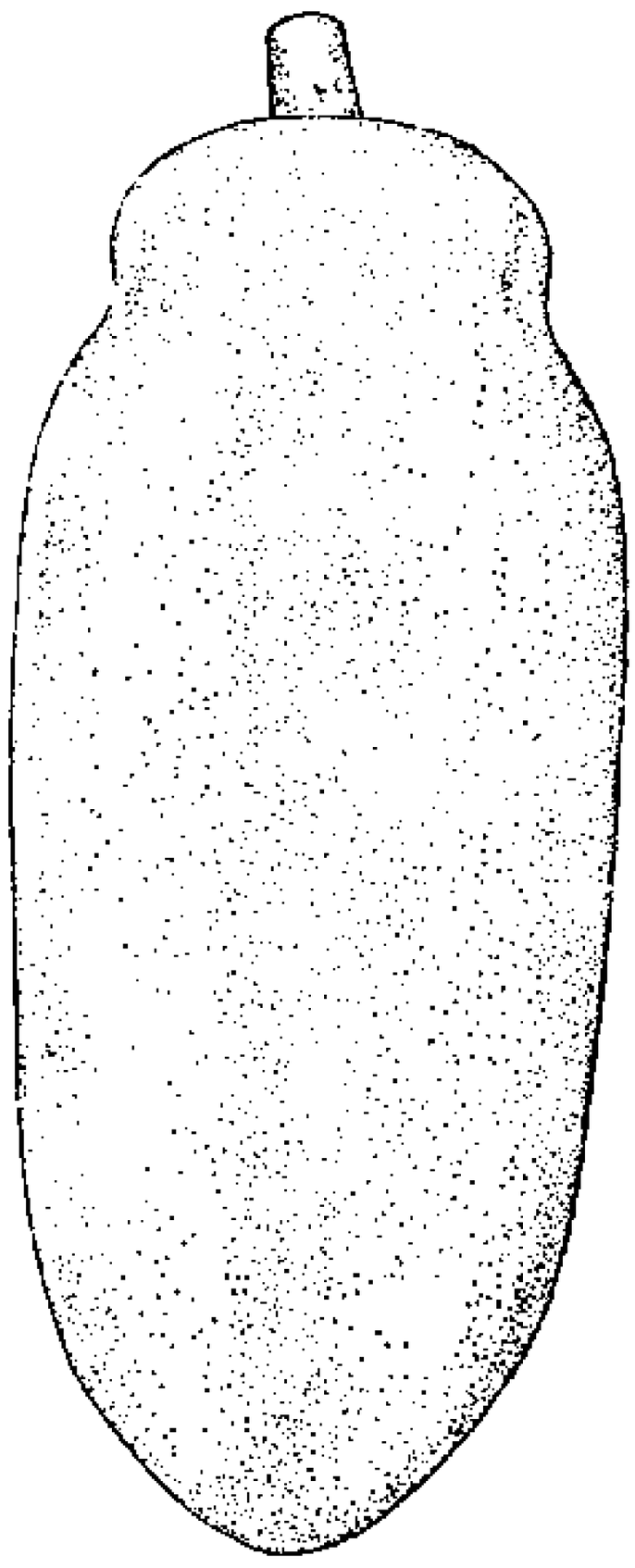
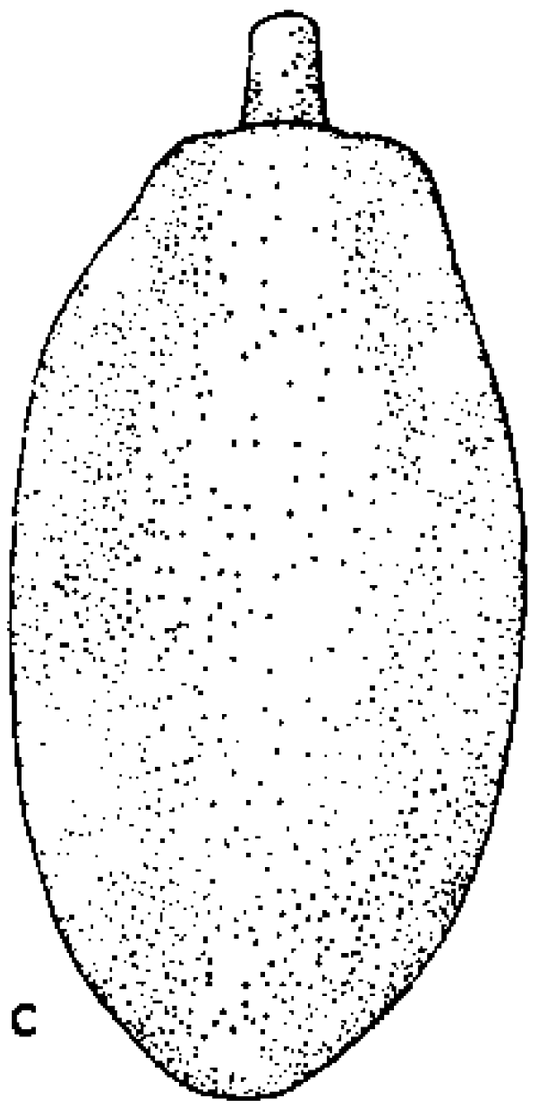
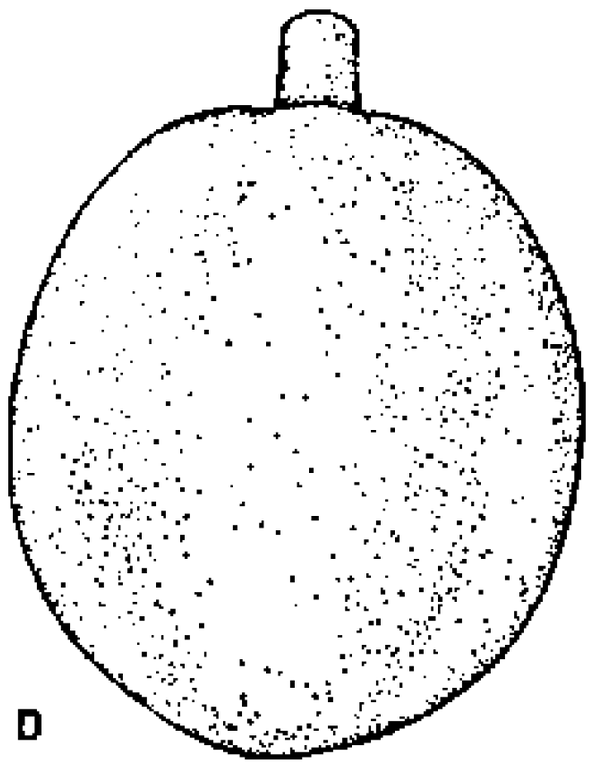


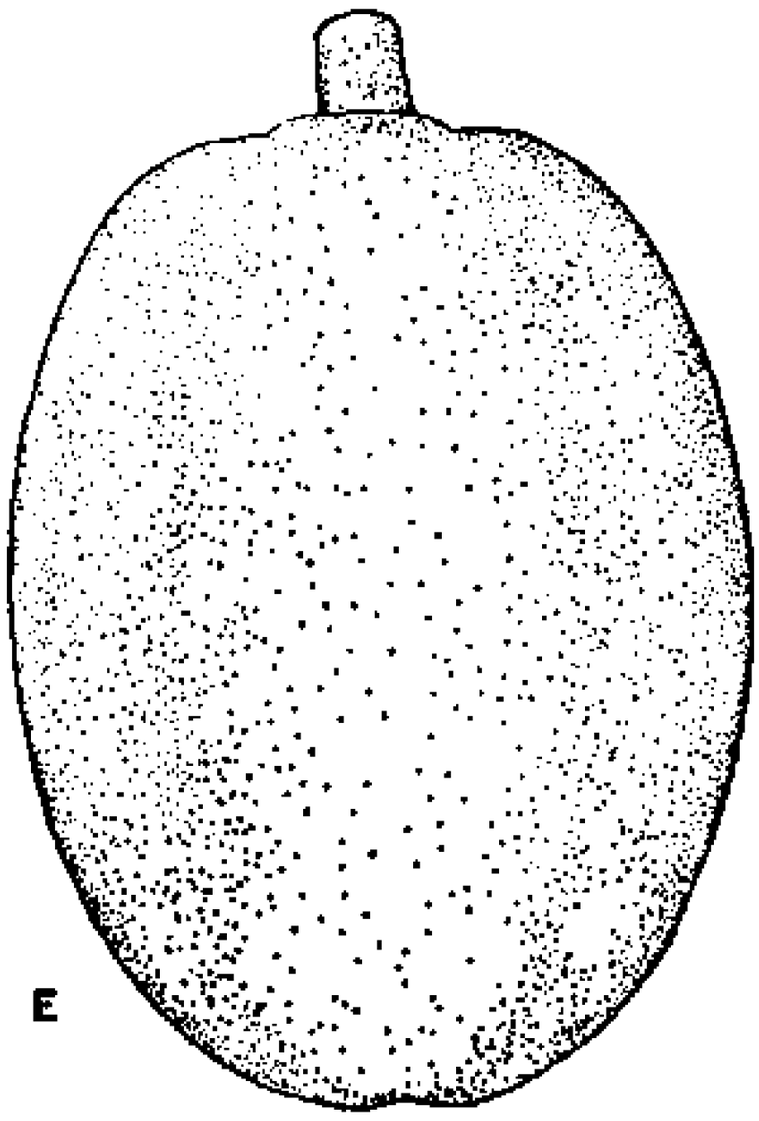
FIGURE 15.—A–I, *Theobroma bernouillii* subsp. *capilliferum* (Holliday 142): A, B, C, peta from inside, outside, and laterally, × 5; D, androecium, × 5; E, stamen, × 10; F, anthers × 20; G, pistil, × 5; H, sepal from inside and outside, × 2; I, bud, × 2. K–R, *T bernouillii* subsp. *bernouillii* (Pittier 4105): K, L, M, petal from inside, outside an laterally, × 5; N, androecium, × 5; O, stamen, × 10; P, anther, × 20; Q, sepal fron inside and outside, × 2; R, pistil, × 5. S–Z, *T. bernouillii* subsp. *asclepiadiflorum* (Wedel 1535): S, T, U, petal from inside, outside and laterally, × 5; V, androecium × 5; W, stamen, × 10; X, anthers, × 20; Y, pistil, × 5; YY, bud, × 2; Z, sepal fron inside and outside, × 2.

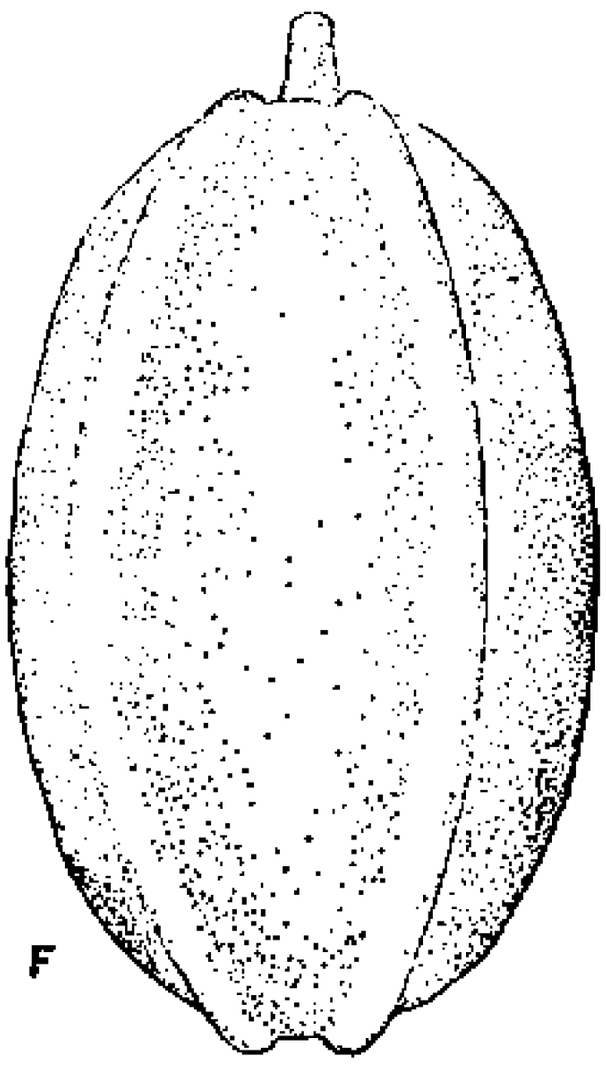












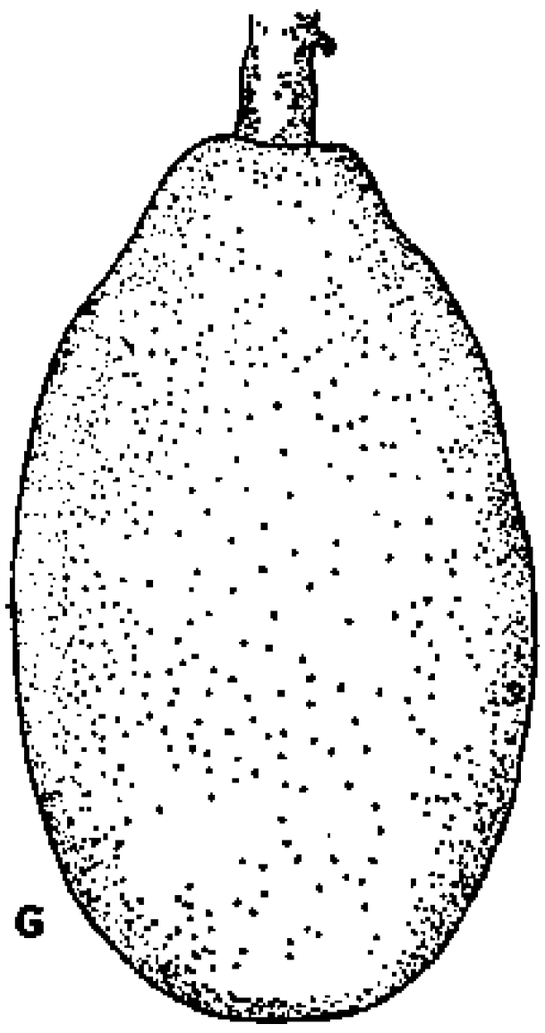


FIGURE 16.—Fruits of *Theobroma*, × ½: A, *bernouillii* subsp. *asclepiadiflorum* (Lucas 1); B, *bernouillii* subsp. *capilliferum* (Cuatr. 17034); C, *glaucum* (Froes 20645); D, *sylvestre* (Froes 20463); E, *speciosum;* F, *velutinum* (Benoist 516); G, *nemorale* (Cuatr. 21291).

"Iter brasiliensis" and then the number 322 at the foot of the label; they are named by Martius as "T. sylvestris Martius." All the specimens agree with each other essentially, although some of them have oblong leaf blades, slightly asymmetrical or symmetrical at the base, and others have broad, oblong-ovate blades, very rounded and asymmetrical at the base; in all of them there is a longer distance between the basal pair of secondary nerves and the next pair than between the other pairs of secondary nerves; two of these specimens bear typical rounded, smooth fruits. One of the specimens which shows the number 891 on a mounting strip (Photo F. M. 19644) may be considered as the holotype of *T. sylvestre* (lectotype); it has a leafy branch with the basal half of a fruit, and a loose, broad, obovate-oblong leaf. Bernoulli, without obvious reasons, considered one of the specimens [890] (Photo F. M. 40709) a different species and described it as *T. nitida* Bernoulli. Another of these specimens [871] was named by Schumann as *T. grandiflorum*, and it is mixed with an authentic *T. grandiflorum* specimen on the F. M. 19641 Photograph. After a close examination of the series of Martius types, it was clear to me that there do not exist basic differences between them and *T. spruceanum* Bernoulli. Most of Martius specimens have somewhat thinner and smaller leaves than the current collections, variations which can be attributed to the habitat and to the age of the collected branches.

Schumann listed *T. sylvestre* Mart. under his "Species dubiae."

The binomial *Theobroma Martii* was published by Schumann as a new name for *T. nitida* Bernoulli, although due to some typographical error this name was not quoted as synonym. But Schumann cited "l.c. 15" and quoted unchanged the diagnosis given by Bernoulli for *T. nitida* on page 15. Schumann considered the name a homonym of his *T. nitidum* (Poepp. & Endl.) K. Schum. (*Abroma nitida* Poepp. & Endl.).

Theobroma sylvestre has been confused with *T. speciosum*, which is usually a larger tree, but its small axillary inflorescences, smaller, scentless and paler brown-reddish flowers, and its green-bluish fruit at maturity, distinguish it readily.

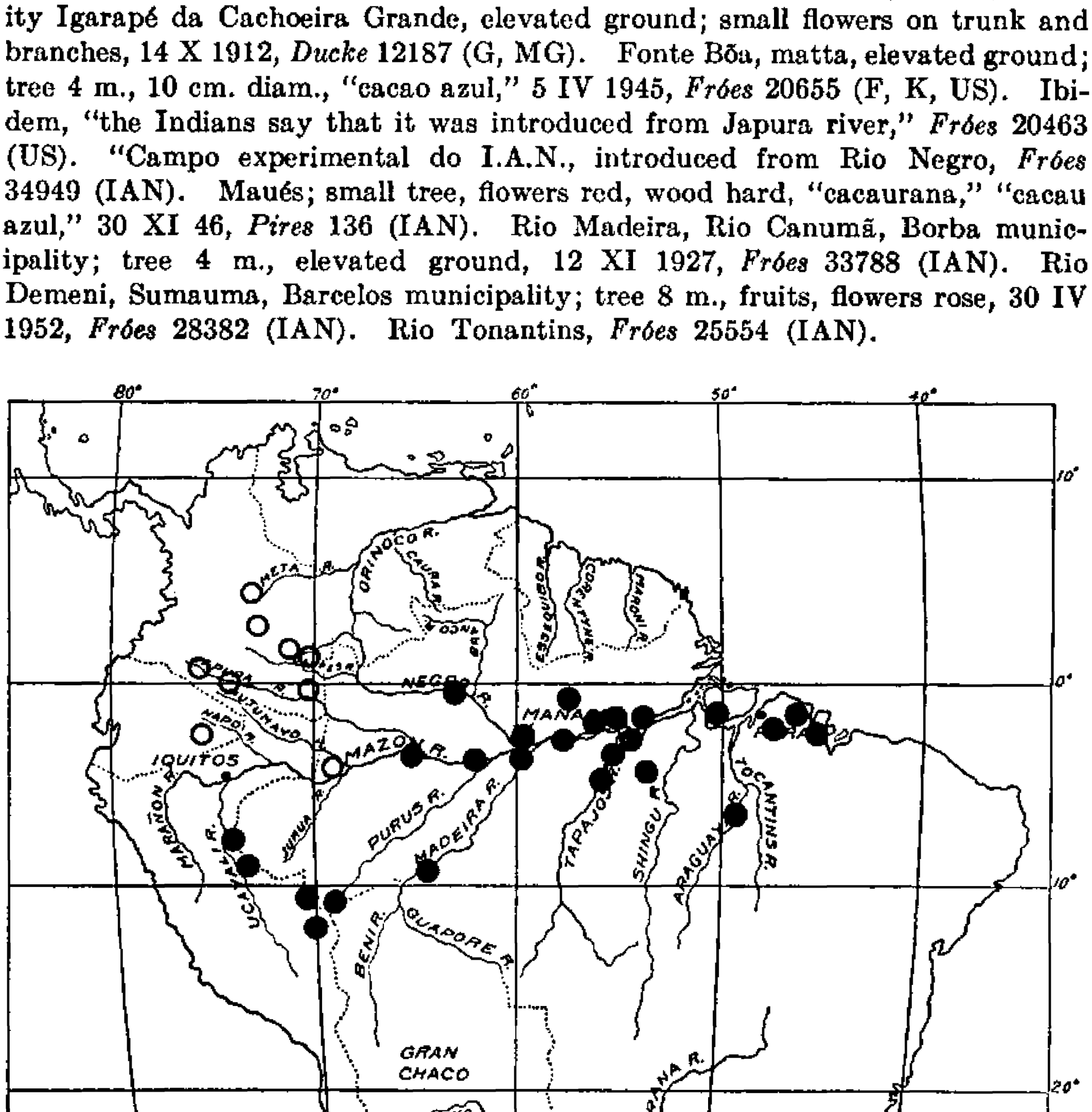
COMMON NAMES.—"Cacao azul" is generally used. Other names recorded are: Cacau azul, cacauí, cacauú, cacao-hú, cacao rana, cacau rana, cacau bravo. Cacao azul refers to the color of the mature fruit (bluish).

USES.—No special uses are recorded.

DISTRIBUTION.—More or less frequent along the Amazon River and lower part of its tributaries from Santarém to Tonantins, eastward from the mouth of the Içá. It grows on elevated ground in rather dry places, and appears frequently in secondary stands.

According to Ducke, it is common around Manaos, especially in relatively dry thickets on clay soils poor in silica.

BRAZIL: AMAZONAS: "Martius Iter brasiliensis 322: *Theobroma sylvestris* Mart. Observ. 2832, *Cacao sylvestris* Aubl., Cacao Rana Incol. Habitat in sylvis ad fl. Solimoes, Prov. Rio Negro," Martius [887] (Photo F. M. 40708) (M, syntype of *T. sylvestris* Mart.). "Martius Iter brasiliensis 322: *Theobroma sylvestris* Mart. in silvis ad Fl. Solimoes," *Martius* [891] (Photo F. M. 19644) (M, lectotype). Ibidem *Martius* [871] (Photo F. M. 40707) (M, syntype). Ibidem *Martius* [888] (M, syntype). Ibidem *Martius* [889] (M, syntype). "Martius Iter Brasiliensis 322, in silvis ad fl. Solimoes," *Martius* [890] (Photo F. M. 40709) (M, type of *T. nitida*). Manaos, Mata do Aleixo, "cacau azul," 16 III 1945, *Frões* 20556 (IAN, NY). Manaos, Colonia João Alfredo, rain forest in noninundatable ground; small tree, flowers pale brown-rose, "cacao azul," 6 XII 1935, *Ducke* 100 (A, F, IAN, K, MG, MO, S, US). Manaos, in noninundatable forest; rather large tree with weak trunk, flowers brownish-flesh color, "cacao azul," VI 1932, *Ducke* 103 (F, Y). Manaos, matta, vicinity Igarapé da Cachoeira Grande, elevated ground; small flowers on trunk and branches, 14 X 1912, *Ducke* 12187 (G, MG). Fonte Bõa, matta, elevated ground; tree 4 m., 10 cm. diam., "cacao azul," 5 IV 1945, *Frões* 20655 (F, K, US). Ibidem, "the Indians say that it was introduced from Japura river," *Frões* 20463 (US). "Campo experimental do I.A.N., introduced from Rio Negro, *Frões* 34949 (IAN). Maués; small tree, flowers red, wood hard, "cacaurana," "cacau azul," 30 XI 46, *Pires* 136 (IAN). Rio Madeira, Rio Canumã, Borba municipality; tree 4 m., elevated ground, 12 XI 1927, *Frões* 33788 (IAN). Rio Demeni, Sumauma, Barcelos municipality; tree 8 m., fruits, flowers rose, 30 IV 1952, *Frões* 28382 (IAN). Rio Tonantins, *Frões* 25554 (IAN).



MAP 5.—Geographical distribution of *Theobroma speciosum* ● and *T. glaucum* ○.

PARÁ: "In vicinibus Obidos, Prov. Para, Dec. 1849," *Spruce* 166 (Photo F. M. 40702) (M, holotype and lectotype of *Theobroma spruceanum* Bernoulli; isotypes BM, WU). Obidos, "cacao azul," 7 I 1904, *Ducke* 4878 (BM, G, MG, P, US); ibidem, matta, 11 V 1905, *Ducke* 7216 (MG). Ibidem, rain forest, elevated ground; small tree, fruit green glaucous when ripe, flowers pale brownish reddish, "cacao-azul," 10 I 1920, *Ducke* 14734 (S, U). São Jorge, municipality of Faro; small tree in rain forest, flower dark red on branches, "cacau azul," 11 XI 1950, *Black & Ledoux* 50–10644 (IAN, UC, U). Oriximiná, Las Trombetas, flowers on trunk and branches, ripe fruit green, "cacao azul," "cacao-hu," 8 XII 1906, *Ducke* 7822 (BM, G, MG, US). Lazo de Faro, above Tanaenera, forest on elevated ground, "cacau azul," 12 II 1910. *Ducke* 10669 (MG). Alenquer, Estrada da Vila do Curuá, municipality of Obidos, sandy ground with vegetation of *Bertholletia* and *Attalea;* tree 2.5 m. in rain forest, 4 III 1953, *Frões & Filho* 29465 (IAN, U). "Km 23 da BR–17 Est. a direita," firm land, sandy, natural forest; flowers yellowish red, edible fruits, 12 X 1955, "cacao bravo," *INPA* (*Dionisio*) 2125 (IAN).

3. Theobroma specciosum Willd.

FIGURES 5, 12, 13, 14, 16, 18; MAP 5; PLATES 2, 3

Theobroma speciosum Willd. ex Spreng. Syst. Veg. **3**:332. 1826; Bernoulli (1869) 8, *pl. 3, fig. 2;* Schumann in Mart. (1886) 74; Jumelle (1899) 30, *fig. 16;* De Wildeman (1902) 95; Huber (1906a) 273; Ducke (1925) 130; (1940) 270, *pl. 1, fig. 3, pl. 2;* (1954) 13; Addison & Tavares (1951), *pl. 5, fig. 2, pl. 6, fig. B, pl. 12, fig. 6;* Cuatrecasas (1956) 658.

Theobroma quinquenervia Bernoulli, Uebers. Art. Theobroma 8, *pl. 3, fig. 3.* 1869.

Theobroma speciosum var. *quinquenervia* (Bernoulli) Schum. in Mart. Fl. Bras. **12**(3):75. 1886: Jumelle (1899) 32, *fig. 16;* De Wildeman (1902) 95.

Theobroma speciosum var. *coriaceum* Huber, Bol. Mus. Goeldi **4**:586. 1906.

Theobroma guianensis sensu Chevalier, Rev. Inter. Bot. Appl. **26**:274. 1946; León (1960) 318, 319, *fig.*, pro parte, non Gmelin.

Sapokaia brasiliensis Rich. ex Chevalier. Rev. Int. Bot. Appl. **26**:275. 1946, as synonym.

TYPES.—*Siber:* "*Hoffmannsegg*" in Herbarium Willdenow no. 3680 (B). *Spruce* 1737, Brazil, Barra do Rio Negro (of *T. quinquenervia*). *Huber* 1567, Peru, Ucayali (of var. *coriaceum*).

Tree up to 15 mm. tall; trunk about 20 cm. in diameter with light gray, smooth bark; sympodial growth by lateral, subterminal upright shoots; primary branches ternate, usually furcate, spreading; branchlets terete, smooth, more or less pulverulently stellate-pilose, later glabrate, grayish brown; crown rather narrow; stipules subulate, short, stellate-tomentose, soon deciduous.

Leaves firmly coriaceous, distichous; petiole robust, subterete, densely stellate-tomentulose, 8–14 (–20) mm. long, 2–4 mm. thick; blades usually large, ovate-oblong or elliptic-oblong, broadly rounded or very obtuse and asymmetrical at base, exceptionally (in orthotropic branches) cuneate and symmetrical, attenuate near the apex, abruptly and acutely acuminate, the margin entire or very slightly sinuose, often slightly revolute, 20–40 cm. long, 7–18 cm. broad, the

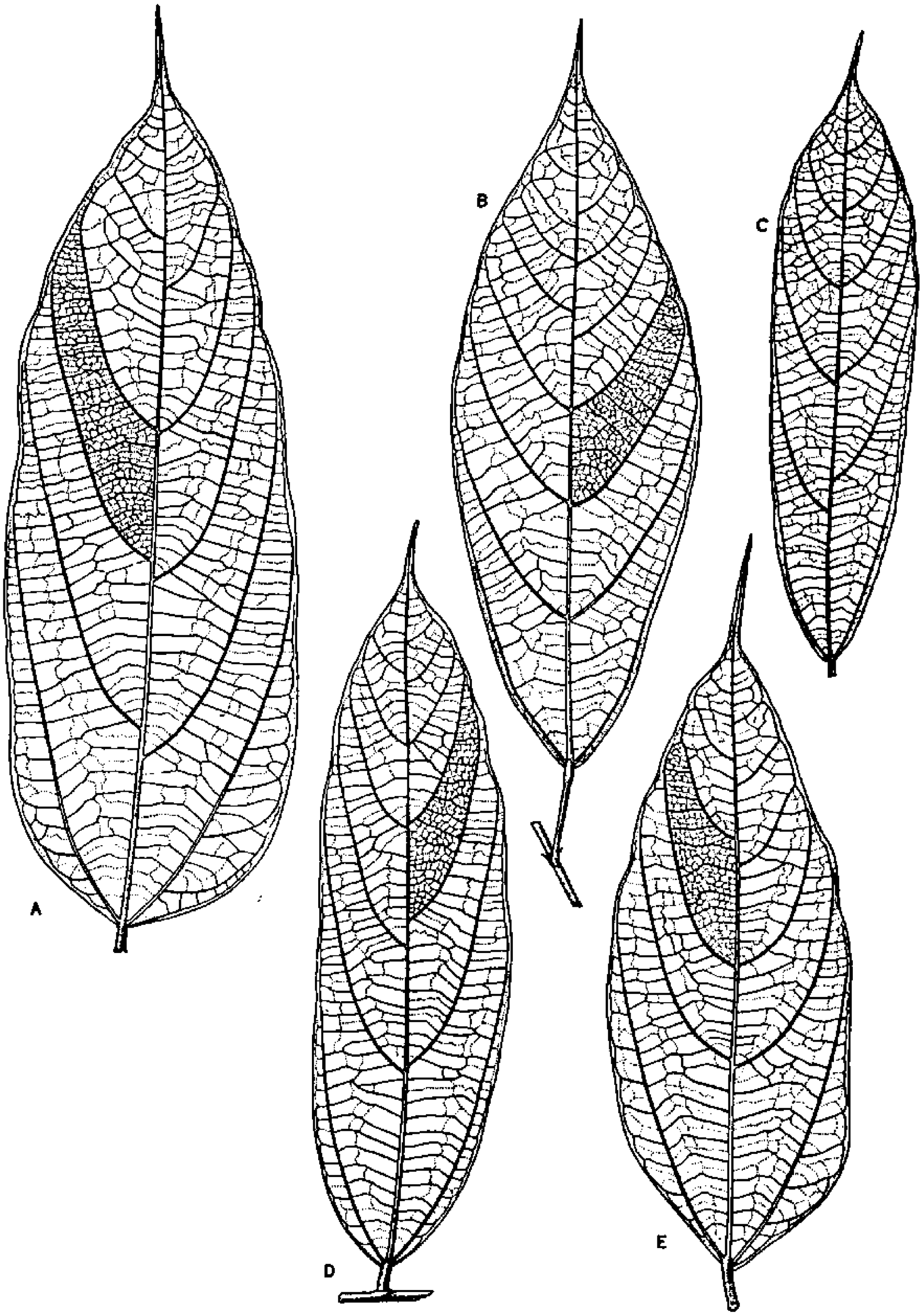


FIGURE 17.—Leaves of *Theobroma*, ×⅓: A, *glaucum*, from lateral branches (Bartley & Holl. 74); B, *glaucum*, from orthotropic branches (Baker 37); C, *bernouillii* subsp. *asclepiadiflorum* (Wedel 681); D, *bernouillii* subsp. *bernouillii* (Pittier 3199); E, *bernouillii* subsp. *capilliferum* (Cuatr. 16160).

acumen 1.5–2.5 cm. long; lustrous above, green, usually pale brown or olivaceous when dry, glabrous, or with a few stellate hairs on the nerves, the costa and main nerves filiform, conspicuous, the minor veins less noticeable or obsolete, pale cinereous beneath with tawny nervation, the costa thick, very prominent, the 6–8 pairs of secondary nerves prominent, subcurvate ascending, near the margin thinner, curving, decurrent and anastomosing, the inferior pair stronger, forming together with the midrib a trinerved base, the transverse tertiary nerves thin but prominent, 5–15 mm. distant from each other, sometimes the basal more conspicuous, forming together with main nerves a basally 4- or 5-nerved leaf; minor veins prominulous, reticulate; main nerves glabrous or subglabrous with sparse, stellate hairs and scattered callose dots, the tertiary glabrous or subglabrous, the minor reticulate veins and the areoles covered by dense minute whitish sericeous tomentum of stellate hairs.

Inflorescences on trunk, forming delicate panicles gathered in many-flowered bunches borne on woody, short, tuberculose branches, often very showy with up to 250 dark-red or purplish-red fragrant flowers; panicles 3–10 cm. long, dichotomously furcate-branched from the base, the branches thin but rigid, reddish and covered with a minute, whitish tomentum, the terminal branchlets (peduncles) thin, flexuous, 10–25 mm. long, 3-bracteolate and articulate to the pedicel at apex; pedicels slender, 5–20 mm. long, minutely tomentulose; bracteoles minute, linear or linear-triangular, 1–2 mm. long, 0.2–0.5 mm. wide, very soon deciduous; buds ovoid, 7–9 mm. high, rather reddish, with 5 longitudinal, white-tomentose, prominulous commissural lines, sparsely stellate-pilose; sepals rather thick, oblong, subobovate-oblong, attenuate toward the base, abruptly narrowed and subobtuse at apex, the margin incurved with a minutely, whitish tomentulose strip inside, the apex shortly cucullate-inflexed, the inside purplish and glabrous, except for glandular trichomes at base, the outside sparingly stellate-pilose, usually one free and the others united one third or almost completely by pairs, 10–12 mm. long, 3.5–4 mm. broad; petal-hoods thick-membranaceous, trinervate, whitish with red lines, oblong-obovoid, attenuate-clawed at base, rounded cucullate at apex, with sparse, thin, spreading hairs outside, 6–7 mm. long, about 4 mm. broad; petal-lamina rather thick, red or dark red, transversely elliptic, subtruncate, slightly emarginate and mucronulate at apex, abruptly cuneate-attenuate at base, entire or slightly erose at margin, conspicuously (especially by transmitted light) reticulate-veined, 5–7.5 mm. long, 7–9 mm. broad; androecium tube thick, about 2–3.5 mm. high, sparsely stellate-pilose; staminodes purplish red, subulate, thick, the apex thinner and curled, minutely muricate-pilose, 5–7 mm. long, 1.2–1.8 mm. wide; filaments glabrous,

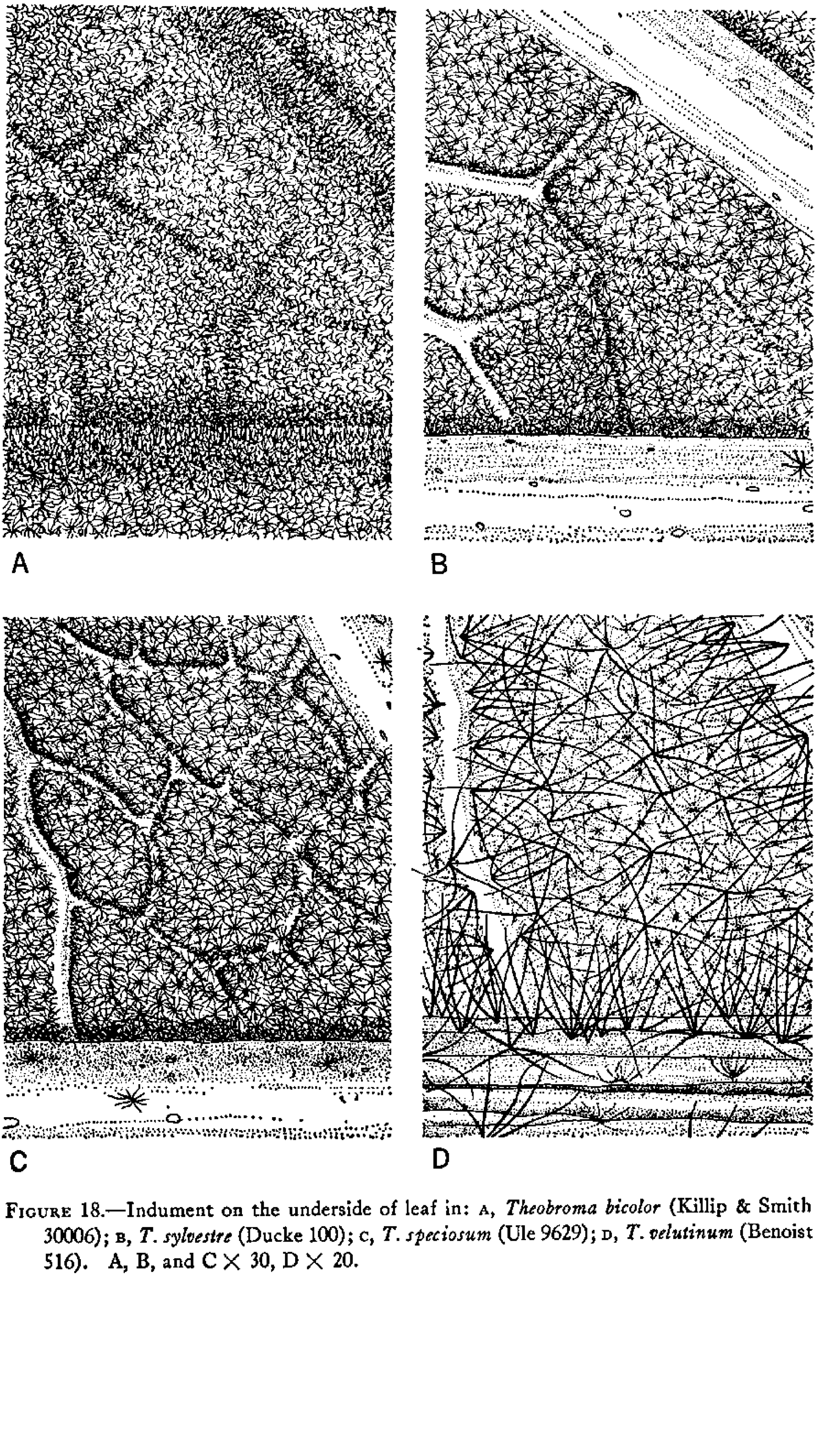


FIGURE 18.—Indument on the underside of leaf in: A, *Theobroma bicolor* (Killip & Smith 30006); B, *T. sylvestre* (Ducke 100); C, *T. speciosum* (Ule 9629); D, *T. velutinum* (Benoist 516). A, B, and C × 30, D × 20.

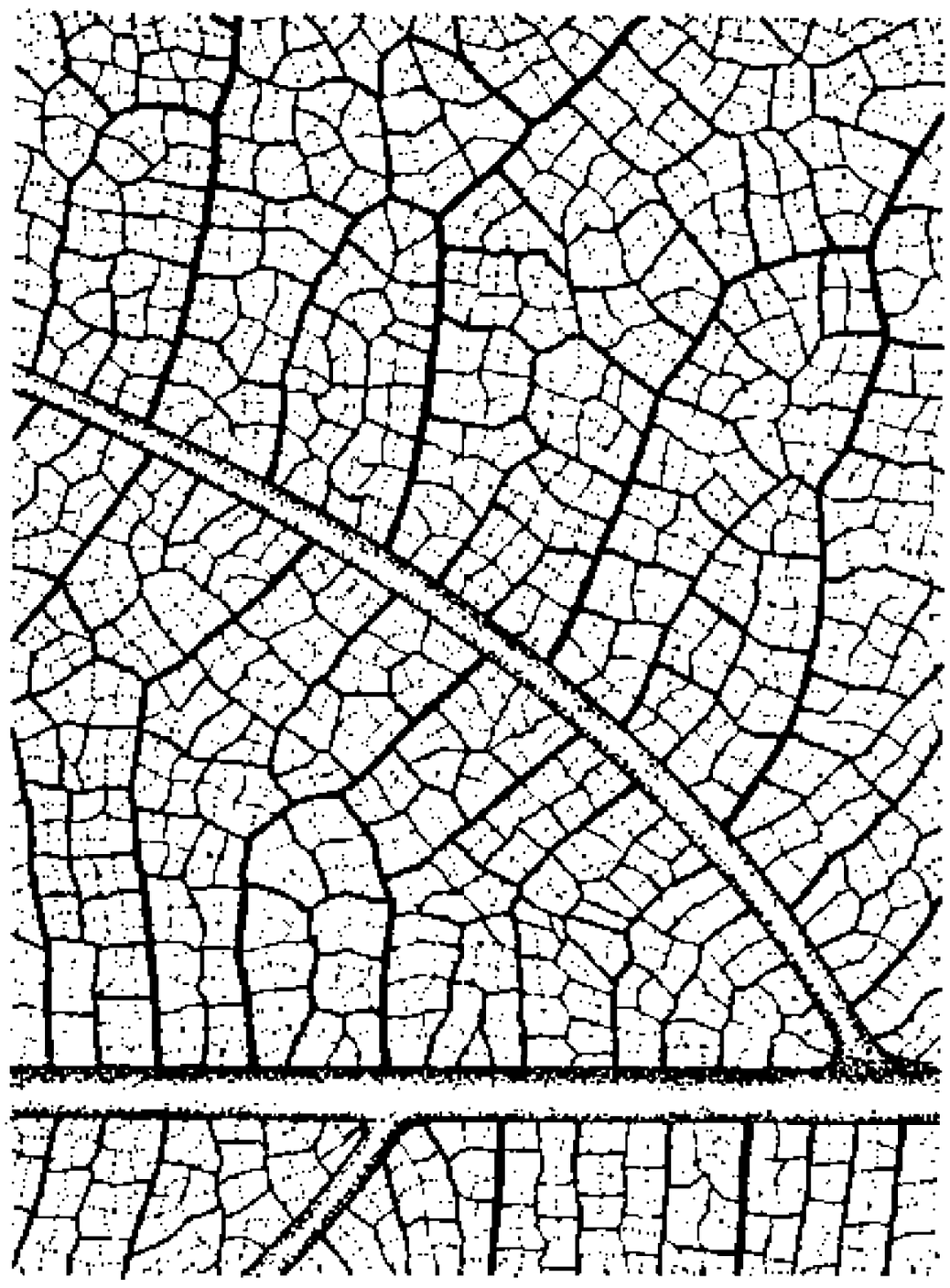
about 2 mm. long, curved, dilated at base, minutely 3-furcate at apex, triantheriferous; anther lobes ellipsoid, about 0.4 mm. long; ovary ovoid-ellipsoid, 2–3 mm. long, 5-ridged, whitish velvety-tomentose; styles 5, subfiliform, 1.2–2 mm. long, glabrous, connivent, only united at base.

Fruit globose-ellipsoid, about 10 cm. long and 7–8 cm. broad, almost smooth, with 5 more or less conspicuous (when dry depressed) costae, shortly and densely tomentose-velvety, yellow when ripe; pericarp about 5–6 mm. thick, the inner layer coriaceous, smooth, very hard, about 0.5–1 mm. thick, the middle tissue about 3–4 mm., carnose, the outer layer coriaceous but less hard than the innermost and becoming rugose after the shrinking of the intermediate layer by drying; seeds about 20–26, surrounded by whitish, sweet, scentless pulp, ovoid-oblong or ellipsoid-oblong, 24–26 mm. long, 13–14 mm. broad, 10–12 mm. thick, the episperm thick (about 1 mm.), coriaceous with the middle layer becoming gelatinous; embryo white, oblong, covered by a very thick pellicle, 22–24 mm. long, 10–11.5 mm. broad, 9–10 mm. thick; germination epigeous.

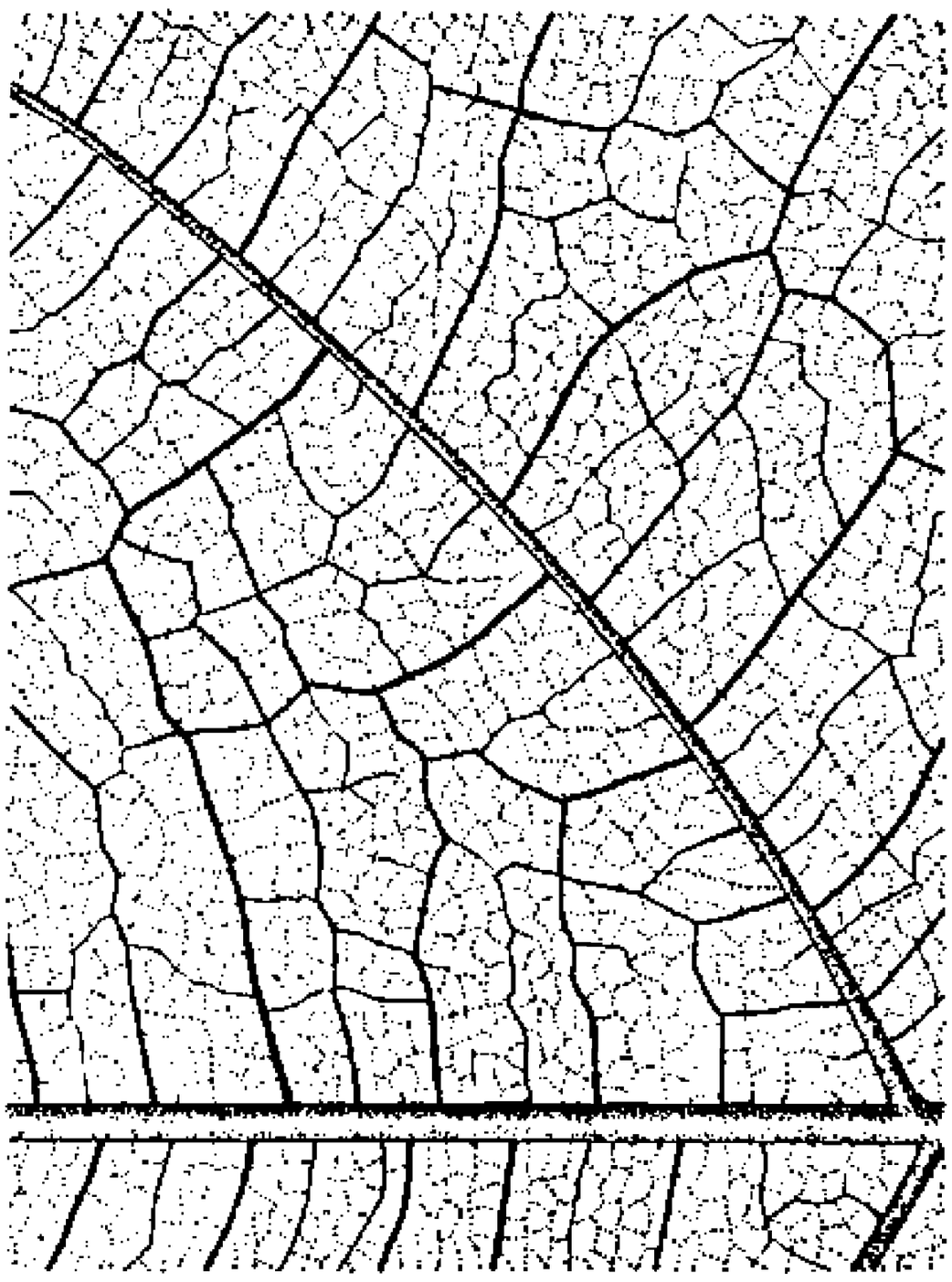
The leaves of the type of *T. speciosum* are long-petiolate, cuneate and trinerved at the base. *Theobroma quinquenervium* Bernoulli was described from a specimen with short-petiolate, broadly oblong leaves, asymmetrically rounded at the base. In the first type the margins of the leaves are close and parallel to the prominent, basal pair of secondary nerves; in the second the margins of the leaves are broadened and remote from the prominent basal pair of nerves, and an additional lower tertiary nerve on each side makes the base of the blade somewhat 5-nerved. The latter type of blade, borne on a short, stout petiole, is the common one in the species. Leaves with slender, long petioles, thickened at both ends, and cuneate blades are seldom found; they appear on young, orthotropic terminal branches. This dimorphism was already noticed by Huber who first united *T. quinquenervium* and *T. speciosum*.

The type specimen was collected near Belém de Pará by Siber who was sent on a collecting trip to Brazil by Hoffmannsegg; it is preserved in the Berlin-Dahlem Botanical Museum in the Willdenow Herbarium. I have been able to study this specimen thanks to the kindness of Prof. Werdermann and Prof. Melchior. The photograph F.M. 9640 is from a specimen at B now destroyed, which agrees perfectly with the type in the Willdenow Herbarium, of which it was undoubtedly a duplicate. In his monograph, Chevalier made this species a synonym of *T. guianense* (Aubl.) Gmel., but this is a confused species, the identity of which is discussed in this paper.

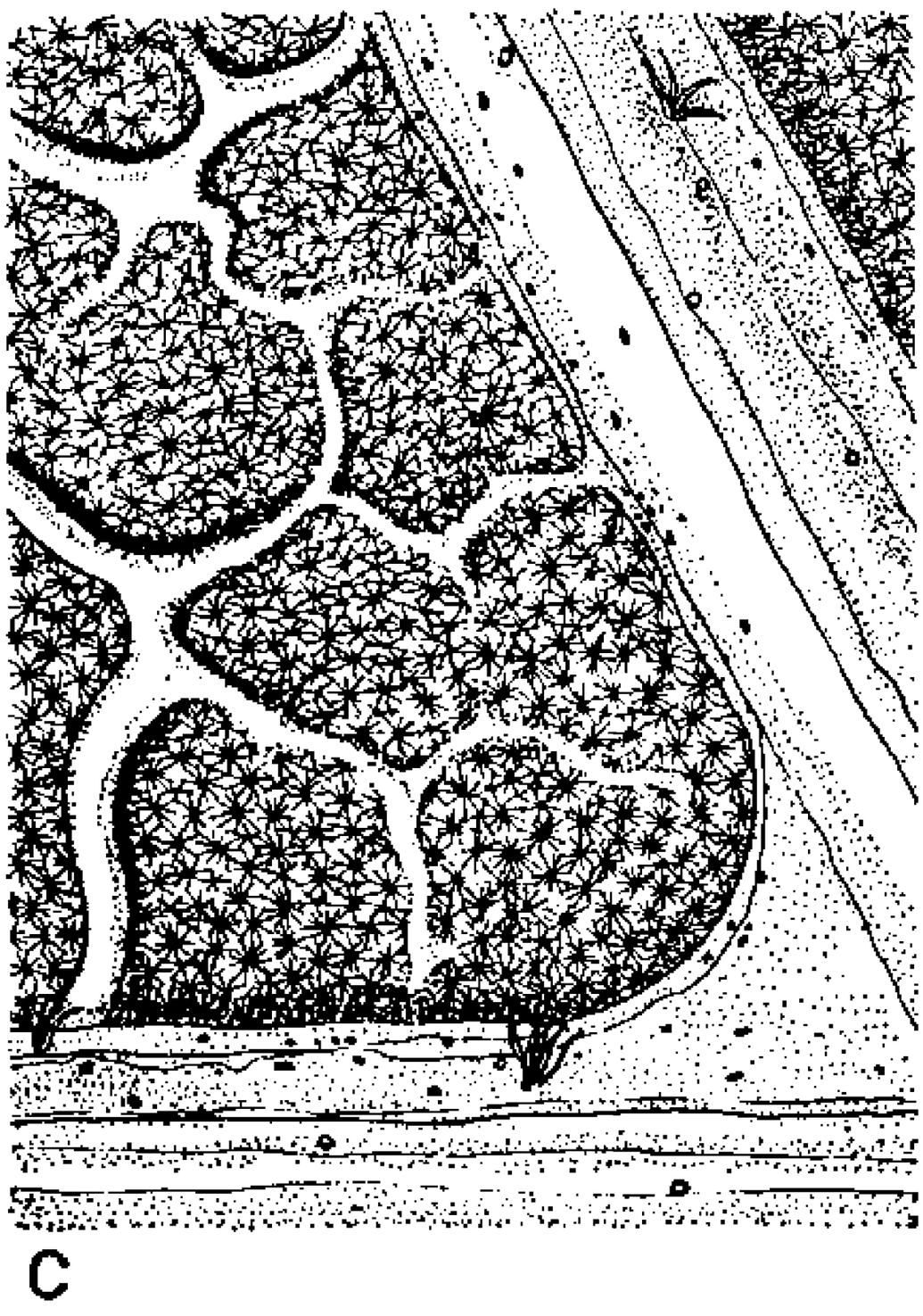
Spruce and Ducke called attention to beauty of this tree in blossom, according to Spruce "one of the prettiest things I have seen."



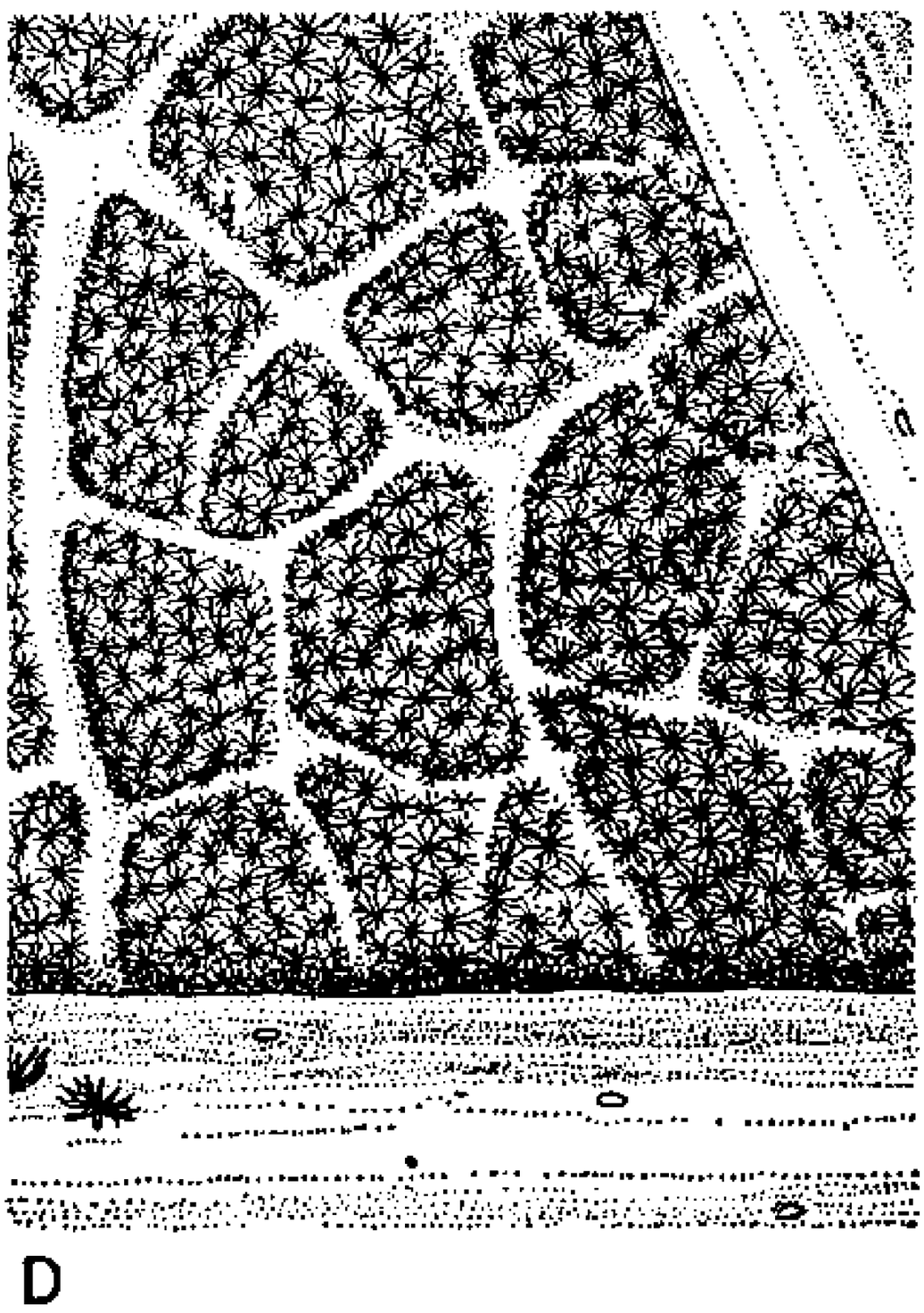
A



B



C



D

FIGURE 19.—A, B, Detail of nervation at the underside of the leaf in: A, *Theobroma speciosum* (Ule 9609); B, *T. cacao* (Cuatr. 7756). C, D, indument on the underside of the leaves in: C, *T. glaucum* (Bart. & Holl. 74); D, *T. bernouillii* subsp. *capilliferum* (Cuatr. 16160). A and B × 2, C and D × 25.

Theobroma speciosum can grow to be 15 m. high, with a few whorls of dichotomous leafy branches near the top of a long branchless stem, which can bear abundant, large, cauline inflorescences. These may form large cushions of showy, blood-red, wine-red, or purplish-red flowers which give off an intense lemon- or orange-skin odor (Ducke). The outer pulp of the seeds is sweet but scentless. It is said to be easy to grow in gardens.

COMMON NAMES.—Cacauí, cacauu. Other recorded names or different ways of spelling are: cacao-y, cacao-u, cacau, cacaohy, cacau-i, cacao-i, cacaoíllo, cacau-rana, cacao-rana, cacao biaro, cupuy, cupuyh, cacao do matta, cupurana, cacao azedo, cacao sacha (Peru), chocolatillo (Bolivia).

USES.—The pulp is eaten by natives. The seeds are used very occasionally to prepare low quality chocolate.

DISTRIBUTION.—This species extends throughout the Amazonian Hylaea except in the northwestern section, from the state of Maranhão at Cururupu to Acre and Madre de Dios in eastern Bolivia and the Ucayali River (Loreto) in Peru. It grows on noninundatable ground in rain forests as well as in not too humid places and it appears also in secondary growth near towns, but it is never of frequent occurrence.

BRAZIL: "Brasil. Herb-Lusit," "*Herrania paraensis*," "*Theobroma subincanum* Mart.?," *Geoffroy* [St. Hilaire?] s.n. (P). "Polyadelphia Decandria Theobroma speciosa foliis acuminatis integerrimis subtus tomentosis. Flores purpurei. Habitat in Para Brasilia," "*Theobroma speciosa* (W.) Spreng. Bernoulli determ." *Hoffmannsegg*, W. (B, Herb. Willdenow 3680, holotypus). "Ex herb. Linn. *Theobroma speciosa* Brasil Col." *Siber* (B), specimen destroyed (photograph F. M. no. 9640); identical with the type in the Willdenow Herbarium.

PARÁ: Belém, noninundatable forest near city; small tree with dark-red flowers on trunk, "cacaohy," IX 1936, *Ducke* 281 (A, F, K, MO, NY, S, US). Belém, Jardim Botánico do Museo Goeldi; slender tree, inflorescence on trunk, petals dark red, sepals reddish stained, fruit 5-parted, yellow when ripe, "cacau-i," 26 VIII 1942, *Archer* 7619 (IAN, K, NY, USDA). Ibidem, slender tree, "cacao-i," 29 X 1942, *Archer* 7721 (IAN, USDA). Ibidem, small tree, flowers deep crimson, calyx light pink, leaves deep green above, gray green beneath, cultivated, 15 VII 1946, *Schultes & Silva* 8066 (GH). Ibidem, 19 X 1945, *Pires & Black* 695 (IAN), 740 (IAN). Bragança, "cacao claro," XII 1899, *Huber* 1748 (G, MG). Taperinha, at Santarém, secondary forest on elevated land; small tree, red flowers on trunk, "cupuy," *Ginzberger* 802 (WU). Rio Curuauna, Cachoeira do Portao, region of Planalto de Santarém, rain forest, XI 1954, *Frões* 31414 (IAN). Santarém, hills, "cacao do Matto," *Jobert* 903 (P). Near Obidos, Prov. Pará, XII 1849, *Spruce* s.n. (K, Herbarium Hookerianum 1867). Forest near Obidos, XII 1845; slender tree 40–50 ft., flowers on the naked stem, leaves on the top of the tree only, "cacao-rana," *Spruce* 456 (K, Herbarium Benthamianum, 1854, P, BM). Monte Alegre, region of Colonia da Mulata, elevated ground; tree 8m., red flowers, 28 IX 1953, *Frões* 30432 (IAN). Breves, VII 1956, *Pires, Frões, & Silva* 5886 (IAN). Belterra, capoeira, way to Pindobal; tree 7 m., red flowers on trunk with lemon scent, leaves white beneath, 31 XI 1947, *Black* 47–1889 (IAN, NY). Region Tapajós, Bõa Vista firm land; tree 4 m.,

10 cm. [diam.], flower color wine, fruits on the trunk, eaten by Indians, "cupuhy," 30 VIII 1932, *Capucho* 397 (IAN, F). Tapajós, Vila Braga; tree, dark-red flowers borne on the trunk, 27 X 1908, *Snethlage* 10044/b (MG). Upper Cupary River, plateau between the Xingú and Tapajós Rivers; tree 25 ft. high, 2 inches in diam. breast high, in high forest, flowers red on old wood, "cacaorana," IX 1931, *Krukoff* 1117 (A, G, K, NY, P). Ibidem; tree near river shore; flowers dark red, borne on large branchlets; wood used for "farinha" containers (to keep it dry), "cacaorana," *Krukoff* 1080 (A, BM, G, K, MICH, MO, NY, S, U). Rio Cumina-mirim, forests at NE; ripe fruit yellow, only on trunk, "cacaorana," 16 XII 1906, *Ducke* 7975 (MG). Oriximina, Las Trombetas, "cacao rana," flowers only on trunk, 8 XII 1906, *Ducke* 7884 (G, MG).

AMAZONAS: Near Barra, Prov. Rio Negro, Aug. 1851; forests south of Rio Negro; tree 20 feet, straight with a whorl of branches only at summit, which are twice or thrice dichot[omous]; trunk almost completely clad with flowers, which have fine odor of bruised orange leaves; petals cucullate, claw pink, white limb dull crimson with dark veins. The subul[ate] processes blood red; one of the prettiest things I have seen, *Spruce* 1737 type of *Theobroma quinquenervium* Bernoulli (M, holotype, Photo F. M. 40703; isotypes: BM, E, F, G, GH, GOET, K, LD, LE, OXF, P, WU) (Photo F. M. 9639 from Berlin). Rio Marmellos, near mouth; flower deep salmon red, buds dark crimson, bark smooth, light gray white, leaves pale dull beneath, dark green glossy above, branches umbelliform at top, trunk 6–7 inches in diameter at base, 20–22 feet tall, inflorescences 200-flowered; seeds give low grade chocolate, 2–12 VIII 1945, "cacao azedo," *Schultes & Cordeiro* 6507 (AMES, F, IAN). Amazonas, Rio Capitare, municipality of Codajas, elevated ground, high forest; tree 8 m., red flowers, 3 IX 1950, *Frões* 26526 (IAN). Manaos, Estrada do Aleixo; tree 5 m., fruits on trunk, 14 V 1953, *Frões* 30180 (IAN).

GUAPORE: Porto Velho, Estrada de Rodagem, Km 8, Viana, disturbed forest, elevated land; small tree, red flowers with lemon scent, 31 V 1952, *Black, Cordeiro, & Francisco* 52-14655 (IAN).

GOIAS: Margen do Rio Araguaia; tree 4 m., red flowers, 13 VI 1953, *Frões* 29732.

ACRE (TERRITORIO DEL): Rio Acre, Seringal San Francisco; tree 5–20 m., black-purplish flowers on stem, VII 1911, *Ule* 9609 (G, K, L), *Ule* 14448 (MG). Near mouth of Rio Macauhan (tributary of Rio Yaco), Lat. 9°20′ S., Long. 69° W., on firm land; tree 40 feet high, 5 VIII 1933, *Krukoff* 5295 (A, F, K, LE, M, MICH, MO, NY, S, U, UC, US).

RIO DE JANEIRO: Quinta de Sao Christovas, 10 I 1876, *Glaziou* 9633 (C, P). Jardim Botánico, flowers on trunk and main branches, V 1944, *Camargo* 2395 (IAN).

PERU: LORETO: Region of the middle Ucayali, rain forest, Yarina Cocha, 155 m. alt., elevated ground; tree 12–15 m., 35 cm. thick, the first branch at 7 m. from ground, flowers with strong anise scent, sepals red crimson, petals dark crimson-striped on white ground, stamens less crimson than petals, pistil whitish, "cacao sacha," 22 IX 1925, *Tessmann* 5398 (G, M, S). Rio Ucayali, Paca, 21 VII 1898, *Huber* 1567 (Holotype of var. *coriaceum* Huber, MG; isotypes BM, US), (photo F. M. No. 1567). 40 km. south of Pucallpa, rain forest of the Amazon basin virgin rain forest on loamy sand, *Ellenberg* 2565 (U).

BOLIVIA: Km. 7 on road Guayaramerin-Cochuela Esperanza, [Prov. Vaca Diez, Depto. Beni], 120 m. alt., "chocolatillo"; growing wild in rain forest; flowers wine red, borne on cushions along the whole, rather slender trunk, dichotomous branches slender, pendent, fruits small. I have seen also a specimen in Brasilia, where it is called "cacau-i"; 9 IX 1954, *Patiño* s.n. (GH). Junction of Rivero

Beni and Madre de Dios; pulp edible and equal to that of *T. cacao*, seeds white, not used, VIII 1886, *Rusby* 654 (BM, E, F, G, GH, K, LE, MICH, MO, NY, P, US). Unduavi, 10,000 ft., *Rusby* 647 (US).

4. **Theobroma velutinum** Benoist, Bull. Mus. Hist. Nat. Paris **27**: 113. 1921. FIGURES 3, 12, 13, 14, 16, 18; MAP 1.

Herrania guianensis Sagot ex Schum. in Mart. Fl. Bras. **12**(3): 75. 1886.
Theobroma speciosum sensu Uittien in Pulle, Fl. Surinam **3**: 45. 1932.
Theobroma sp. 4, Uittien in Pulle, Fl. Surinam **3**: 46. 1932.
Herrania guyanensis Sagot in Chevalier, Rev. Int. Bot. Appl. **26**: 275. 1946 (as synonym).

TYPE.—*Benoist* 516, French Guiana.

Branches terete, subcinereous, densely appressed stellate-tomentose or becoming glabrate, grayish brownish; branchlets densely tomentose.

Leaves large, firmly coriaceous; petiole robust, subterete, densely appressed cinereous-tomentose, when old transversely rimose, 12–14 mm. long; lamina oblong-ovate or ovate-oblong, broadly rounded and more or less asymmetrical at base, suddenly narrowed and long-acuminate at apex, the margin slightly revolute, entire or very slightly sinuose, 28–40 cm. long, 16–21 cm. broad, including the acumen, this about 3 cm. long, pale olivaceous above (when dry), subnitidous, slightly and broadly bullate, glabrous except for the midrib, this sparsely pilose towards the base, the costa and secondary nerves thin, the tertiary nerves filiform, the minor veins less apparent or obsolete, softly velutinous beneath, ochraceous-cinereous, the midrib very prominent, the 5–7 pairs of secondary nerves prominent, ascending, curved near the margin and anastomosing, the longer pair stronger, more separated from the next, the transverse tertiary nerves prominent, others broadly reticulate, prominulous, the lesser veins forming a minute, prominulous reticulum, the minor reticulum and its areoles densely tomentose with minute, white, dense, subappressed, stellate hairs, the other nerves and the sides of the midrib covered with abundant, long, delicate, stellate hairs with long, thin, spreading rays.

Inflorescences many-flowered, borne on lignose, tuberculate branches on the trunk, the panicles fasciculate, ramose from the bases, 5–12 cm. long, the branchlets moderately thin, cinereous, hirtellous-tomentellous with thin, mediocre, stellate hairs, the terminal (peduncles) thinner with 2 or 3 deciduous bracteoles at the end; pedicels slender, 6–18 mm. long; bracteoles at the joints minutely lanceolate, hirtellous, deciduous, 1–1.5 mm. long; sepals thick-membranaceous, spreading, shortly united at base, lanceolate-oblong, subacute, glandular at base, otherwise glabrous inside, with fine stellate hairs copious on the outside, the margin minutely tomentulose, about 10 mm. long and 3.5–4.5 mm. broad, usually one free, the others united by pairs. Petal-hoods 6–7.2 mm. long, about 3 mm. broad, membranaceous, obovate-oblong, cucullate-rounded at apex, 3-nervate, the median

vein furcate, outside sparsely, weakly pilose, the end auriculate-emarginate, articulate to the erect lamina, 6–7.2 mm. long, about 3 mm. wide; petal-lamina sessile, subtrapezoid, subtruncate or often slightly sinuate or 3-toothed at apex, abruptly narrowed into a short claw at base, moderately thick, but venation conspicuous by transmitted light, glabrous, somewhat rugulose-papillose toward the base, 5 mm. long, 6–6.5 mm. broad; androecium-tube about 2 mm. long and 2.4 mm. broad, minutely papillose-pilose; staminodes purplish red, lanceolate-subulate, thick, suddenly narrowed into a short, crisp, acute acumen at apex, minutely muricate-pilose, about 6 mm. long and 1.5 mm. wide; filaments triantheriferous, 2.5 mm. long; ovary ovoid-oblong, about 2.2 mm. long, 5-ridged, tomentose; styles 5, connivent, adherent, easily separable, glabrous, 2 mm. long.

Fruits ellipsoid, densely and softly stellate-pilose-velutinous, 5-costate, the ribs thick, very prominent, the surface smooth, 8.2–9 cm. long, 6–6.3 cm. broad, the pericarp 3–4 mm. thick; seeds usually 25–30 in each pod.

This species is closely related to *T. speciosum*, having very similar flowers and leaf outline. However, *T. velutinum* is very different on account of the structure of the fruits and the indument. The ellipsoid, densely velvety fruits have 5 longitudinal, very prominent, typical ribs, a character only known in this species. The leaves beneath have a soft, velvety indument of long, thin, stellate or dendroid, more or less densely distributed hairs on the whole nervation and a lower layer of a short, dense tomentum of minute, stellate, intricate hairs covering the areoles and the minor reticulate veins. Also, the terminal branches are densely tomentose and the inflorescence branchlets and pedicels have copious, rather long, fine hairs.

Theobroma velutinum is only known from French Guiana and the neighboring Dutch side of Maroni River valley. The excellent foliage and fruiting collections made by Benoist and recent other collections by members of French and Dutch Forest Services, especially the flowering specimens B. B. S. 1161, have facilitated a complete description of the species. Its inflorescences are cauline, many-flowered, and often showy, like those of *T. speciosum*. The Sagot collection 1206, preserved in several herbaria and consisting only of large inflorescences, belongs to this species. Sagot named it *Herrania guianensis* and left an accurate unpublished description which is attached to the specimens in Paris.

COMMON NAMES.—Bouchi-cacao, cacao sauvage, cacao.

USES.—Reported to yield edible seeds comparable to cacao but no information is given on the quality of the product.

DISTRIBUTION.—French and Dutch Guiana in the valley of Maroni River.

SURINAM: 4 X 1950, B. W. 1161 (U). Placer l'Arver, 31 X 1918, *Gonggryp* 4108 (U). Flur of Marowyne, Reu naar L. etwa en Tupanahoni, No. 47 Marowyne, 26 XI 1918, *Gonggryp* 4127 (U). Flur Tapanahoni, III 1922, No. 33 Tapanahoni, *Gonggryp* 4148 (U).

FRENCH GUIANA: A 1 kilometre plus ou moins du camp de transportés de Charvein, le long de chemin qui conduit a la leproserie de l'Acarouany, 8 I 1914, *Benoist* 516 (P, holotype, foliage and fruits). Crique Serpent, rive droit à 1 kilometre de la crique terrain en pente, à proximité immediate d'un ravin rocheuse; arbuste ayant été repéré au moment de sa fructification en février 1951; abattu depuis et pourvu de rejets de 3 m. de haut; produit de gousses côtées contenant des grains comestibles, "bouchi cacao" (*Paramaka*), 12 XII 1952, BAFOG 136M (P). Placean No. 2, Carreau No. 3, route de mana, terrain sablonneaux; fruits jaunâtres, gousses ovoides de 7 à 8 x 10 à 12 cms. déhiscents, sparses sur le tronc de l'arbre, "bouchi cacao," "cacao sauvage," 19 III 1956, BAFOG 7386 (P). Karouany, 1858, "Flores atropurpurei suaveolentes, fructus ovatus, pentagonus, breviter tomentosus cacao sativa paulo minor, folia non vidi, flores e ligno prodeunter, "cacao," "*Herrania guianensis* Sagot," 1858, *Sagot* 1206 (BM, G, K, P, U, WU); type of *Herrania guianensis* Sagot (only inflorescences and flowers in all the specimens; a long and accurate description made "in vivo" by Sagot is attached to the specimens at Paris).

5. **Theobroma glaucum** Karst.

FIGURES 2, 10, 14, 16, 17, 19; MAP 5; PLATE 4

Theobroma glaucum Karst., Linnaea 28:447. 1856; Triana & Planch. (1862); Bernoulli (1869) 10; Jumelle (1899) 34; De Wildeman (1902) 97; Chevalier (1946) 277.

Theobroma calodesmis Diels, Notizbl. Bot. Gart. Berlin 14:336. 1939; Baker, Cope & al. (1954), *figs. 10, 12;* Cuatrecasas (1956) 655; León (1960) 314, 317, *fig.*

TYPES: *Karsten* s.n. Colombia, San Martín. *Schultze-Rhonhof* 2312, Ecuador, Papayacu (of *T. calodesmis*, formerly in Berlin).

Tree 8–15 m. high; stem up to 30 cm. in diameter, with grayish, inside reddish bark and white wood; sympodial growth by lateral, subterminal, upright shoots; primary branches ternate, regularly dichotomous, spreading, deciduous when old, the terminal minutely stellate-pulverulent with additional simple, spreading hairs, soon glabrate, smooth, rather shining, dark brown or somewhat purplish; stipules linear-subulate, 4–5 mm. long, sparsely stellate-pilose, soon deciduous.

Leaves coriaceous, rather rigid, distichous; petiole robust, densely ferruginous or brownish tomentose with stellate hairs, transversely rimose when dry, 0.8–1.8 cm. long; blades oblong-ovate or ovate-oblong, broad in the lower third, obtusely cuneate at base, narrowed near the apex, prolonged with a long slender appendage, the margin entire or slightly sinuate and slightly revolute, 16–36 cm. long, 7–13 cm. broad, the acumen 2–3.5 mm. long, shining above, green, pale olivaceous brown when dry, apparently glabrous but with sparse mediocre stellate hairs and callose scar-dots on the nerves, the costa and secondary nerves prominently filiform, the others slender, more or

less noticeable, somewhat cinereous beneath, glaucous or pale rosy, with a glabrous aspect but the rather shining, pale brownish principal nerves sparsely callose-dotted and with very scarce ferruginous, stellate hairs, the small veins glabrous, the areoles covered with a very appressed microscopic tomentum of minute, white, stellate hairs, the costa very prominent, the 4 or 5 pairs of secondary nerves prominent, the basal one at an acute angle (remote from the margin), ascending, the others curved-ascending, near the margin becoming slender, decurrent, curving, anastomosing, the cross-tertiary nerves thinner, prominent, 3–10 mm. distant from each other, the lesser veins minutely prominulous-reticulate; leaves of the orthotropic spreading-puberulous branches long-petiolate, with the blades attenuate-cuneate at base, the lower pair of nerves very close to the margin, the petiole slender, 3.5–4 cm. long.

Inflorescences on the trunk, often many-flowered and showy, with up to 200 flowers, the base woody-tuberculate; branches 3-many, mediocre, 4–6 cm. long, furcate-ramose from near the base, the branchlets fastigiate, angulate, rather rigid, ferruginous-tomentose, the terminal (peduncles) moderately robust, 3–4 mm. long, articulate to pedicel, this 5–15 mm. long, striolate, slightly thicker, tomentellous, the subtending bracteoles minute, ovate-lanceolate, about 1 mm. long, very soon deciduous; buds ovoid, round at base, subacute at top, densely stellate-tomentose, 8–9 mm. long, about 6 mm. broad.

Calyx umbilicate; sepals thick, lanceolate-oblong, acute, inflexed at apex, connate for 2 mm. at base, densely and appressed stellate-tomentose outside, within minutely, whitish stellate-pilose near the margin and glandular at base, otherwise subglabrous, 12–13 mm. long, 3.5–4 mm. broad, curved-spreading after anthesis.

Petal-hoods light red, oblong-obovate, shortly unguiculate at base, rounded cucullate at apex, the end emarginate, biauriculate, articulate to the lamina, the 3-nerves prominent inside, thin, with spreading, weak, sparse hairs outside, 5–6 mm. long, 2.5–3 mm. broad; petal-lamina red crimson, thick, minutely rugose, and more or less translucid-venulose, glabrous, suborbicular or broadly elliptic, subsessile at base, abruptly contracted into a short claw, minutely sinuate at margin, 5.5–7 mm. long, 5–6.5 mm. broad, the claw 0.5 mm. long.

Staminal tube about 2 mm. high and 2.5 mm. in diameter; staminodes red crimson, erect, lanceolate-subulate, acute at apex, fleshy, minutely muricate-pilose, 10–12 mm. long, 1.4–1.8 mm. wide above base; filaments flexuose, 2.5–3 mm. long, glabrous, shortly 2 or 3 furcate at apex, bearing 2 or 3 anthers, the loculi ellipsoid, convergent, 0.5–0.6 mm. long; ovary oblong, about 2 mm. long, 5-ridged and sulcate, hirsute-tomentose; styles connivent, 3 mm. long, united only at base.

Fruits ellipsoid-oblong, obtusely pentagonal, broad and umbilicate at base, more or less attenuate and subacute at apex, the pericarp 1 cm. thick, coriaceous, rigid, densely and minutely velutinous-tomentose, bluish greenish, 11–13 cm. long, 5.5–9 cm. broad; seeds 2–2.3 x 1.2–1.4 x 0.9 cm.; fruiting peduncle robust, 7–8 cm. long, 1–1.5 cm. thick; germination epigeous.

According to Baker and his associates the cotyledons are white and the pulp is pale orange and of a very sweet taste.

The type collection of *T. calodesmis* was destroyed during the war in Berlin; it was collected by Hertha Schultze-Rhonhof near Papayacu at about 200 m. altitude on the Bonanza River, a tributary of the Pastaza River in eastern Ecuador. The description given by Diels makes it possible to identify his species perfectly with several Amazonian collections from nearby regions of Colombia, Peru, and Brazil. The sterile type specimen of *Theobroma glaucum*, collected on the Llanos de San Martín, agrees perfectly with a specimen that is almost a topotype, collected by Philipson, Idrobo, and Fernández in the foothills of the Sierra Macarena, Intendencia del Meta. I have no doubt that all these collections represent the same species, which extends from the upper Orinocia to upper Amazon basin on both sides of the great river.

Diels did not see fruits but gave an accurate description of the foliage and flowers; he related his species to *T. speciosum* on account of the texture and tomentum of the leaves, and also to *T. bernouillii*, but he says that the leaves are broader, the inflorescences larger, the flowers larger, and the staminodes longer.

COMMON NAMES.—Cacao de monte, cacao silvestre, chucú (Rio Papayacu [*Schultze-Ronhof*]), "bicco" Río Apaporis).

USES.—According to Karsten, the seeds are used as cacao by the natives, being very similar to the true cacao. Schultze-Rhonhof gives the indigenous name "chucú" for the fruit which, according to her, is very much appreciated by the natives.

DISTRIBUTION.—This species grows in the upper Amazon basin (northwestern section) along the rivers Caquetá, Caguán, Putumayo, Vaupés, Guainía, Inírida, and Apaporis in Colombia and along the Colombian boundary with Ecuador, Peru, and in western Brazilian Amazonas; at the northern end of its range it enters the Orinoco basin into the Meta drainage in Colombia.

It grows in the humid rain forests from the lower level of the great rivers to an altitude of 450 m. in forested hills.

COLOMBIA: META: Villavicencio, Llanos de San Martín, *Karsten*, s.n. (WU, holotype) (photo F. M. 32205). Sierra Macarena, Caño Yerly, 450 m., dense, humid forest; unbranched tree 10 m. high, bunches of cauliflorous fruits green, 24 XI 1949, *Philipson, Idrobo, & Fernández* 1552 (BM, COL, US).

PUTUMAYO: Vicinity of Mocoa; tree 6–7 m., growing fully exposed in meadow, trunk 23 cm. thick at base, branched inflorescence (dead) borne on trunk and branches, pod broadly pentagonal with 5 very shallow furrows, 13 cm. long, 9 cm. diam., blue green in colour, fruit pedicel 8 cm. long, 1.5 cm. diam., with abscission ring 1.5 cm. from pod base, in colour pale green with fine white hairs, 17 III 1953, *Holliday & Cope* T/79 (COL, TRIN, US). Ibidem; sterile tree 15 m. in forest, undoubtedly similar to T/79, shoots from below jorquette, *Holliday & Cope* T/79A (COL, TRIN, US). Río Leguízamo, Laguna Primavera, 3 IV 1953; tall tree 15 m., obviously cauliflorous, *Holliday & Cope* T/94 (COL, TRIN, US). Río Leguízamo; tree 16 m., with old trunk inflorescences, no flowers or fruits, 5 IV 1953, *Holliday & Cope* T/96 (COL, TRIN, US).

CAQUETÁ: Rio Caguán, Camp 4; branched tree 10 m., found in good flowering condition, flowers in large inflorescences on trunk, 27 IV 1953, *Holliday & Cope* T/118 (COL, TRIN, U, US). Ibidem; tree 15 m., branched, two immature pods, on sloping land near T/114, 26 IV 1953, *Holliday & Cope* T/115 (TRIN, US).

VAUPÉS: Río Guainía, near Victorino, river level; tree without flowers or fruit but with stipules; said by the local Indians to be a type of cacao with small smooth pods, native in the forest, 3 II 1952, *R. E. D. Baker* 37 (TRIN, US). Río Inírida, Santa Rosa, 300 m.; tree 15 m., trunk about 30 cm. in diameter, bark greenish, cortex light red, wood white, no terminal growing point, young shoots arising from below jorquette, cauliflorous, pod surface 10-ridged, also with transverse ridges, fruit pedicel about 4 cm. long with abscission layer 3 cm. from trunk, 25 I 1953, *Bartley & Holliday* T/69 (COL, TRIN, US). Left bank of Río Inírida, San Joaquín, 200 m. from river bank, 300 m. alt.; tree 10 m., trunk base 15–20 cm. in diameter, one dead cymose inflorescence seen, 28 I 1953, *Bartley & Holliday* T/70 (COL, TRIN, US). Río Inírida, Río Papunana; tree 10 m., trunk about 30 cm. in diam., bluish gray in appearance, bark red, wood white, three branches at each jorquette, dichotomous branch habit, inflorescences on upper part of trunk, 18 II 1953, *Bartley & Holliday* T/74 (COL, TRIN, U, US).

AMAZONAS: Río Apaporis, Jinogojé, river level; tree 40–50 ft., 8″–9″ diameter at base, jorquettes of 3 branches, subsequent growth from below, ultimate branches repeatedly bifurcating, flowers in large clusters, sepals, ligules, and staminodes dark crimson, 8 IX 1952, *Baker & Cope* 11 (COL, F, TRIN, US). Ibidem (boundary Amazonas-Vaupés) between Río Piraparaná and Río Popeyaca, 250 m., Caño Unguyá; tree 8 m., calyx red, petals white, purplish red at apex, "bicco," 3–11 XI 1952, *García-Barriga* 14380 (COL, US).

BRAZIL: AMAZONAS: Sao Paulo de Olivença, on elevated land; tree 10 m., 12 cm. [in diam.], "cacau azul," 18 V 1945, *Frões* 20942 (NY). Cidade Fonte Bôa ("introduzida pelos indios do Japurá"); tree 10–12 m., 12–15 cm. diam., "cacau azul," "cachu azul," 4 IV 1945, *Frões* 20645 (K, USDA). B. constant, tree 10 m., "cacau azul," 9 V 1945, *Frões* 20885 (NY). Macacacain, Rio Jutahi, Barreira Branca; tree 15–25 feet, small, main branches in whorls of 3, each bifid, 31 I 1875, *Traill* 62 (GH, K, P).

6. Theobroma bernouillii Pittier

FIGURES 2, 6, 7, 15, 16, 17, 19; MAP 4; PLATE 5

Theobroma bernouillii Pittier, Repert. Sp. Nov. Fedde **13**:319. 1914. Chevalier (1946) **26**: 277; León (1960) 314.

Theobroma asclepiadiflorum Schery, Ann. Mo. Bot. Gard. **29**:360. 1942.

Theobroma capilliferum Cuatr. Rev. Acad. Colomb. Cienc. **6**:547, *figs. 3a, 4a, pl. 34*. 1946.

TYPES.—*Pittier* 4105, Panama. *Wedel* 1535, Panama (of *T. asclepiadiflorum*). *Cuatrecasas* 16160, Colombia, Pacific coast (of *T. capilliferum*).

Tree 15–20 m. high; stem up to 25 cm. in diameter, with grayish-brown, rugulose bark 5 mm. thick and yellowish-white wood; sympodial growth by lateral, subterminal, upright shoots; primary branches ternate, grayish brown or blackish brown, dichotomous, the oldest falling off, leaving the stem naked, the terminal stem leafy, terete, dark brown, minutely, subappressed tomentulose, when older puberulous or glabrate; stipules linear-oblong, attenuate at apex, acute, pubescent, about 8 mm. long, 2.5 mm. wide.

Leaves coriaceous, more or less rigid, entire; petiole thick, 4–12 mm. long, terete, densely and minutely tomentulose, transverse rimose when dry; blades rather asymmetrically ovate, ovate-oblong, or elliptic-oblong, obtusely cuneate-attenuate and mostly very asymmetrical at base, triplinerved, narrowed toward the apex, ending in a long, linear, acute tip, the margin entire or very slightly sinuate, slightly revolute, 13–30 cm. long, 5.5–18 cm. broad, including the acumen, this 1.5–6 cm. long, 2–4 mm. broad, green or pale brownish above when dry, shining, the main nerves filiform, prominent, the others reticulate, slightly prominulous, pale greenish ochraceous or ashy beneath, apparently glabrous but the tawny shining veins with very sparsely minute stellate hairs and the areolae covered with very appressed, white tomentum of smaller, microscopic, entangled stellate hairs, the midrib and 5–7 secondary nerves on each side very prominent, the basal pair acutely ascending, the others distally curved-ascending, decurrent and anastomosing near the margin, the transverse tertiary nerves thin but prominent, the minor veins prominulous, minutely reticulate.

Inflorescences on the main trunk usually many-flowered, borne on short, tuberculate, woody branches, the panicles abundant, 4–10 cm. long, spreading, bristly, the axes slender (0.4–1.5 mm. thick), rigid, striolate, stellate-tomentose in the upper third or rarely from the base, cymose-bifurcate, corymbiform, the branchlets rigid, erect at acute angle; peduncles (ultimate branchlets) capillary, tomentulose, 2–20 mm. long, 3-bracteolate at apex; bracteoles narrowly linear, 1–2 mm. long, very soon deciduous; pedicels thicker than the peduncles, about 5–20 mm. long at anthesis, minutely stellate-tomentellous like the branchlets; buds ovoid, densely and shortly tomentose.

Flowers crimson; sepals moderately thick, lanceolate-oblong, rather acute, shortly united at base, often first temporarily united in pairs but separated later, 8–10 mm. long, 3 mm. wide, reddish, with sparse slender, flexuous, sericeous hairs inside, ferruginous, rugulose, and

stellate-tomentose outside, minutely tomentulose at the margin inside, with thick, glandular hairs crowded at the insertion at base; petal-hood red, oblong-obovate, rounded-cucullate at apex, narrowed at base, 3-nerved, prominent inside, hirtellous pubescent outside, 4–5 mm. long, about 2 mm. wide, at base 0.6 mm. wide; petal-lamina crimson, sessile, shortly unguiculate-articulate, moderately thick, rugulose, glabrous, orbicular or suboricular or elliptic, minutely crenulate, 2.5–4 mm. long, 3–4 mm. broad; staminal tube about 1.5–2 mm. high; staminodes 6–9 mm. long, erect in bud, purplish red, sublanceolate-linear-subulate, thick, suddenly narrowed toward the apex, covered with minute, spreading, acute, conical trichomes; fertile filaments glabrous, flexuous, about 2.5 mm. long, 2-antheriferous; ovary 5-sulcate-costate, tomentose, 1.2 mm. high; styles five, 2 mm. long, adherent into a column but separable.

Fruit 15–20 (12–25) cm. long, 6–7.5 (5.2–8) cm. broad, ellipsoid-oblong, more or less prismatic, obtusely 5-angulate, abruptly narrowed subacute or subobtuse at apex, umbilicate at base, more or less constricted near the base or not; pericarp thick, rigid, coriaceous at maturity, the epicarp and endocarp hard coriaceous, the mesocarp fleshy, shrinking in drying, dull brown, dense velvety-tomentose; seeds compressed-ovoid, 16–22 x 9–14 x 9–11 mm., the testa reddish, papery, the cotyledons white; pulp white, flavored, acidulous; germination epigeous.

This species, as here broadly considered, includes heteromorphic elements described as three species, two of which came from the Atlantic coast of Panamá, and the third from the Pacific coastal region of Colombia. The Colombian population (*T. capilliferum*) is the best known, being represented by several collections with fruits and flowers, showing morphological uniformity throughout its area. The original *T. bernouillii* is known only from flowering material of one collection (the type), which has some minor differences from the Colombian plants in the shape of the leaves and details of flowers. The other described Panamanian species, *T. asclepiadiflorum*, was based on discordant elements collected by von Wedel in Water Valley. Schery wrote: "Although fruiting material of this species is lacking, floral and vegetative characters distinguish it sufficiently to warrant description as a new species." The glabrous branches and leaves of the type specimen, which resemble those of *T. cacao*, do not belong to a *Theobroma;* they belong actually to the Lauraceae. The inflorescences and flowers are similar to those of *T. bernouillii*, type specimens of which were collected by Pittier not very far away. The question about what kind of leaves belong to the described flowers of *T. asclepiadiflorum* is answered by the collection *Wedel* 681 from the same locality, Water Valley; the flowers of this collec-

tion are identical to those of the type of *T. asclepiadiflorum* and the leaves are exactly like those of *T. bernouillii*. There are minor differences between the flowers of these two types, but considering the vicinity of the geographic range of these two populations, it may be safe to consider them mere forms of one species. Fruits from the type locality of *T. bernouillii* have never been collected, but Allan Lucas did collect fruits of *T. asclepiadiflorum* in Water Valley. The flowers of *T. asclepiadiflorum* are almost identical to those of *T. capilliferum*, but the fruits are smoother and not constricted.

In view of these facts, I consider all these Colombian and Panamanian plants to belong to one species; since the three forms are geographically separated the observed differences warrant subspecific recognition.

DISTRIBUTION: Pacific coast and the Chocó region of Colombia and the Atlantic coast of Panama. In the underforest of the tropical rain forest, from sea level and lowland swamps to heavily forested hills about 100 m. altitude.

Key to Subspecies of *Theobroma bernouillii*

1. Leaves broadly ovate or ovate-oblong, very asymmetrical, rigid, 5–12 x 2–6 cm. Petal-lamina orbicular 2.5–3.5 mm. long; petal-hood 4–5 x 2 mm.; staminodes subulate, densely pilosulous, 7–8.5 mm. long; inflorescences long, with thin branches, the peduncles 5–20 mm. long, the pedicels about 10 (5–20) mm. long; fruits obtusely pentagonal with smooth, conspicuous ridges, 12–25 x 5–8 cm., umbilicate constricted above the base.
   6c. subsp. **capilliferum**
1. Leaves oblong-elliptic, slightly asymmetrical, thinner, less rigid.
   2. Staminodes lanceolate, slightly pilose, 5.5–6 mm. long, 1.5–2 mm. broad at base; petal-lamina suborbicular, 3 x 3–4 mm. long; petal-hood 4–5 x 2–2.5 mm.; peduncles 2–5 mm. long; pedicels 5–8 mm. long; fruit unknown.
      6a. subsp. **bernouillii**
   2. Staminodes subulate, densely pilose, 9–10 mm. long, 1.5 mm. broad; petal-lamina elliptic, 4 x 3 mm.; petal-hood 5 x 3 mm.; peduncles 6–12 mm. long; pedicels 10–12 mm. long; fruit oblong, 17 x 7 cm., very slightly pentagonal, attenuate at apex, not contracted at base, with a filiform, impressed, furrow on each inconspicuous ridge.
      6b. subsp. **asclepiadiflorum**

6a. Theobroma bernouillii Pittier subsp. **bernouillii**

DISTRIBUTION.—Atlantic coast of Panama.

PANAMA: Prov. Colón, in forests near Fató, Loma de la Gloria (Nombre de Dios), 10–104 m., 4 VIII 1911, *Pittier* 4105 (US holotype; isotypes BM, BR, C, F, GH, K) (Photo USNH 3199).

Further collections at the type locality are necessary to know the nature of the fruits.

6b. Theobroma bernouillii Pittier subsp. **asclepiadiflorum** (Schery) Cuatr., stat. nov.

Theobroma asclepiadiflorum Schery, Ann. Mo. Bot. Gard. **29**:360. 1942; León (1960) 316, 321, *fig.* (as. *T. bernouillii*).

TYPE.—*Wedel* 1535, second sheet, flowers (MO, lectotype).

DISTRIBUTION.—Atlantic coast of Panama.

PANAMA: Bocas del Toro: Water Valley, vicinity of Chiriquí Lagoon; tree 90 feet, flowers red, 8 XI 1940, *H. von Wedel* 1535 (second sheet MO, lectotype); the first sheet of this collection (MO) belongs to the Lauraceae. Bocas del Toro, Water Valley, 10 IX 1940; tree 80 ft.; flowers maroon red, *H. von Wedel* 681 (MO). Bocas del Toro, Water Valley, V 1949, *Allan Lucas* 1 (F, TURRI).

The fruit of this subspecies is known through one specimen brought by Allan Lucas (TURRI), which is 17 x 7 cm., ellipsoid-oblong, very slightly pentagonal with 5 filiform furrows on the obtuse angles; the surface is slightly rugose due to the drying; the apex is shortly attenuate and the base is subtruncate and umbilicate. The shape differs clearly from that of the fruits of subsp. *capilliferum* and *T. glaucum;* it must be a mutant form geographically isolated.

6c. Theobroma bernouillii Pittier subsp. **capilliferum** (Cuatr.) Cuatr., stat. nov. PLATE 5

Theobroma capilliferum Cuatr. Rev. Acad. Colomb. Cienc. **6**:547, *figs. 3a, 4a, pl. 34.* 1946; Baker, Cope & al. (1954) 13, *figs. 17, 18;* León (1960) 314, 317, *fig.*

TYPE.—*Cuatrecasas* 16160, Colombia, Pacific coast.

COMMON NAMES.—Chocolate de monte, cacao de monte bravo, cacao de monte (Colombia).

USES.—On the Pacific coast of Colombia and in the Chocó area, the fruits are known as wild cacao (chocolate de monte, cacao de monte, cacao de monte bravo). Their white seeds are considered a high quality cacao, but the fruits remain abandoned on the trees, the people not making actual use of them, although monkeys and other animals break or pierce them, sucking the pulp or eating the seeds.

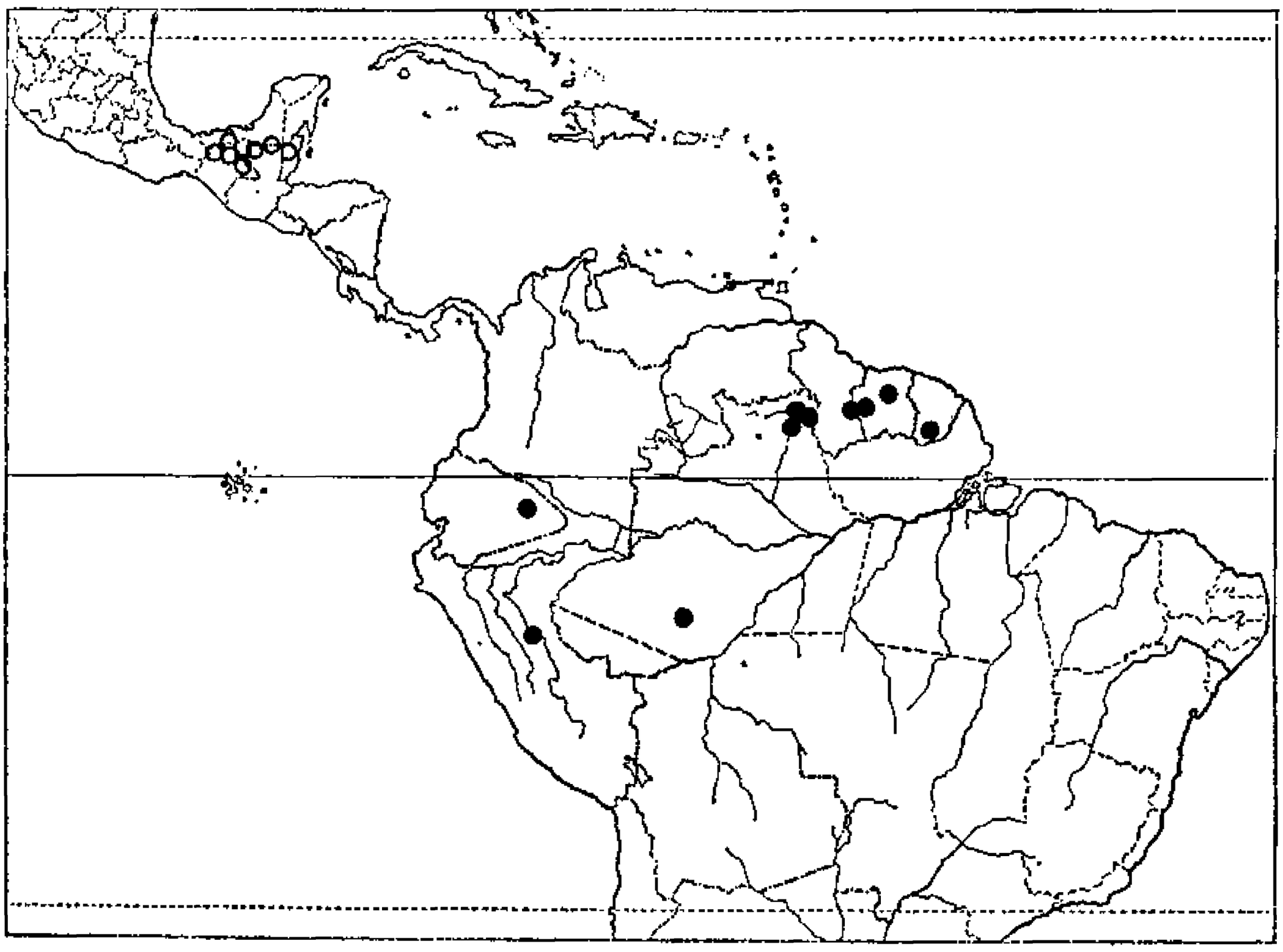
DISTRIBUTION.—Pacific Coast and the Chocó region of Colombia. In the under story of the rain forest, from the lowland swamps next to the mangroves to the forested hills about 100 m. in altitude.

COLOMBIA: EL VALLE: Pacific Coast, Río Yurumanguí, Veneral, swampy rain forest in Quebrada del Zancudo, 5 m. elevation; tree 15 m., 25 cm. diam. at base, bark granulate-rugose, brown or grayish, its section 5 mm. thick, producing abundant mucilage; wood yellowish white; fruits 11–12 x 6 cm. (immature), ellipsoid-prismatic, thick, umbilicate at base, more or less constricted above the base, with 5 furrows or flat sides, and 5 well-marked angles, apex acute and slightly umbilicate, the surface minutely tomentose, greenish ferruginous, peduncles 6–10 cm. long, thick, fruits abundant, hanging on trunk, leaves coriaceous, rigid, green above, pale green beneath, long-tailed (Cuatr. photographs C-2202, 2203), 10 II 1944, *Cuatrecasas* 16160 (VALLE, holotype; isotype, F). Pacific

Coast, Río Cajambre, Barco, forest on hill at the right margin of Quebrada de Agua Clara, 40–100 m. elevation; tree 20 m., stem 25 cm. diam., leaves coriaceous, pale yellowish green above, cinereous beneath, distichous and pendulous, the lower ones larger and thicker, dry inflorescences with thin, long branchlets, fruiting peduncles 8–10 cm. long, 10–12 mm. thick, fruits with 5 furrows and 5 thick angles, surface sinuate-rugose, velvety-tomentose, pale tawny, 16–20 cm. long, 6.5–7.5 cm. broad, umbilicate at both ends, usually constricted above the base, cotyledons whitish, wood yellowish white, 23 IV 1944, *Cuatrecasas* 17034 (F, VALLE). Same locality and date, seedlings, *Cuatrecasas* 17034A (F, VALLE). Río Cajambre, San Isidro, hill forest on left margin of Quebrada de Veneno, about 50 m. alt.; tree 20 m., stem 20 cm. diam., bark yellowish white, leaves coriaceous, rigid, yellowish green above, greenish cinereous beneath, fruits hanging on trunk, 4 V 1944, *Cuatrecasas* 17350 (F, VALLE). Same locality, seedlings, *Cuatrecasas* 17350A (F, VALLE). Río Calima, Caño de la Brea, about 5–10 m. elev.; tree 15–20 m. high, 20–25 cm. diam. at base, crimson flowers in dense cushions on upper portion of trunk only, 29 VI 1943, *Holliday* T/142 (TRIN, US). Río Calima, Estación Agroforestal, about 5–10 m. alt.; tree 12–15 m. in forest clearing, crimson flowers in dense cushions on upper part of trunk only, dry fruit up to 25 x 8 cm., ridged, 29 VI 53, *Holliday* T/145 (TRIN, US).

Chocó: Lloró, young tree, sterile, 4 VIII 1953, *Holliday & Bartley* T/177 (TRIN, US). Ibidem; tree 6 m., *Holliday & Bartley* T/178 (TRIN, US). Río San Juan, Remolino, young tree 2 m., sterile, 1 VIII 53, *Holliday & Bartley* T/172 (TRIN, US).

Nariño: South of Tumaco, in heavy rain forest; tree 10 m., fruits on trunk, olivaceous, 18 X 1955, *Romero Castañeda* 5405 (COL).



Map 6.—Location of known spontaneous, wild, populations of *Theobroma cacao* subsp. *cacao* ○ and subsp. *sphaerocarpum* ● which may be the origin of the present cultivated varieties.

Section 3. Theobroma

Theobroma sect. *Theobroma* FIGURES 3, 4
Theobroma sect. *Cacao* (Aubl.) Bernoulli, Uebers. Art. Theobroma 4. 1869.

Sect. *Eutheobroma* subsect. *Cacao* (Aubl.) Pittier, Rev. Bot. Appl. **10** (110):779. 1930.

Petal-laminas spatulate, long-attenuate stipitate. Petal-hoods 3-nerved. Staminodes linear-subulate, erect in aestivation. Filaments 2-antheriferous. Fruit ovoid-oblong or ellipsoid, more or less pentagonal, the pericarp thick, firmly fleshy glabrous. Cotyledons epigeous at germination. Leaves glabrous or sparsely pilose. Inflorescences on the trunk and on leafy branches. Sympodial growth of stem by orthotropic adventitious, lateral-subterminal shoots. Primary branches in 5's, persisting in age.

TYPE SPECIES.—*Theobroma cacao* L.

7. Theobroma cacao L.

FIGURES 1, 2, 3, 5, 6, 20, 21, 22, 23, 24, 25, 26; MAP 6; PLATE 6

Theobroma cacao L. Sp. Pl. **2**:782. 1753; Syst. Nat. ed. 12, **2**:508. 1767; H. B. K. (1823) 316; Richard (1845) 183 (1845a) 73; Bernoulli (1869) 5, *pl. 1, 2;* Baillon (1884) 792–795, *figs.;* Schumann in Mart. (1886) 72, *pl. 7;* Jumelle (1899) 11, *figs. 1–9;* Preuss (1901), *pls. 1, 2;* De Wildeman (1902) 91, *figs. 16, 18, 20, 21.* 1902; Standley (1923) 805; Ducke (1925) 130; (1940) 268, *pl. 1, fig. 1,* (1954) 11; Fawcett & Rendle (1926) 158–160, *fig. 60;* Uittien in Pulle, Fl. Surinam **3**:45. 1932; Ciferri (1933) 604; Standley (1937) 688; Chevalier (1946) 269–274, *pl. 5;* Standley & Stey. (1949) 423; Holdridge (1950) 4; Addison & Tavares (1951) 25, *pl. 7, pl. 13, fig. 7;* Lemée (1952) 379; Baker, Cope & al. (1954) 9–11; Cuatrecasas (1956) 653; León (1960) 311–313.

Cacao Clusius, Exot. Libr. Dec. 55. 1605; Ray (1688) 1670; Sloane (1696) 134; Tournef. (1700) 660, *pl. 444;* 1700; Merian (1705), *pl. 26;* Sloane (1725) 15, *pl. 160;* Ray (1733) 158; Weinm. (1739) 1–11, *pl. 277, 278;* Geoffr. (1747) 409; Catesb. (1747) 6, *pl. 6;* Blackwell (1739) 373; Hernández (1630) 79, (1946) 908–914.

Amygdalis similis guatimalensis, Avellana mexicana Bauh. Pinax Theat. Bot. 442. 1623.

Arvor cacavifera americana Pluk. Almagest. Bot. 40, *pl. 268.* 1696.

Theobroma foliis integerrimis Linn. Hortus Cliff. 379. 1737.

Cacao guianensis Aubl., Pl. Guian. **2**:683, *pl. 275, figs. 1–15.* 1775, *pro parte (tantum flores).*

Cacao sativa Aubl., Pl. Guian. **2**:689. 1775; Lam. Encycl. Meth. **1**:533, *pl. 635.* 1797.

Cacao minus Gaertn. Fruct. & Sem. 190, *pl. 122.* 1791.

Cacao Theobroma de Tussac. Fl. Antill. **1**:101, *pl. 13.* 1808.

Theobroma integerrima Stokes, Bot. Med. **4**:83. 1812.

Theobroma caribaea Sweet. Hort. Britt. 67. 1830 (nom. nud.)

Theobroma pentagona Bernoulli, Uebers. Art. Theobroma 6–7, *pl. 2.* 1869; Preuss (1901) 199, 255, *pl. 3, 5;* De Wildeman (1902) 94; Standley & Stey. (1949) 427.

Theobroma leiocarpa Bernoulli, *op cit.* 6, *pl. 2;* Standley (1937) 688; Standley & Stey. (1949) 426.

Theobroma Saltzmanniana Bernoulli, *op. cit.* 7, *pl. 2.*
Theobroma Kalagua De Wild., Bull. Herb. Boiss. 7:957, *pl. 11.* 1899 (*tantum folia*, sed lectotypus).
Theobroma sativa (Aubl.) Lign. et Le Bey, Bull. Soc. Linn. Norm. V, 8:263. 1904; Chevalier (1946) 270.
Theobroma sphaerocarpa Chevalier, Veget. Util. Afr. Trop. Fr. 4:12. 1908.
Theobroma sapidum Pittier, Bol. Soc. Venez. Cienc. Nat. 1:183. 1932, *nom. nud.*
Theobroma cacao var. *typica* Ciferri, Monogr. 604. 1933.
Theobroma cacao var. *leiocarpa* (Bernoulli) Ciferri, Monogr. 604. 1933.
Theobroma cacao var. *typica* x *T. cacao* var. *leiocarpa*, Ciferri, 604. 1933.
Theobroma cacao forma *leiocarpum* (Bernoulli) Ducke, Rodriguesia 4:274. 1940.
Theobroma sativa var. *leucosperma* Chevalier, Bull. Inter. Bot. Appliq. 26: 270. 1946.
Theobroma sativa var. *melanosperma* Chevalier, *loc. cit.*
Theobroma cacao subsp. *leiocarpum* (Bernoulli) Cuatr. in Macbr. Fl. Peru, Field Mus. Publ. Bot. 13 (3A):654. 1956.
Theobroma cacao subsp. *sativa* (as (Lam.) Lign. & Le Bey) León in Hardy's Cacao Man. 312. 1960.
Theobroma cacao subsp. *pentagona* (Bernoulli) León, *loc. cit.*

TYPE.—Sloane Herbarium vol. 5, p. 59 (BM, lectotype); Paratype: Tournefort *pl. 444*, fruit-lectotype.

Tree usually 4–8 m. high, rarely taller (up to 20m.), with the growth of the sympodial stem by subterminal, lateral, upright shoots (chupons); primary branching by successive whorls of normally spreading branches; young branchlets terete, grayish green or brownish, densely or sparsely pubescent, with slender, patulous, acute, simple or furcate hairs 0.1–0.3 mm. long, later glabrate, more or less striate, rugulose and sparsely lenticellate; stipules subulate, very acute, 5–14 mm. long, 0.5–1.5 mm. wide at base, pubescent or puberulous, deciduous.

Leaves coriaceous or chartaceous, more or less rigid, alternate, distichous on the normal branches, green; petioles pubescent or tomentose, with simple, acute, slender, rather dense, spreading hairs, thickened pulvinate at the ends, 1.5–2 (1–3) cm. long, on orthotropus stems 3–10 cm. long; blades subobovate-oblong or elliptic-oblong, slightly asymmetrical, rounded or obtuse at base, attenuate and cuspidate at apex, acute or subacute, usually entire or slightly and irregularly sinuate, green above, pale when dry, glabrous except for the pubescent or puberulous midrib, the midrib linear, prominent, the secondary nerves filiform, the fine veins reticulate, often slightly prominent, lighter green beneath, glabrous or with very sparse, minute, simple, furcate or stellate hairs, rarely puberulous, the midrib thick and prominent, the secondary nerves 9–12 each side, prominent, subpatulous, then ascending, near the margin curving, slendering, anastomosing, the tertiary nerves prominent, the minor veins reticulate and prominulous, 15–50 cm. long, 4–15 cm. broad, the acumen 1–2.5 cm. long.

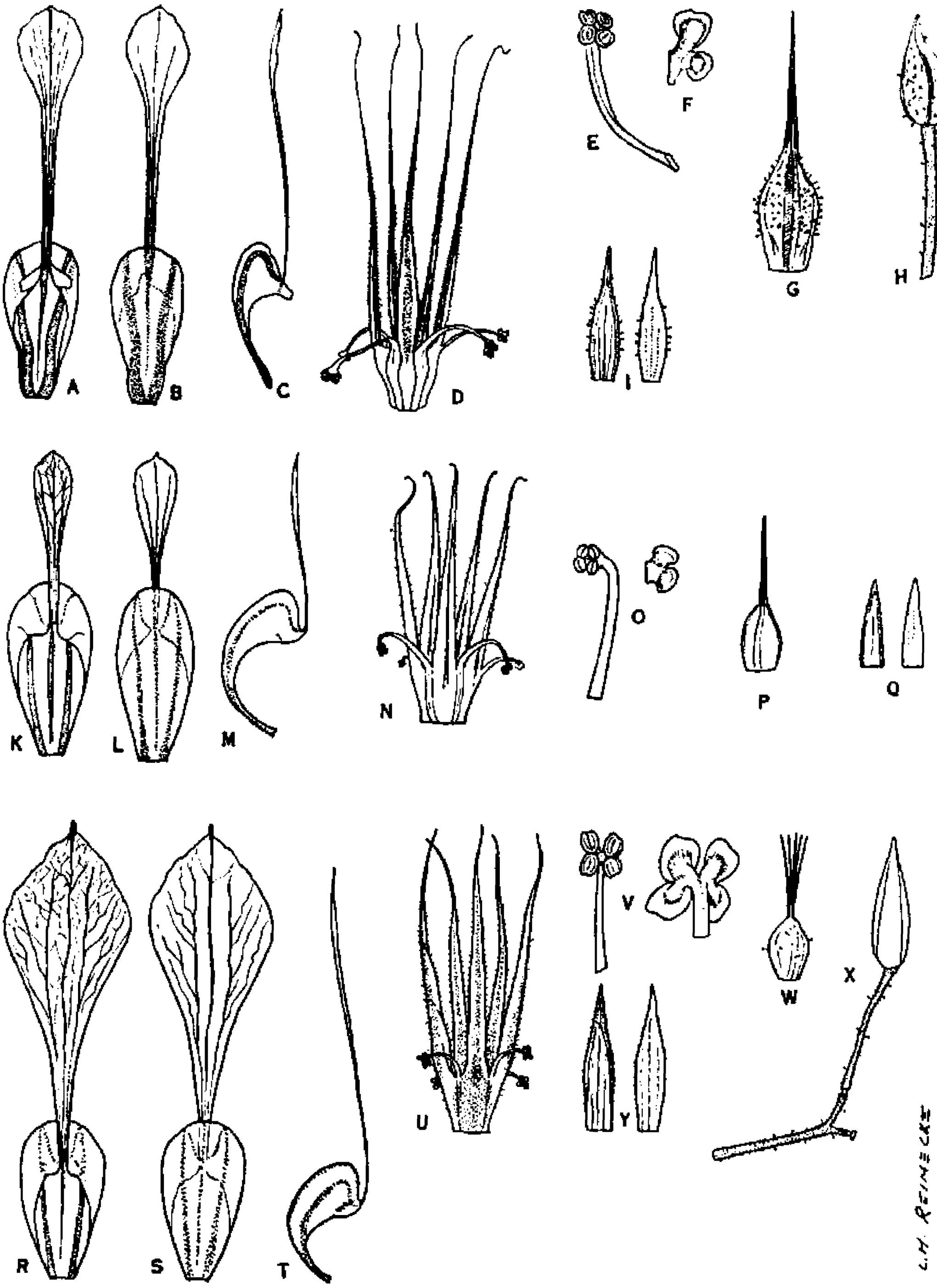


FIGURE 20.—A–I, *Theobroma cacao* subsp. *cacao* fma. *pentagonum* (Cuatr. 26004): A, B, C, petal from inside, outside and laterally, × 5; D, androecium, × 5; E, stamen, × 10; F, anther, × 20; G, pistil, × 10; H, bud, × 2; I, sepal from inside and outside, × 2. K–Q, *T. cacao* subsp. *sphaerocarpum* (Cuatr. 7756): K, L, M, petal from inside, outside and laterally, × 5; N, androecium, × 5; O, stamen, × 10 and anther, × 20; P, pistil, × 5; Q, sepal from inside and outside, × 2. R–Y, *T. cacao* subsp. *cacao* (Nelson 2490): R, S, T, petal from inside, outside and laterally, × 5; androecium, × 5; V, stamen, × 10 and anther, × 20; W, pistil, × 5; bud and pedicel, × 2; Y, sepal from inside and outside, × 2.

Inflorescences on the trunk and branches, usually borne on small tubercles, the cymose branchlets short, knotty, persistent, the cymose peduncles 1–3 mm. long, stellate-pubescent, hirtellous and with scattered glandular trichomes; bracts ovate or ovate-oblong, amplectant, pubescent; bracteoles ovate-oblong, acute or subacute, 0.5–1.2 mm. long, pubescent, deciduous; pedicels capillary, rigid, pale green, whitish or reddish, 5–15 mm. long, hirtellous with rather dense, thin,

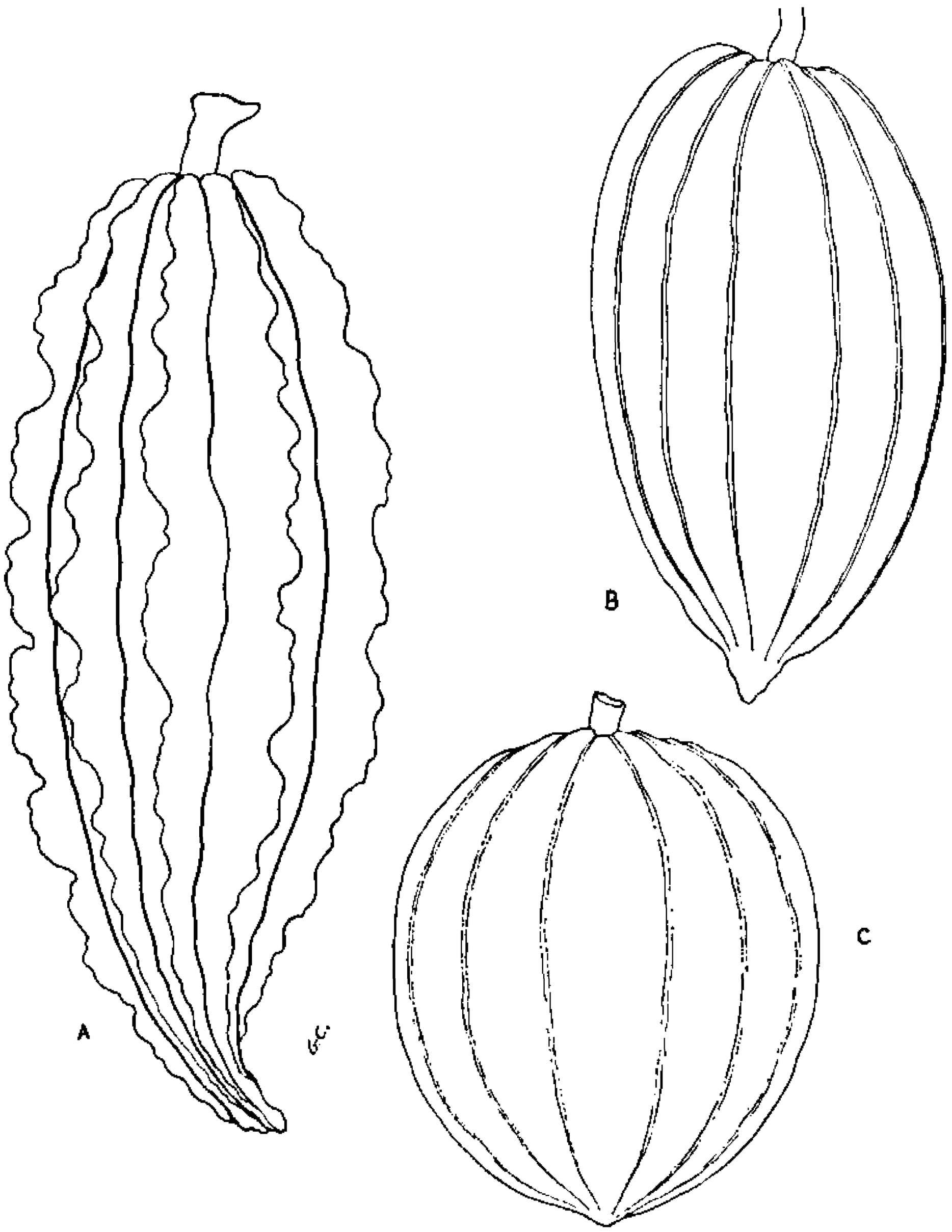


FIGURE 21.—Sketches of fruits of *Theobroma cacao* from classical and recent literature: A, in Tournefort plate 444, clearly representing a "criollo type"; B, in Sloane, pl. 160; C, in Chevalier 1946, pl. 5 (*T. sphaerocarpum* Chev.).

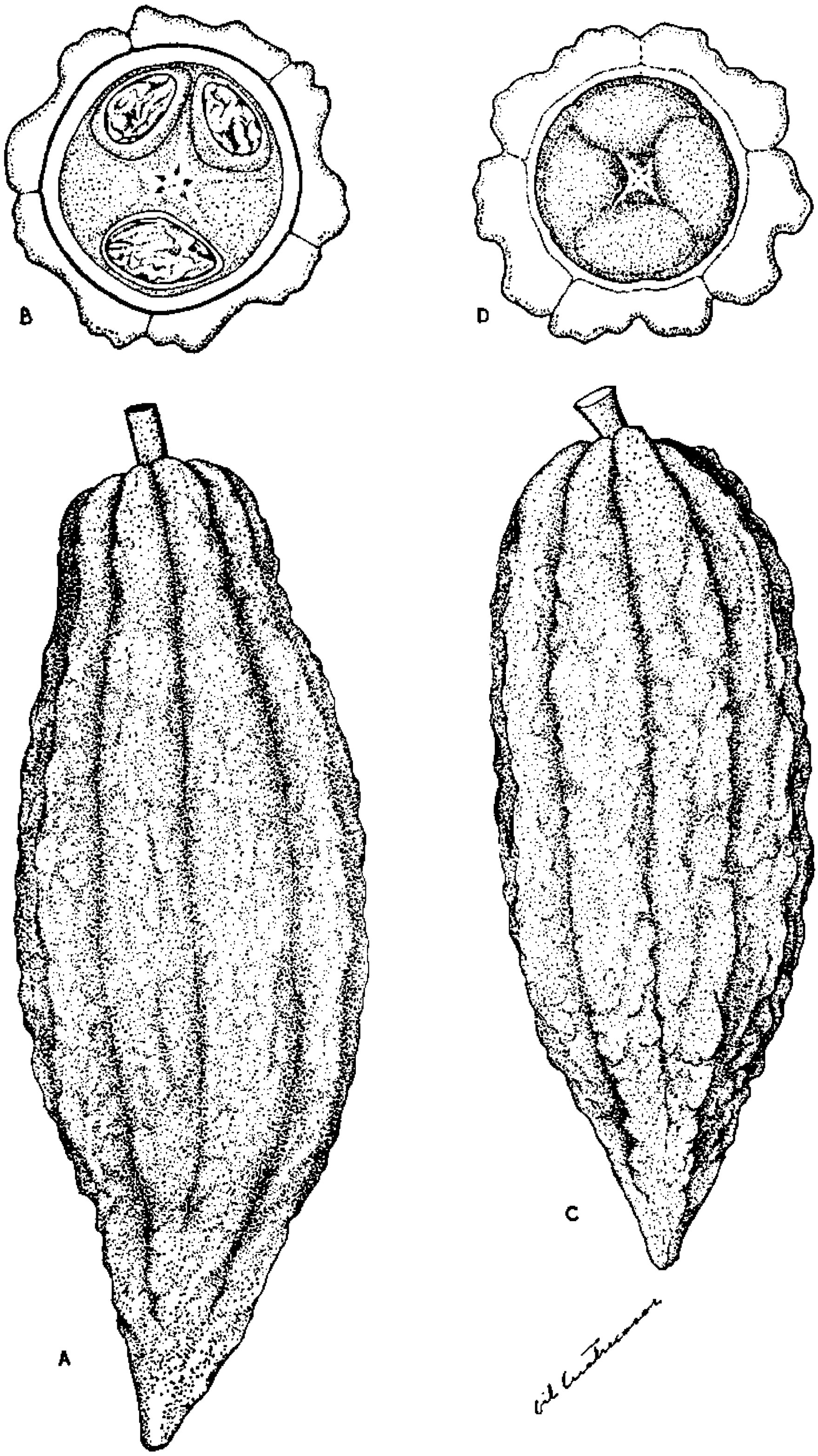


FIGURE 22.—A, Fruit of *Theobroma cacao*, cultivar "cundiamor" (Cuatr. 26492 from Colombia). B, Cross section of same showing structure of pericarp and arrangement of seeds each surrounded by their pulp. C, *T. cacao* subsp. *cacao*, cultivar "criollo" ("Caldas") (Cuatr. 26006 from Colombia). D, Section of same. All × ½.

acute, patulous, stellate or furcate hairs and sparse pluricellular, glandular, capitate trichomes; buds white, whitish green, lilac, or reddish, ovoid or oblong-ovoid, acute, 5–7 mm. long, subglabrous or sparsely puberulous with slender stellate hairs and thicker, glandular,

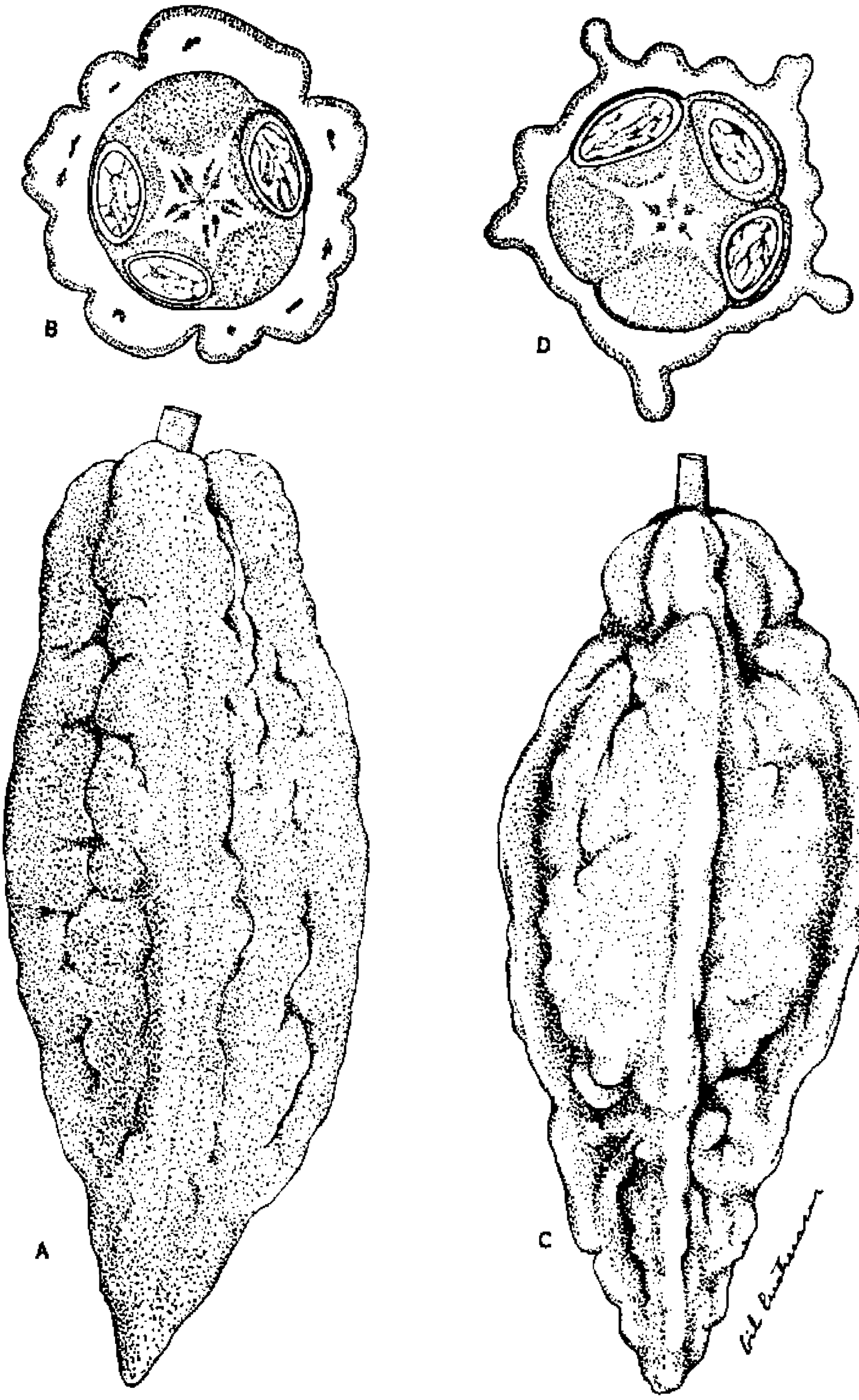


FIGURE 23.—A, Fruit of *Theobroma cacao* subsp. *cacao* fma. *pentagonum* (Cuatr. 26004 from Colombia) with some degree of introgression from fma. *cacao*. B, transection of the same showing the great reduction of the structure of pericarp (mesocarp represented by isolated bundles). C, *T. cacao* subsp. *cacao* fma. *pentagonum*, typical (Cuatr. 26540 from Costa Rica). D, transection of the same, showing the pericarp reduced to one layer. All × ½. Cultivar "lagarto."

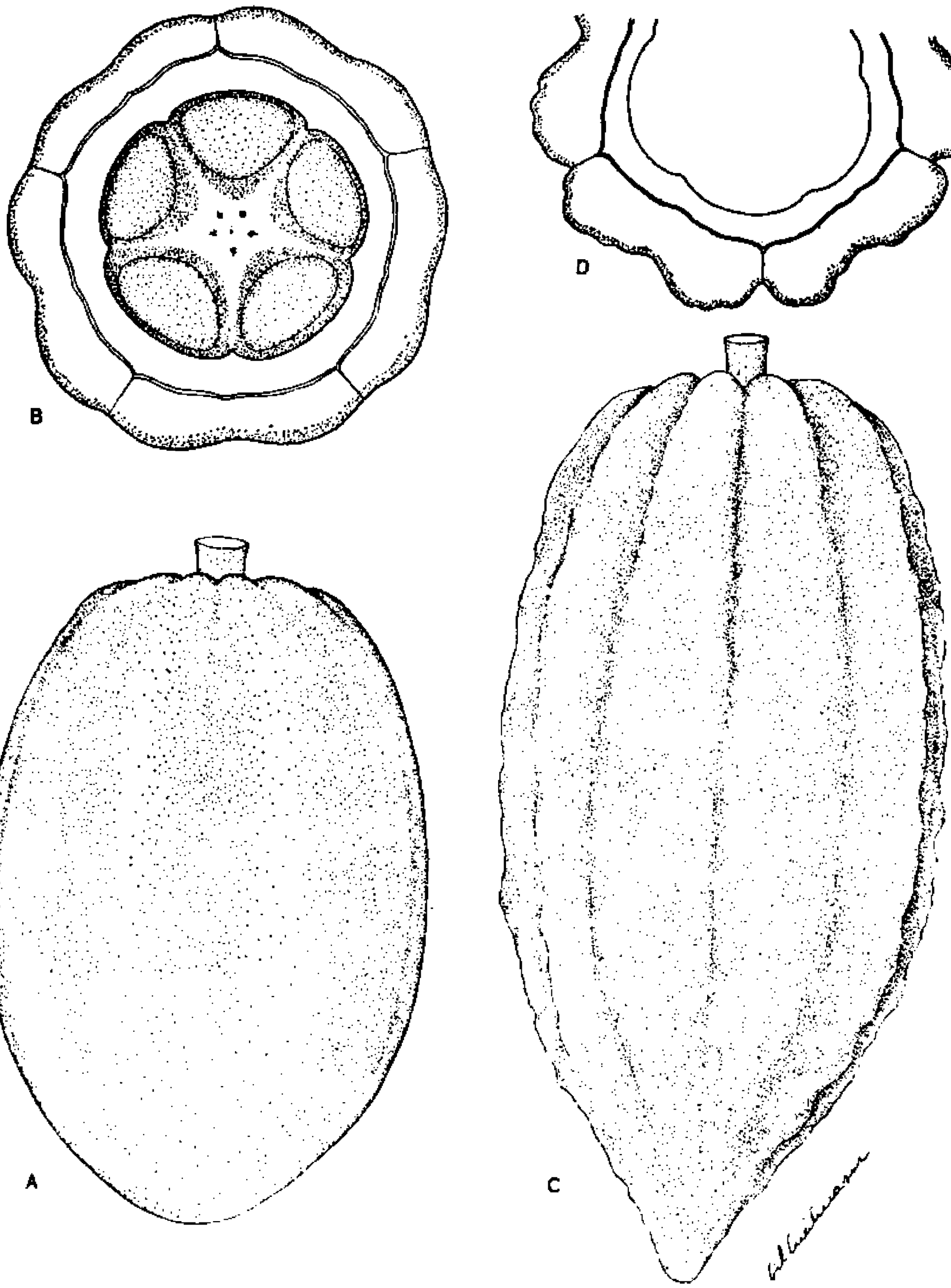


FIGURE 24.—A, Fruit of *Theobroma cacao* subsp. *sphaerocarpum*, cultivar "amelonado" (Cuatr. 25805 from Venezuela, Barlovento). B, transection of the same. C, fruit of *T. cacao* cultivar "angoleta" (Cuatr. 26494 from Colombia). D, transection of same. All × ½.

stipitate trichomes; sepals thick-membranaceous, lanceolate or oblong-lanceolate, acute, white, greenish white, pale violaceous or reddish, slightly 3-nerved, shortly (0.5–1 mm.) united at base, 5–8 mm. long, 1.5–2 mm. wide, minutely tomentose at margin, outside sparsely pubescent with stellate and glandulose hairs, or glabrous, inside glabrous or with rare glandular trichomes; petals contorted in aestivation, thick-membranaceous, the hood 3–4 mm. long, 5–2 mm. wide,

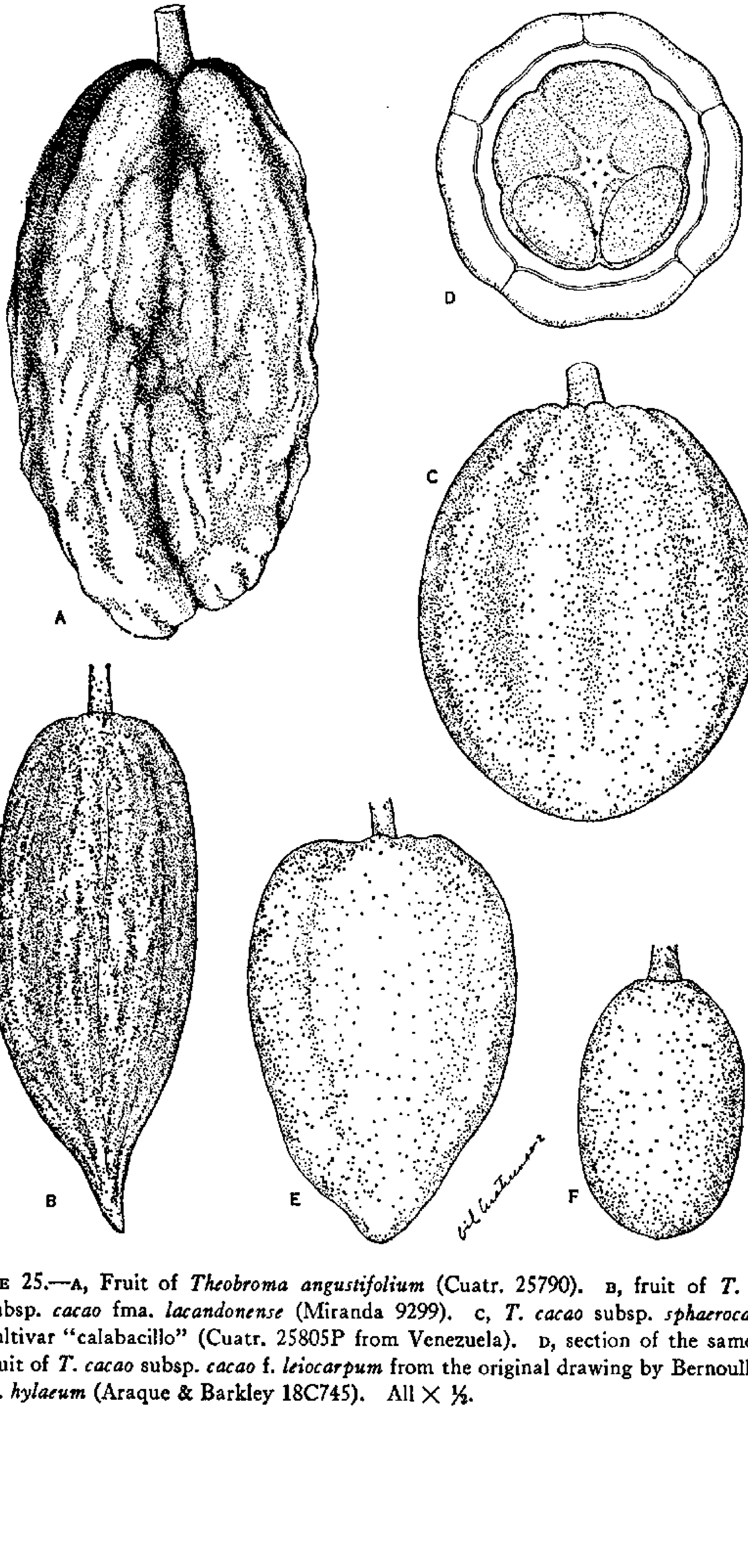


FIGURE 25.—A, Fruit of *Theobroma angustifolium* (Cuatr. 25790). B, fruit of *T. cacao* subsp. *cacao* fma. *lacandonense* (Miranda 9299). C, *T. cacao* subsp. *sphaerocarpum* cultivar "calabacillo" (Cuatr. 25805P from Venezuela). D, section of the same. E, fruit of *T. cacao* subsp. *cacao* f. *leiocarpum* from the original drawing by Bernoulli. F, *T. hylaeum* (Araque & Barkley 18C745). All × ½.

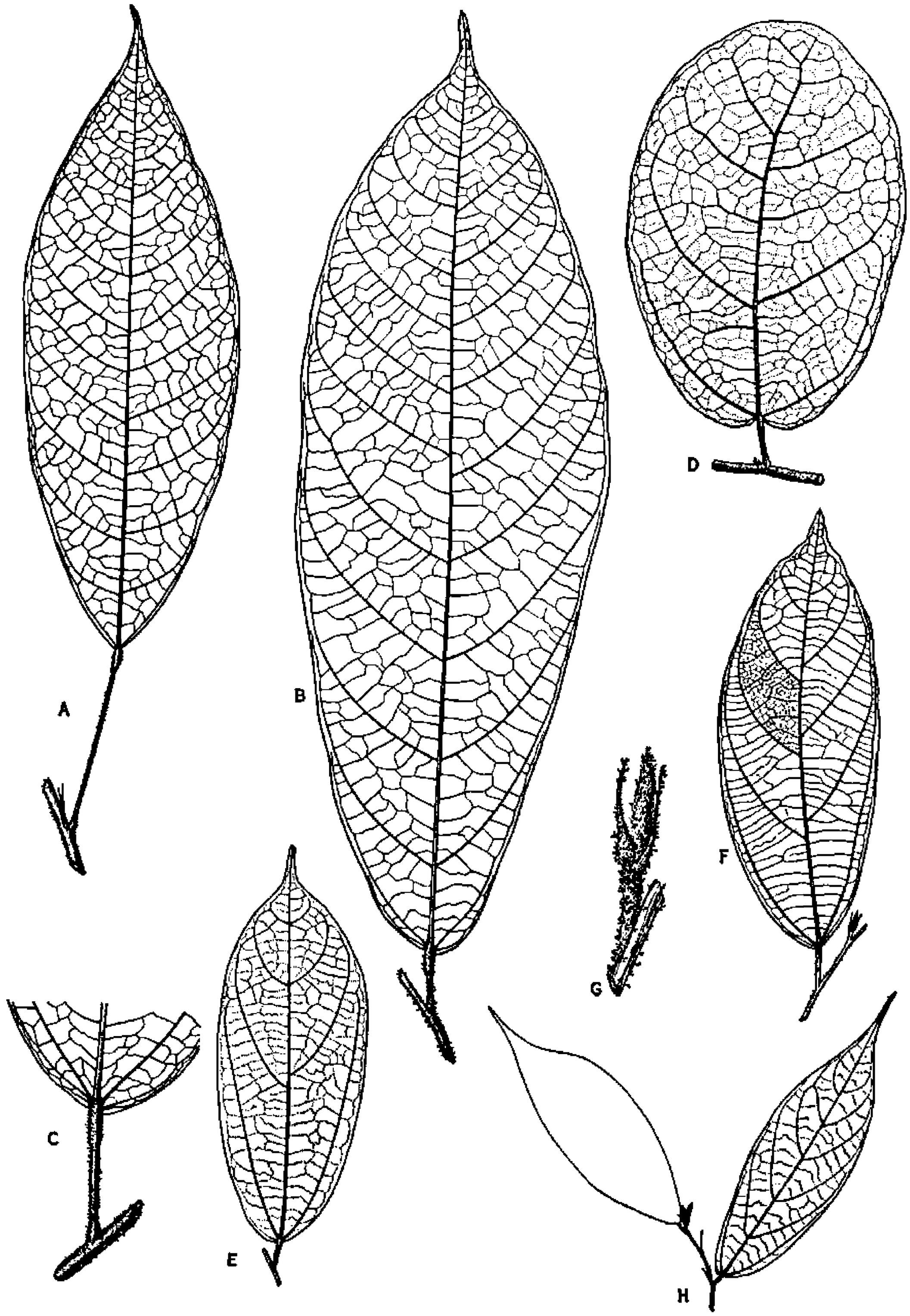


FIGURE 26.—A–C, Showing the characteristic elongated, bipulvinate petiole in *Theobroma cacao:* A, *T. cacao* from orthotropic stem (Steyermark 54143); B, *T. cacao* from lateral branches (Cuatr. 7756); C, *T. cacao* from young, lateral branches (Steyermark 49218). D, exceptional, broad, rounded leaf of *T. cacao*, a cultural mutation (León 5078). E, F, *T. microcarpum* (Fróes 23963 and Holliday & Cope 125). G, young shoot showing pubescens and stipules of *T. microcarpum* (Holliday & Cope 125). H, *T. gileri* (Giler 162). C, × 3; leaves, × ⅓.

obovate, rounded at apex, white, 3-nerved, the nerves papillose inside, the lateral ones very thick, usually purplish or red, the medial prominent only upwardly; petal-lamina pale yellowish, 1.5–2.5 mm. long, 1.5–2 mm. wide, obovate or rhombic-obovate, attenuate at apex, acuminate or subtruncate and shortly mucronate, rarely blunt, entire or sinuate at margin, pedicellate at base, the pedicel linear, 3-nerved and sometimes 4- or 5-nerved at apex, 2–4 mm. long, 0.2–0.5 mm. wide; androecium tube rather thick, 1.2–1.5 mm. long, glabrous; staminodes 4–6 mm. long, 0.6–0.7 mm. broad at base, narrowly subulate, very acute, erect in bud, erect or somewhat flexuous in anthesis, the middle vein thick, angular, red or purplish, minutely papillose-pilose, the thin margin whitish, more or less revolute, ciliate, with slender, flexuose simple hairs; stamens diantheriferous, the filaments glabrous, patulous or recurved, 1.5–2 mm. long, the anthers about 0.4 mm., with rounded cells; ovary oblong-ovoid, obtusely pentagonal or 5-ridged, about 1.5 mm. high, 0.8 mm. thick, glabrous or usually glandular, covered with more or less copious white or reddish, pluricellular, stipitate glands; styles 5, glabrous, adherent, 1.5–2.5 mm. long.

Fruit subbaccate, variable in shape, from globose to fusiform and acute, and with a very smooth to a strongly ridged and rugose or verrucose surface; pericarp consistently fleshy and thick (5–15 mm.), and usually made of two, more or less conspicuously different, carnose layers (epicarp and endocarp) separated by a thin, ligneous membrane (mesocarp), the endocarp limited by a firm epidermis inside, the inner wall of the shell, the epicarp sometimes differing in color and firmness, rich in mucilaginous cells, limited outside by the hard epidermis of the fruit, the mesocarpic membrane sometimes reduced to isolated bundles of fibers or lacking, the endocarp also sometimes lacking.

Seeds (20–40) usually arranged in 5 rows, but sometimes when large arranged in 4 or 3 rows, the five radial walls initially separating the 5 cavites in the earlier stages reabsorbed long before the maturation of the fruit; seeds ovoid, ellipsoid, amygdaloid, more or less complanate through mutual pressure or almost round in cross section, variable in size (20–40 mm. long, 12–20 mm. broad), the integuments brown, subcoriaceous, the surrounding pulp white, sweet, the cotyledons white, purplish, violet, or intermediate in color.

Theobroma cacao is variable in its characters, especially with regard to the color, size, and shape of the parts of the flower and the fruits. These are variations to be expected of an ancient crop spread throughout a very wide area.

Based on some of these more or less consistent variations, Bernoulli described three species, *T. pentagonum*, *T. leiocarpum*, and *T. saltz-*

mannianum, and Chevalier *T. sphaerocarpum*. The shape of the fruit is the main defining character, except for *T. saltzmannianum*, which was based on petal characters, probably from an abnormal specimen. The few floral characters given for the other three species are irrelevant or inconstant. *Theobroma pentagonum* is defined by having elongate, gradually and acutely narrowed, warty pods which are strongly pentagonal and 5-ridged; it has white seeds. It was described from the Atlantic coast of Guatemala and is called "cacao lagarto." *Theobroma leiocarpum* was characterized by ovoid pods, almost smooth, with five very shallow furrows and a glabrous ovary; the color of the seeds was not stated; it was found in plantations on the Atlantic coast of Guatemala, and stated to be rather rare. *Theobroma sphaerocarpum* was described from cultivated specimens on São Tomé island, western Africa, characterized by its nearly spherical, slightly 10-furrowed, almost smooth or slightly rough pods, and violet cotyledons. Schumann considered the three Bernoulli species as mere local variations of *T. cacao* and therefore unworthy of taxonomic consideration. Some authors have followed Schumann in this view, but there is a tendency to accept *T. pentagonum* as a different species, because of its characteristic fruit form and thinner pericarp.

For many years there has evidently been confusion in the taxonomy of cultivated cacaos, the main problem being insufficient knowledge of the wild populations of *T. cacao*. There are many citations of places in Central and South America where *T. cacao* is said to have been found wild, which may have been true in some cases, but not in others where we may be dealing with the remains of abandoned plantations. The discovery of wild cacao by Stahel in the rain forests of Mamaboen Creek in Surinam (confirmed later by Myers) and a few other places very distant from populations, is very significant; the cacao is of the Amelonado type. Ogilvie also found it in abundance on Black Creek, a branch of the Essequebo River, and along the Berbice River in British Guiana. He found it along the Rupunumi River at Rewa and Quitaro Creeks, at Kuduwini Kassikedju or Dewar Wow, etc., on the upper Essequebo River, and also on the Quitari River (according to Myers). Robert Schomburgk also cited wild cacao in several places in British Guiana on the Cutari, at the head of the Correntyne River, and also at Quitaro, and Richard Schomburgk found it on the Upper Pomeroon River. Wild cacaos also have been found, according to Stahel, in the Upper Oyapok in French Guiana (Myers), all of the Amelonado type, implying that this population of the Guiana highland area westwards to the Amazon valley may have been the home of this cultivated variety. In Brazil there has been found wild cacao near the Guianas and, according to Ducke, at the upper Rio Branco, northeast of Obidos, and at Francez

on the middle Tapajóz; he adds that the area of spontaneous *T. cacao* includes a greater part of the Hylaea and that it is of the form "*leiocarpum*." Preuss (1901, p. 247) found wild cacao in eastern Ecuador, also of the Amelonado type. Huber found spontaneous cacao in the upper Purus river, and along the Río Ucayali, Peru. Pound also claimed to have found spontaneous cacaos in the upper Amazon basin. The spontaneous cacao trees found by the Anglo-Colombian Expedition in the forests of Caguàn (Caquetá) and Río San Miguel offer some doubt about their indigenousness. I found myself, in 1939, in the rain forests of Río Guaviare wild trees of *T. cacao*, tall and well developed, but we have to be cautious in accepting them as indigenous, because the Guaviare River is said to have had more extensive plantations on its banks in earlier times. An interesting find was made in British Honduras by Sampson, who encountered wild trees of the Criollo type in the Southern forests. In Mexico, Miranda recently found a completely indigenous cacao tree in a forested region of Chiapas (Selva Lacandona), very distant from any population; the natives (Lacandones indians) reported that other trees of such cacaos are found scattered; this cacao has a somewhat scandent stem and produces small, elongated, pointed, slightly 10-ridged and rugose fruits. Standley and Steyermark (Fl. Guat. 426) say that in the lowlands of Guatemala sometimes cacao is found more or less wild in the forest, especially in Alta Verapaz, and that it is not improbable that it is native in the wet North Coast region.

Many forms of the cultivated cacaos have received local or regional names which after the many introductions of cultivars from one country to another have brought confusion to the complicated system of cacao types. Morris was the first to make a classification of cultivars, arranging them in two main groups: Criollo and Forastero. Hart (see page 396) modified this, making three groups (Criollo, Forastero, and Calabacillo), later separating *T. pentagonum* (cultivar "Lagarto") into another group, as a different species from *T. cacao*. The classification of Hart has been followed by many authors of cacao treatises until recent times when van Hall, simplifying, went back to the basic two groups of Morris: Criollo and Forastero.

Pittier, a botanist with much experience both in Central and South America, recognized the existence of two different, original, spontaneous forms of cacao, Criollo with elongated, ridged, pointed fruits and white cotyledons, and Forastero, with short, roundish, almost smooth fruit and purplish cotyledons; he believed that they corresponded with two different species, *T. leiocarpum* generally spread throughout tropical South America, where it is still found spontaneous, and *T. cacao*, spontaneous in Central America and which was the

source of the prehistoric cultivation and selection of cacao, all of the Criollo type, in Mexico and Central America. Introduction of Criollo types in South America and West Indies and conversely of the smooth type into West Indies and Central America created the cross-varieties which multiplied with the years. Although there is much speculation in this, the theory is a workable and reasonable one, because the available historical data favors the recognition of the earlier Central American and Mexican cacaos as being of the Criollo type. The finding of spontaneous cacao of this type in Chiapas and British Honduras also supports this theory. Another favorable fact is the uniformity of the Venezuelan Criollo, supposed to have been introduced from Central America to Venezuela in the earlier times of the Spanish conquest.

Soria, after visiting (1961) important plantations in Mexico where new Forastero types have been abundantly introduced in recent times, recognized that in Mexico before 1900 varieties of the Criollo type almost exclusively were cultivated. He observed in large, old (more than 50 years) plantations a great variation in the Criollo type, but the seeds were always white and the pods, variable in shape, were always pointed, with surfaces varying from tuberculate to rugose, from light green, through green, to reddish; the trees were small, slow growing, and often with fewer branches (5–3 in each whorl) than is normal in the species; the petal-laminas are bright yellow.

Pittier's theory was very much welcomed by botanists and cocoa experts; Chevalier supported it, and Ducke also in its basic idea. Cheesman adhered to it at first (1932), but later (1944) developed a new theory that all cultivated Criollo cacaos came "from an offshoot of a general cacao stock in the headwaters of the Amazon carried over the Andes into southern Colombia, and developed many of their present characters in association with man." But historical knowledge at present can only closely relate cacao to Central American man, especially to the Mayans and not to the South American Indians. Central American Indians undoubtedly developed the art of planting and selecting of cacao through several thousands of years, finally obtaining the high quality produce which the Spaniards found at the time of the conquest.

It may be assumed that in early times a natural population of *Theobroma cacao* was spread throughout the central part of Amazonia-Guiana, westward and northward to the south of Mexico; that these populations developed into two different forms geographically separated by the Panama isthmus; and that these two original forms, when isolated, had sufficiently consistent characters to be recognized as subspecies. As they intermingle readily by crossing, giving fertile

and robust hybrids, they cannot be considered distinct species. Both types in cultivation have originated many mutations, some of them persistent, thanks to ecological adjustment, selection, and isolation. Because the cultivation and selection has been very active for some thousand years in the Central American-Mexican area, it is in these areas where we find the richest variety of forms. When the subspecies (with their different forms) interbred the products gave the great and confusing variety of existing types.

Another theory is that most of the stable forms of cacao might have originated by mutations from a widespread, uniform original specific type. In such a way the forms *pentagonum*, *leiocarpum*, Criollo, Cundiamor, Angoleta, Nacional Ecuador, Trinitario, etc., and their variants could have originated. This theory does not exclude hybridization as a factor in the multiplicity of forms, but its influence would be secondary instead of basic, as postulated by the Pittier theory.

TYPES OF THEOBROMA CACAO.—The only specimen of *T. cacao* in the Linnaean herbarium is the number 934–1, but this specimen is posterior to the publication of Species Plantarum (1753), since it bears the annotation "Pl. Surin. 1775. p. 13." The type has to be sought among the bibliographic references of Linnaeus. In Species Plantarum, Linnaeus refers to Hortus Cliffortianus. At my request, Mr. Sandwith was kind enough to examine the Hortus Cliffortianus herbarium at the British Museum and found no specimens of *Theobroma* in it. However, Hortus Cliffortianus page 379 seems to give a key to the matter, where Linnaeus writes "Flores a nullo bene depicti, multo minus descripti sunt, . . . Sloane mihi inspiciendi copiam fecit, . . ." and gives the quotation "Hist. Jam. *pl. 160.*" Linnaeus was especially preoccupied with the flowers; he wanted to know exactly the structure in order to be able to place *Theobroma* in the right place in his sexual system; the previous literature did not give him the answer, and neither did the Sloane plate. However, from the above paragraph we may infer that Sloane sent him flowers at his request, surely very few, which may be the reason why there are none of them in the Linnaean herbarium; from Sloane's flowers Linnaeus found the floral structure of *Theobroma* by himself and drafted his diagnosis. The original flowers (surely dissected) having disappeared, the corresponding specimens in the Sloane Herbarium have to be considered the isotype. Messrs. Dandy and Sandwith found the specimens in the Sloane Herbarium at the British Museum. Mr. Sandwith writes: "We found the corresponding specimen in the Sloane Herbarium and it is obviously the source of (in fact part of) the plate, though not identical; there are leaves, detached flowers, frag-

ments of fruit and one seed; it is the vol. 5 p. 59." There is the possibility that Sloane lent Linnaeus these specimens, but even if this were not the case, we may assume that Linnaeus used flowers taken from this specimen which would thus be an isotype; therefore, the sheet page 59, volume 5, of the Sloane Herbarium is to be chosen as lectotype for the flowers and leaves. According to Sandwith and Dandy "there is also what appears to be a duplicate, leaves only, in the Plukenet Herbarium volume of Herb. Sloane. The leaves of both specimens are reddish brown and glabrous beneath with reticulate tertiary veins."

Sloane's plate 160 is a paratype, but another even more important paratype is Tournefort's plate 444. Tournefort is the only reference given by Linnaeus in his original description of the genus in Genera Plantarum (1754), and its citation precedes the reference to Sloane in Hortus Cliffortianus. I propose it as the lectotype for the fruit, because the Tournefort drawing is perfectly defined, leaving no doubt that the characters are of the Criollo type. On the other hand, the fruits shown on Sloane's plate 160 are not unquestionable, even though they are very pointed; they are among the variations found in Criollo populations. But the reasons which compel me to consider the flower specimens in the Sloane Herbarium as the lectotype do not apply to the fruit, the origin of which may have been different from the origin of the flowers and leaves, for Sloane collected in several places and countries. A fruit typification by the Tournefort plate fits well the definition of *T. cacao* L. *sensu stricto* given by Pittier and later authors. It is obvious that all these authors described cultivars and that the cacao described by the earlier authors was of the type Criollo, as can be inferred from the illustrations, and also from the descriptions of Hernandez, Pison, Plukenet, Merian, Weinmann, Tournefort, Catesby, and Gaertner.

Synonyms.—*T. pentagonum* Bernoulli was characterized by the shape of the fruit and by smaller flowers. Last character is inconstant but the fruit form is a very particular one and constant, fruit always easily recognized. This type was described in vivo by Bernoulli from the Atlantic coast of Guatemala; there is no type specimen of the fruit, but it was well drawn (*Pl. 2, fig. III*) and the drawing may be considered the type. It is my belief that *T. pentagonum* is just a cultivar. It crosses easily with other forms of cacao giving intermediate products. Gross morphological study also supports this view. The pericarp in *Theobroma* is composed of three visible layers, one of these being more or less consistently woody; in *T. cacao* the woody layer is the middle one, the mesocarp. It seems that in cultivation there is a tendency for the pods to change, the shells

becoming thinner in the best quality Criollos. This reduction is extreme in *T. pentagonum* which lacks the firm mesocarp and the fleshy endocarp, the whole pericarp being only half as thick as in other cultivars; *pentagonum* trees are also weaker than others. I have no doubt that *pentagonum* is a fixed product of mutation selected for better fruits. I must agree with Soria (1959) when he writes "*Pentagona* is nothing more than one of the extremes in the variability of the complex of types forming the species *T. cacao*." The name must be kept but only at the rank of forma.

Theobroma leiocarpum was also described by Bernoulli from living specimens in cultivation on the Atlantic coast of Guatemala; there are no type specimens of the fruits recorded, and so the published drawing (*Pl. 2, fig. II*) must be chosen as the type. This plant was characterized by a glabrous ovary and smaller flowers (an insignificant feature) and by ovoid, shallowly 5-sulcate, almost smooth fruits. The color of the cotyledons was not mentioned. For a long time this form was identified with the widespread South American "Calabacillo" or "Amelonado" fruit types, especially since Pittier published his theory, it being supposed that the Venezuelan "Calabacillo," with thick-shelled, rounded or ellipsoid, obtuse, slightly 10-furrowed fruits, and violet cotyledons, was *T. leiocarpum*. All workers followed this nomenclature, myself included. It was Cheesman (1944, p. 14) who called attention to the differences between Calabacillo and Central American *T. leiocarpum*. The Bernoulli cacao has thin, ovoid attenuate shells, with only 5 furrows, and plump seeds which are probably white or light violet. Preuss had written previously that the seeds were different. I saw Calabacillo in Nicaragua with very light-violaceous seeds. The recent observation by Soria (1961) in Mexico of the great variety in external form of Criollo in an old plantation of Criollo makes it clear that *T. leiocarpum* is a mere segregate form or mutant from the Criollo type of *T. cacao*, originating in a similar way to *T. pentagonum*. I consider it only as a cultivar.

Theobroma sphaerocarpum was described by Chevalier from cultivation in Isla São Thomé, in the South Atlantic Ocean west of tropical Africa, conforms perfectly with the "Calabacillo" cultivar of Venezuela and other South American plantations. It is an extreme form of the widespread South American subspecies. The type is a preserved fruit in the Museum in Paris. This name has to take the place of the subspecies which Pittier and later authors have called *T. leiocarpum*.

Cacao sativa Aubl. is a nomenclatural synonym of *T. cacao*, and cannot be used as a substitute for the latter. Any imprecision implied by the binomial *T. cacao* is implied also in *Cacao sativa*, and *Theobroma sativum*.

Theobroma sapidum Pittier may well have been unintentionally published as a *lapsus calami* for *T. sativum;* it corresponds to *T. cacao sensu stricto* of Pittier, restricted to the Criollo type. But the binomial is a *nomen nudum*, because it was not formally published, not being accompanied by a description and with no indication of any type.

Cacao minus Gaertn. was published without mention of specimens or locality. It agrees well with some forms of the Criollo type. It cannot be *T. pentagonum* because in *T. pentagonum* the ridges are always very prominent and smooth. The type of the binomial consists of two fruits identical with the original drawing, labeled *Cacao minus*, Gaertner at Paris.

Cacao theobroma de Tussac, *T. integerrima* Stokes, and *T. caribaea* Sweet are nomenclatural synonyms.

Theobroma saltzmannianum was established by Bernoulli, the emarginate petal-laminae being the only difference from *T. cacao* (ligulae lamina anguste obovata, apice truncata emarginata). According to Bernoulli the shape of the ligula was a constant character in *T. cacao* and *T. leiocarpum;* having found at Kew some specimens collected by Salzmann near Bahia, in which he saw the petal-lamina emarginate, he did not hesitate to make a new species. Schumann could not identify this character in any of many flowers collected in Bahia by Salzmann, and inferred that Bernoulli had examined some exceptional, teratological flower. Rombouts in 1948 (Kew Bull. 1948: 104) studied in detail the type specimens at Kew and arrived at the same conclusion as Schumann, that Bernoulli did base his species on an accidental character. Chevalier had already expressed the same view (1946, p. 270). I also can confirm the above opinions after having examined several Salzmann collections at different times and the type specimen in 1954 at Kew.

Theobroma sagittata Pavon was published by Chevalier in his revision (1946: 274) as a microspecies of the complex of *T. cacao*. The binomial, however, is not validly published for lack of the required Latin diagnosis. Moreover, I have identified the type specimen, which is preserved in Paris, as a 3-leaflet fragment of a leaf of *Herrania nitida* (Poepp.) Schultes. *Theobroma hastata*, a name mentioned by Chevalier in the footnote on page 273, presumably is a *lapsus calami* for *T. sagittata.*

The varieties *leucosperma* and *melanosperma* published by Chevalier without reference to any type specimens are fortunately not validly published for lack of Latin diagnoses. It would be very difficult to ascribe these two supposed varieties to any recognized taxonomic entity relying only on the seed color.

COMMON NAMES.—Cacao, cocoa, cacao dulce, cacao criollo, cacao calabacillo, cacao forastero, cacao amelonado, cacao trinitario, cacao lagarto, and many other adjectives according cultivar varieties and regional or local cultivar forms. Also: Bizoya, yagabizoya (*Reko*), deghy (*Otomi*), caocauatzaua (*Zoque*), kako (*Mixe*), cahequa (*Tarascán*), Chudechu (*Otomi*) in Mexico after Standley; cacahuatl, cacahoatl, cacahoaquahuitl, quauhcacahoatl, mecacahoatl, xochicacahoatl, tlacacahoatl, cacahoacuahuitl, cacaotlquahuitl (*Nauhatl*), kicou, kicob, cuculat, pacxoc, cucuh, caco in Costa Rica and Guatemala; cacao chuncho in Peru. For Costa Rica and Chiriquí, Pittier (1902) gives the following Indian names: ko (*Térreba*), koó (*Brunka*), kajo (*Guatuso*), kuá (*Guaimí*), kno (*Penonomé*), doló (*Doraske*), tsirú (*Bribrí*), (*Cabécara*); according to him the *Bribrí* Indians use the following names for some varieties of cacao: murú-uak, tsipá-uak, xi-uak, and betsún-uak; Standley (1937) mentions, also for Costa Rica: kuk (*Rama*), tsirú-kurú (*Cabécara*), kao-krá (*Brunka*) and kau (*Tiribí*). Cacao silvestre, cacao de monte, wild cacao, are names often used in different countries whenever a cacao tree is found apparently spontaneously growing. It is a fact that although the other species have native Indian names, for *Theobroma cacao* only the name "cacao" is recorded from the whole of South America, whereas this species has many indigenous names in Central America.

SUBSPECIFIC DIVISIONS.—A correct classification of all forms will only be possible after careful and extensive genetic research. In the meanwhile we cannot do more than use a provisional, conservative approach, confining the nomenclature to names already used.

The summarized classification given below of cultivated varieties follows Morris, who was the first to give status to the most popular common names of cocoa cultivars; the adaptation in general use made by van Hall is followed in this paper, with few modifications. See also my reviews of Preuss (1901), and Hart (1892, 1900 and 1911) in the Historical Sketch above. The reader will find more extensive information on this subject in special treatises (van Hall, Baker in Urquhart, Hart, etc.).

Key to subspecies and forms of *Theobroma cacao* L.

1. Fruit elongate, claviform, fusiform or ovoid-oblong, tapering and pointed, more or less strongly 10-costate or 5-costate and verrucose; pericarp moderately thick, the woody mesocarp thin; seeds ovoid or ellipsoid, usually rounded in cross section; cotyledons white or yellowish white . . 7a. subsp. **cacao**
2. Fruit 10-costate . . . . 1. f. **cacao, lacandonense** and unnamed forms.
2. Fruit claviform, strongly 5-costate, the ridges prominent and smooth, the sides strongly verrucose, the pericarp thinner, lacking the woody mesocarp and endocarp . . . . . 2. f. **pentagonum**
2. Fruit ovoid, shallowly 5-furrowed, almost smooth, obtusely attenuate at apex . . . . . 3. f. **leiocarpum**

1. Fruit ellipsoid, almost globose or more or less oblong, rounded at both ends, smooth or slightly verrucose, more or less shallowly 10-furrowed; pericarp very thick, the woody mesocarp firm; seeds ovoid, more or less compressed; cotyledons purplish or dark violet. . . . . 7b. subsp. **sphaerocarpum**

7a(1). Theobroma cacao subsp. **cacao** FIGURES 20, 21, 22

Cacao minus Gaertn. 1791.
Theobroma sapidum Pittier, 1932.
Theobroma cacao var. *typica* Ciferri, 1933.
Theobroma sativa var. *leucosperma* Chevalier, 1946.

TYPE.—Sloane Herb. (flowers, leaves) (BM, lectotype); Tournefort *pl. 444* (fruit-lectotype).

COMMON NAMES.—The leading name is cacao criollo or criollo.

DISTRIBUTION.—Originally from Mexico and Central America, and cultivated more or less extensively in other tropical countries. Corresponds to the Criollo cultivars.

Among the collections examined are:

MEXICO: VERACRUZ: Colonia San Rafael, flowers and pods, January, 1946; forests from Colima to Chiapas, *Olivia Converse* 74 (UC). Fortuño, Coatzacoalcos River, 30–50 m., III 1937, "cacao"; tree 15–25 feet tall, crown fairly dense, trunk branching from base, inner bark reddish or reddish brown, wood light brown, fruit yellow about 8 in. long, 4 in. wide, often cultivated and growing wild in lowlands slightly humid or subject to seasonal floods, (*Ll.*) *Williams* 8457 (F, P).

OAXACA: Santa Maria de Chimilapa, I 1927, "wild cacao," *Mell* 29 (US).

BRITISH HONDURAS: Stann Creek Valley, Mountain Cow Ridge; tree 5 in. diam., 30 III 1940, "wild cacao," *Gentle* 3292 (MO, NY, US). Middlesex, 200 ft. alt.; tall tree of upright habit of growth, generally found growing along river banks, fruits dark red, occasional, 19 XI 1929, specimen with fruits, *Schipp* 178 (UC). El Cayo district, Mountain Pine Ridge, 8 V 1931, *Bartlett* 13108 (F, NY).

7a(2). Theobroma cacao subsp. **cacao** forma **pentagonum** (Bernoulli) Cuatr., comb. nov. FIGURES 5, 6, 20, 23

Theobroma pentagona Bernoulli, Uebers. Art. Theobroma 6–7, *pl. 2, fig. III.* 1869.
Theobroma cacao subsp. *pentagona* (Bernoulli) León in Hardy's Cacao Man. 312. 1960.

TYPE.—Bernouilli, *op. cit., plate 2, fig. III*, isotype, *Bernoulli* 98 (GOET).

COMMON NAMES.—Cacao lagarto, alligator.

USES.—One of the best quality cacaos known.

DISTRIBUTION.—Only known in cultivation, being probably a mutant cultivar from *T. cacao* L. originally from Central America; mainly cultivated in southern Mexico and Central America, seldom in other areas. It is a weaker variety, for which reason it is being displaced by more robust and disease resistant varieties, in spite of the high quality of its product.

Collections examined (cultivated):

GUATEMALA: Mazatenango, "cult. Marz. 1865 *Theobroma pentagonum* n. sp.?"; specimen with two leaves and one seed, *Bernoulli* 98 (GOET, isotype) Retaluleu, Apr. 1878, *Bernoulli & Cario* 3151 (GOET).

COSTA RICA: Turrialba; fruit red, "lagarto" seed white, 7 XI 1961, *Cuatrecasas & Soria* 26540 (US).

COLOMBIA: El Valle: Finca Esmirna, "lagarto rojo"; seeds white, 16 X 1961, *Cuatrecasas & Barros* 26004 (US); *ibidem*, "lagarto amarillo"; seeds white, *Cuatrecasas & Barros* 26005 (US).

7a(3). Theobroma cacao subsp. **cacao** forma **leiocarpum** (Bernoulli) Ducke, Rodriguesia 4:274. 1940. FIGURE 25

Theobroma leiocarpa Bernoulli, Uebers. Art. Theobroma 6, 7, *pl. 2, fig. II.* 1869: (not *T. leiocarpum* of current authors).

Theobroma cacao var. *leiocarpum* Ciferri, Real Accad. Ital. Mem. Cl. Sci. Fis. Mat. e Nat. 4:604. 1933, as to basionym.

Theobroma cacao subsp. *leiocarpum* Cuatr. *in* Macbride, Field Mus. Publ. Bot. 13 (3A): 654. 1956, as to basionym.

TYPE.—Bernoulli, *op. cit., pl. 2, fig. II;* isotype, *Bernoulli* 97 (GOET).

COMMON NAME.—Cumacaco (Guatemala).

USES.—A current cocoa of high quality.

DISTRIBUTION.—Atlantic coast of Guatemala and rarely in other parts of Central America and southern Mexico. Only known in cultivation, probably being a mutant cultivar of *T. cacao* L. The commercial type known as "Porcelaine Java Criollo" probably represents this form.

Collections examined (cultivated):

GUATEMALA: Mazatenango, "cult. Marz. 1865, *Theobroma laeve* n. sp.?.," *Bernoulli* 97 (GOET, isotype). Retaluleu, "April 1878, *Theobroma laeve* Bern.," *Bernoulli & Cario* 3152 (GOET).

Theobroma cacao subsp. **cacao** forma **lacandonense** Cuatr., forma nov. FIGURE 25

Fructus ovoideo-oblongus, acutus, 10-angulatus, 12 cm. longus, 5.3 cm. diam., pericarpio 5 mm. crasso, epidermide dura, epicarpio molli 2–3 mm. crasso, mesocarpio cartilagineo, endocarpio molli circa 2–3 mm. crasso; semina oblonga 20–22 x 14 x 8–10 mm.

Type in the U.S. National Herbarium, No. 2404633, collected near Caribal Lacanjá ("selva lacandona"), northeast of Chiapas, Mexico, in high primary forest (about 50 m. high), 550 m. alt. by F. Miranda (No. 9299); half-vine, about 7 m. tall, with very long branches; trunk 15 cm. diam. The Lacandona Indians call it "cacao."

DISTRIBUTION.—Only known from the type locality. It is a very interesting variety due to the fact that it is a true wild plant and therefore a possible ancestor of the present cultivated cacao.

MEXICO: CHIAPAS: Selva Lacandona, Caribal Lacanja, 550 m. alt. in primary forest, X 1960, *F. Miranda* 9299 (US, holotype).

7b. Theobroma cacao subsp. **sphaerocarpum** (Chevalier) Cuatr., comb. nov.

FIGURES 20, 24, 25

Theobroma sphaerocarpa Chevalier, Veget. Util. Afr. Trop. Fr. 4:12. 1908.
Theobroma cacao subsp. *leiocarpum* sensu Cuatr., excl. basionym *T. leiocarpum* Bernoulli.
Theobroma leiocarpum sensu Pittier et auctt., excl. basionym *T. leiocarpum* Bernoulli.
Theobroma cacao var. *leiocarpa* sensu Ciferri, excl. basionym *T. leiocarpum* Bernoulli.
Theobroma cacao f. leiocarpum sensu Ducke, excl. basionym *T. leiocarpum* Bernoulli.

TYPE.—São Tomé, *Chevalier*, preserved fruit (P).

COMMON NAMES.—Calabacillo, amelonado, Amazonian forastero, forastero, etc. (South America). Laranja (São Tomé, West Africa).

USES.—A currently used cocoa of variable quality; the original type gives the lowest quality of the cultivated varieties.

DISTRIBUTION.—Native in South America, found spontaneous in the Hylaea from the Guianas and middle Amazonia north and westward to the Andes. Its several cultivars and forms are planted throughout the tropics, especially in South America and Africa. Being hard and robust trees, and fast-growing plants, they are spreading steadily in plantations.

Some of the collections examined are:

BRITISH GUIANA: Mataruki River, upper Essequebo; small riparian tree' *Myers* 5829 (K).

COLOMBIA: META: San Jose del Guaviare, forest on left side of the Guaviare River, 240 m. elev.; fruits 18 x 7 cm., abundant, apparently spontaneous trees, in the lower tree-layer of forest, 14 XI 1939, *Cuatrecasas* 7756 (COL, F, US). Sierra de la Macarena, train between Güejar River and Caño Guapayita, Caño Yerli, 500–600 m. elev.; slender tree 35 ft. tall, 20–28 XII 1950, *Idrobo & Schultes* 784 (COL, US). Ibidem, tree 12 m. tall, 20–28 XII 1950, *Idrobo & Schultes* 940 (COL, F. US). Ibidem, Caño Yerli, dense humid forest; shrub 3 m. tall, 25 XI 1949, *Philipson, Idrobo, & Fernández* 1565, 1569 (BM, COL, US).

AMAZONAS: La Pedrera, Caquetá River, river level; old trees possibly planted long ago and not truly wild on the river banks and islands, pods green, ripening yellow, 20 X 1952, *Baker & Cope* 15 (COL, F, US, TRIN).

CAQUETÁ: Río Caguán, Cartagena; tree 7–8 m., found distant from river bank, white-based pod, smooth and scarcely furrowed, all beans pigmented, 20 IV 1953, *Cope & Holliday* 105 (COL, TRIN, US). Ibidem; tree 8 m., numerous small fruits smooth, distinctly 10-ridged, somewhat pigmented, very dark purple beans, 20 IV 1953, *Cope & Holliday* 107 (COL, TRIN, US).

MAGDALENA: Poponte, in forest of Magdalena valley; tree 30 ft., leaves dark green, flowers yellow, fruit red, 16 XII 1924, *Cyril Allen* 880 (MO). Ibidem; fruit green yellow, *Allen* 881 (MO).

BRAZIL: AMAZONAS: Esperança, at mouth of Rio Javary, in noninundatable rain forest; small tree, flowers whitish, spontaneous "cacao," 25 IX 1942, *Ducke* 1095 (IAN, MG, MO, NY, US); ibidem, *Ducke* 23976 (US). "B." Constant,

inundatable ground; tree; "cacau silvestre," 9 V 1945, *Frões* 20882 (IAN, NY); ibidem, *Frões* 20573 (IAN, NY). Rio Solimoes, on an island below Tabatinga; rain forest, slightly inundatable, small tree, flowers white, spontaneous "cacao," 24 IX 1931, *Ducke* 23970 (P).

PERU: LORETO: Río Ucayali, Laguna de Canchahuaya, 28 × 1898, *Huber* 1392 (MG). A specimen collected by Asplund near Tingo Maria (No. 13408) may well represent a new species. I did not study this, the material having been lent to Dr. Schultes, Botanical Museum, Cambridge.

The cultivars of Cacao are grouped as follows:

Fruit elongated and pointed, warty, 10-furrowed, with 5 ridges more prominent than the alternate, or only 5, sometimes almost smooth and only attenuate not pointed; shell medium thick, easy to cut; seeds usually rounded in cross section, white or yellowish white inside, and slightly bitter in taste. (Figs. 5, 20, 21, 22, 23.) . . CRIOLLO

Fruit ellipsoid, rounded at both ends or somewhat narrowed toward the apex, rather smooth, with 10 more or less marked furrows; shell thick and harder to cut; seeds usually flattened, violet inside, bitter in taste. (Some varieties with deep furrows or warty surfaces, and pale violet or white beans, being intermediate forms with Criollo. (Figs. 5, 6, 20, 22, 24, 25.) . . . . . FORASTERO

CRIOLLO Morris (1882, pp. 12, 13). This is the type developed and propagated since prehistoric times in Central America and southern Mexico and which later acquired importance in western Venezuela (cacao Caracas). It comprises the best qualities of cocoa, but the plants are vulnerable to diseases. Criollo is widely cultivated throughout the tropics, the following cultivars being especially known by the growers: Venezuela criollo, Nicaragua, Java, Ceylon, Samoa, Madagascar, Surinam, and Porcelaine Criollos. See van Hall for more information. Among the Criollos has to be included "Alligator" or "Lagarto" mentioned above as *T. cacao* f. *pentagonum*. It seems to me that "Porcelaine Criollo" corresponds to *T. cacao* f. *leiocarpum*. Figs. 5, 20, 21, 22, 23.

FORASTERO Morris (1882, pp. 12, 13). This group of cultivars was divided by Hart into two: Calabacillo and Forastero, the former containing the most typical, shortly ellipsoid, smooth forms. It comprises the hardiest, easiest and fastest growing types, but also those with lower qualities of cocoa; most Forasteros are an interbreeding product of Calabacillo and Criollo and their segregates. Some varieties have developed a good combination of characters. They originated and spread in South America and Trinidad, especially in the Amazon and Orinoco Valley. The most common known types of Forastero are the four listed by van Hall: Angoleta, rather deeply ridged and warty, about twice as long as broad, with a wide base; Cundeamor, strongly ridged and warty, narrower than half of its length, rather acute at the apex, constricted above the base; Amelonado, oblong, ellipsoid, obtuse, rather smooth with rather shallow

furrows and not constricted above the base; Calabacillo, shortly ellipsoid or almost round, the surface smooth with very shallow furrows. Figs. 5, 6, 20, 22, 24, 25.

The *Trinitarios* also are Forasteros with features intermediate to Criollo, being variable in shape and in seed characters. They probably originated by interbreeding in the Venezuelan Orinoco basin, from which they were introduced to Trinidad where they acquired new genes from old Criollo plantations and developed extensively. Later they were brought to Venezuela (receiving the name Trinitario), to Ceylon, and more recently to other countries. Trinitarios are cocoas with well-balanced conditions of hardness and quality of product. Cacao Nacional of Ecuador is another special Forastero of superior quality. (See van Hall, Baker, etc.)

At the Eighth Inter-American Cacao Conference (1960) an "International Register of Cacao Cultivars" was established, to be organized under the chairmanship of Dr. B. G. D. Bartley, of Trinidad.

Section 4. Telmatocarpus

Theobroma sect. *Telmatocarpus* Bernoulli, Uebers. Art. Theobroma 11. 1869.

FIGURE 4

Sect. *Bubroma* subsect. *Telmatocarpus* (Bernoulli) Pittier, Rev. Bot. Appl. **10**(110):779. 1930.

Petal-lamina lacking. Petal-hood 5-nerved. Staminodes long-caudate, flagelliform, ovate-enlarged at base, flexuose in aestivation. Filaments 3-antheriferous. Fruit ovoid, ellipsoid or globose, the pericarp thick, costate-nervate-reticulate and lacunose, pilose, or tomentulose, the endocarp rigid, thin-woody. Leaves beneath puberulous or subglabrous. Germination hypogeous. Inflorescences axillary on trunk, small, the peduncles solitary or 2 or 3. Main axis sympodial with pseudoapical growth; orthotropic shoots from axillary buds of the terminal jorquette. Primary branching ternate.

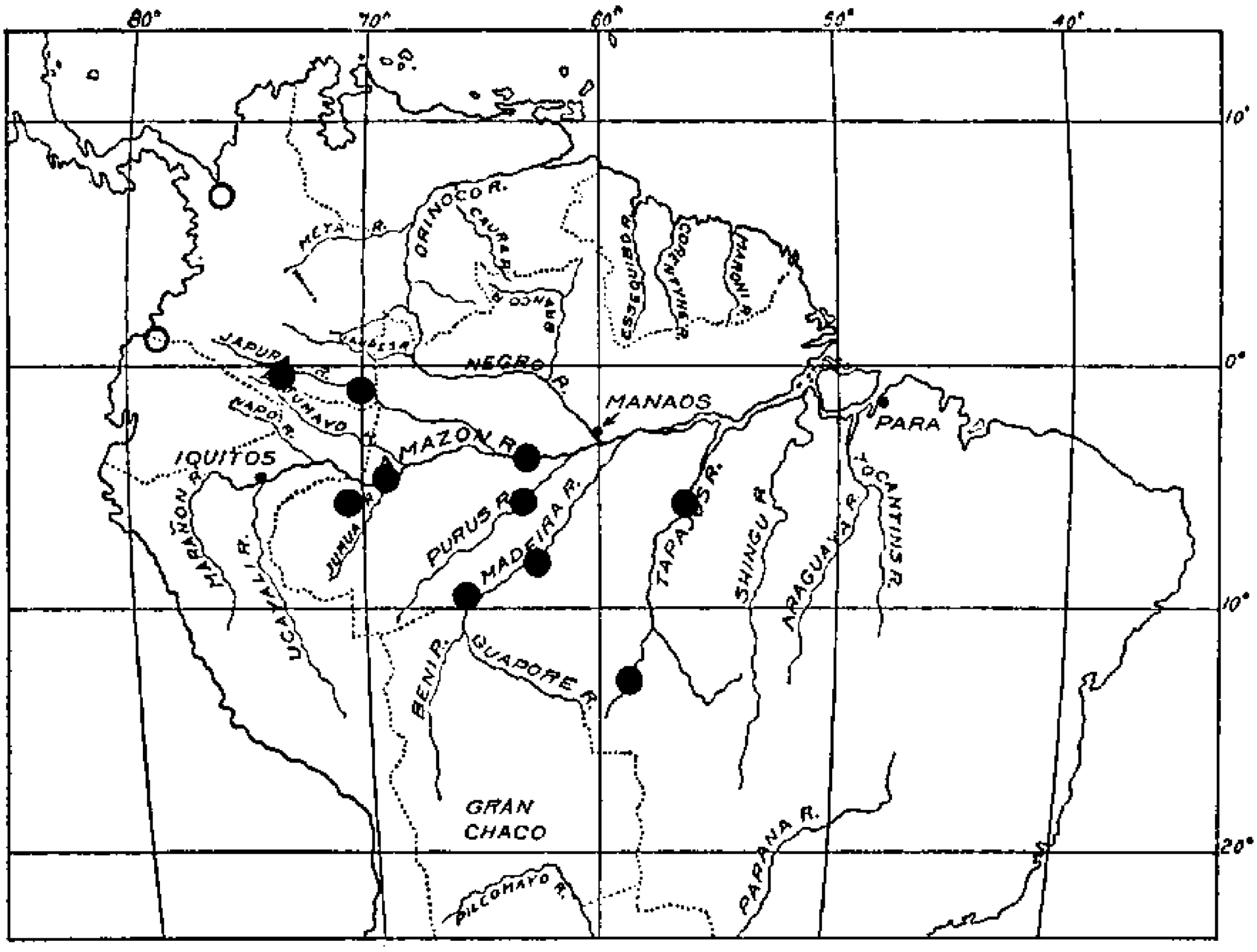
Type species: *Theobroma microcarpum* Mart.

8. Theobroma gileri Cuatr. FIGURES 5, 6, 26, 27, 28, 29; MAP 7

Theobroma gileri Cuatr. Rev. Intern. Bot. Appl. **33**:562, *fig. 1.* 1953; Baker, Cope & al. (1954) 13, *fig. 19;* León (1960) 316, 315. *fig.*

TYPE.—Esmeraldas, Ecuador, *Manuel Giler* 162 (flowers), 168 (fruits).

Small tree up to 14 m. high; growth pseudoapical; trunk 20 cm. in diameter, brownish, the bark orange in section, the wood white, rather hard; primary branches ternate-verticillate, light brown, warty lenticellate, glabrous; terminal branchlets thin, the hornotinous stellate-puberulous or pubescent; stipules narrowly subulate, minutely stellate-pubescent, 5–8 mm. long, deciduous.



MAP 7.—Geographical distribution of *Theobroma microcarpum* ● and *T. gileri* ○, the two vicariant species (eastern and western of the Andes) of the sect. *Telmatocarpus*.

Leaves distichous, thin-coriaceous; petioles 3–5 mm. long, mediocre, subterete, stellate-tomentulose, 3–5 mm. long; blade elliptic-lanceolate, narrowed and caudate at apex, asymmetrically rounded at base, entire, 6–22.5 cm. long and 1.5–8 cm. broad (usually 7.5–13 x 2–4 cm.) including the acumen, this acute, 12–25 mm. long, shining above, sparsely stellate-puberulous when young, glabrous or subglabrous when adult except for the midrib, sparsely callous-granulate, the midrib and secondary nerves conspicuous, with scattered appressed stellate hairs beneath, these more copious on the main nerves, but the prominent midrib stellate-tomentulose with smaller stellate hairs, the 5 or 6 secondary nerves each side filiform, conspicuously prominent, arched-ascending, near the margin decurrent and anastomosing, the transverse tertiary nerves prominent, the lesser veins prominulous loosely reticulate.

Inflorescences on tubercular growths on trunk and on the branches, the cymes few-flowered, often reduced to one flower, the axis very short, knotty, bracteate; peduncle erect, filiform, 5–25 mm. long, 3-bracteolate at apex, the pedicel 7–8 mm. long, somewhat thickened toward the apex, scattered pilose; sepals ovate-lanceolate, rather thick, reddish or purplish, glabrous inside, greenish or ochraceous and stellate-tomentulose outside, minutely tomentulose at margin,

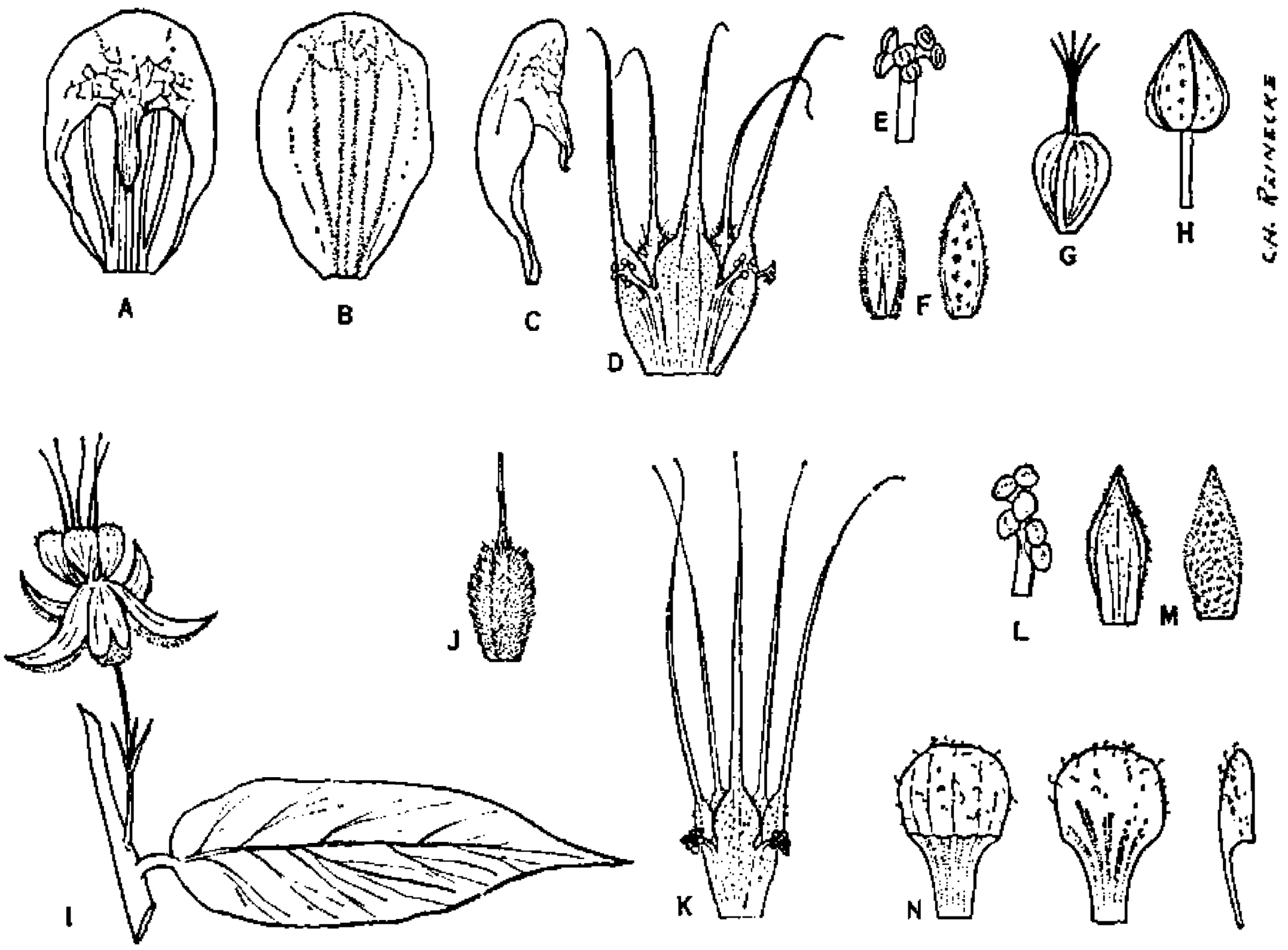


FIGURE 27.—A–H, *Theobroma microcarpum* (Ducke 21045): A, B, C, petal from inside, outside, and laterally, × 5; D, androecium, × 5; E, stamen, × 10; F, sepal from inside and outside, × 2; G, pistil, × 5; H, bud, × 2. I–N, *T. gileri* (Giler 162): I, flower on branch; J, ovary, × 5; K, androecium, × 5; L, stamen, × 10; M, sepal from inside and outside, × 2; N, petal from inside, outside, and laterally, × 5.

united 1–1.5 mm. at base, about 6 mm. long, 3 mm. broad; petal-hoods purplish-red obovate, very narrowed in the lower third, rounded-cucullate, muticous or emarginate at apex, with no appendix, sparsely covered with slender hairs above, with 5 prominent minutely pilose nerves inside, 3–3.2 mm. long, 2.2 mm. broad; androecium purplish red, the tube about 1.2 mm. high, minutely puberulous; staminodes about 7 mm. long, the base laminar, ovate, 1 mm. long and wide, with minute, thick hairs, suddenly narrowed at apex into a subulate, flexuous, flagelliform, glabrous appendix about 6 mm. long; filaments white, rather thick, glabrous, shortly trifurcate, triantheriferous; anthers bilobate, the thecae ellipsoid; ovary ovoid or ellipsoid 5-angulate, densely stellate-tomentose; styles glabrous, about 1 mm. long, coherent.

Fruit ovoid or ellipsoid at maturity, 7.5–11 cm. long, 7.5–9 cm. broad, brownish green or olivaceous, appressed stellate-tomentose, with 5 longitudinal prominulous ribs and irregularly, loosely, reticulate prominulous nerves, the intermediate surface shallowly depressed; pericarp 1 cm. thick, with a pelliclelike epicarp, a thick carnose, very mucilaginous mesocarp, and an inner, 1 mm. thick, coriaceous,

ligneous, hard endocarp, inside with a sweet, flavorous, ochraceous-white pulp surrounding the seeds; seeds ovoid or ovoid-oblong, 2.5–3 cm. long, 1.8–2 cm. broad, 1.5 cm. thick, usually 20–25 in a pod, the

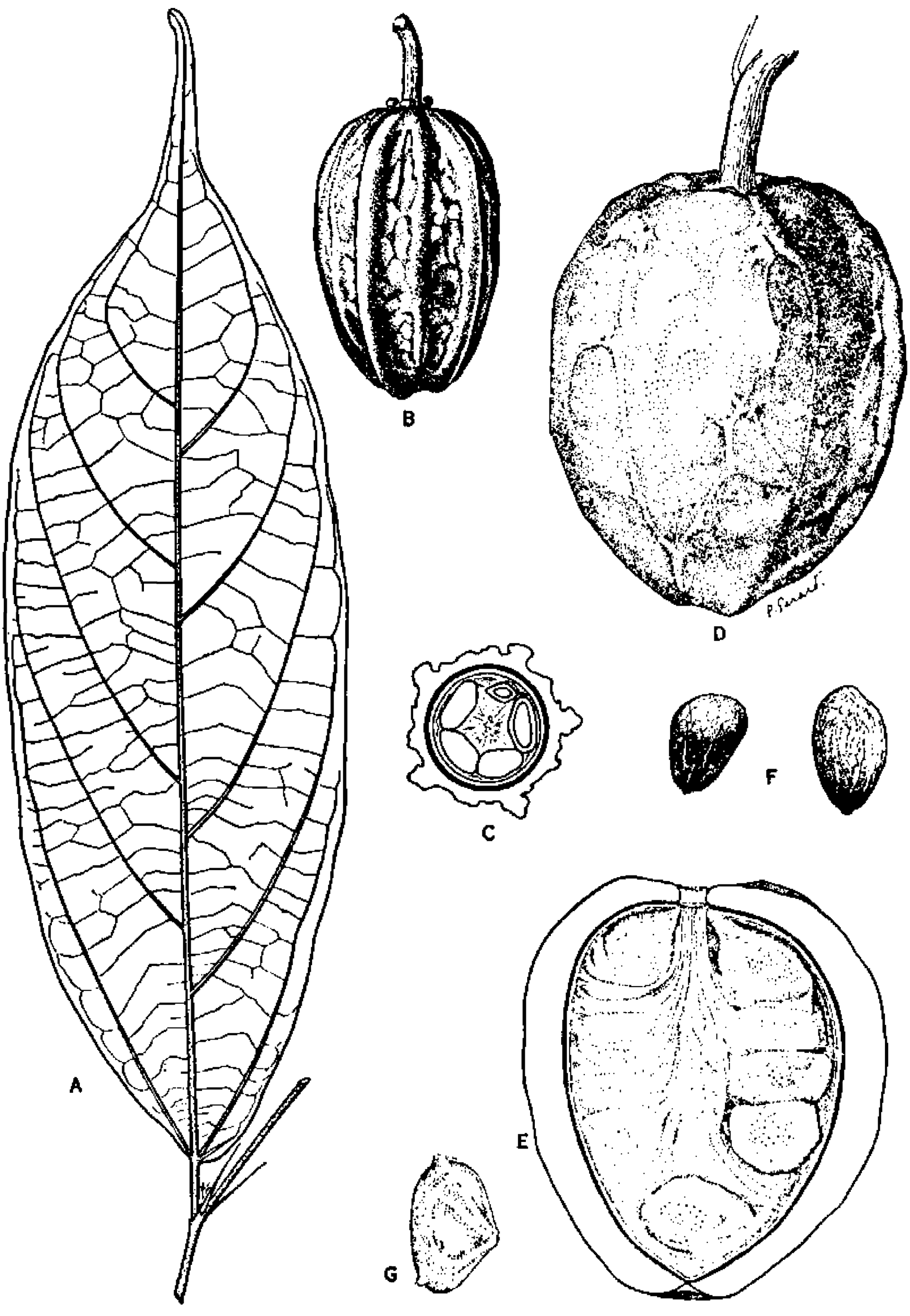
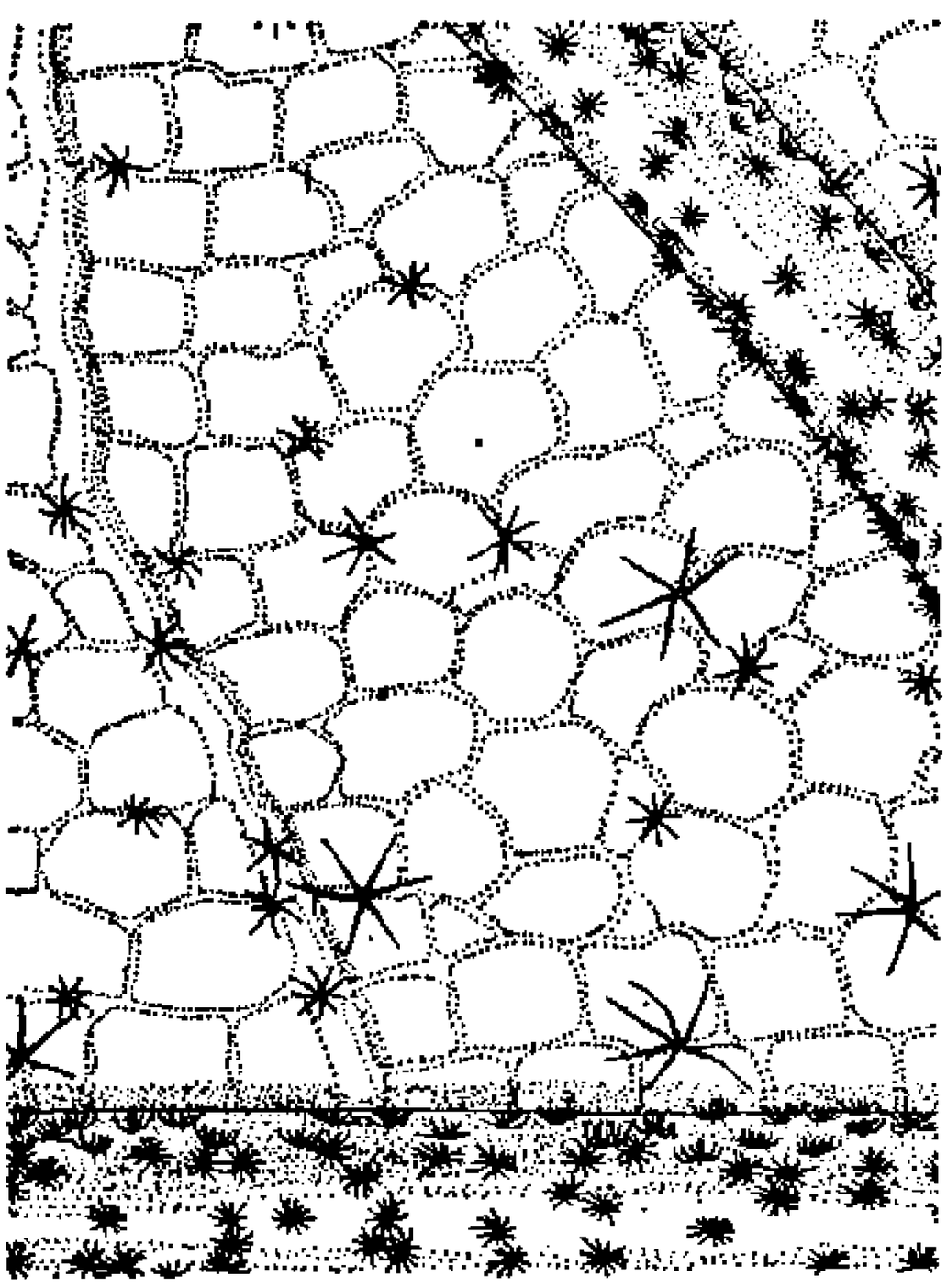
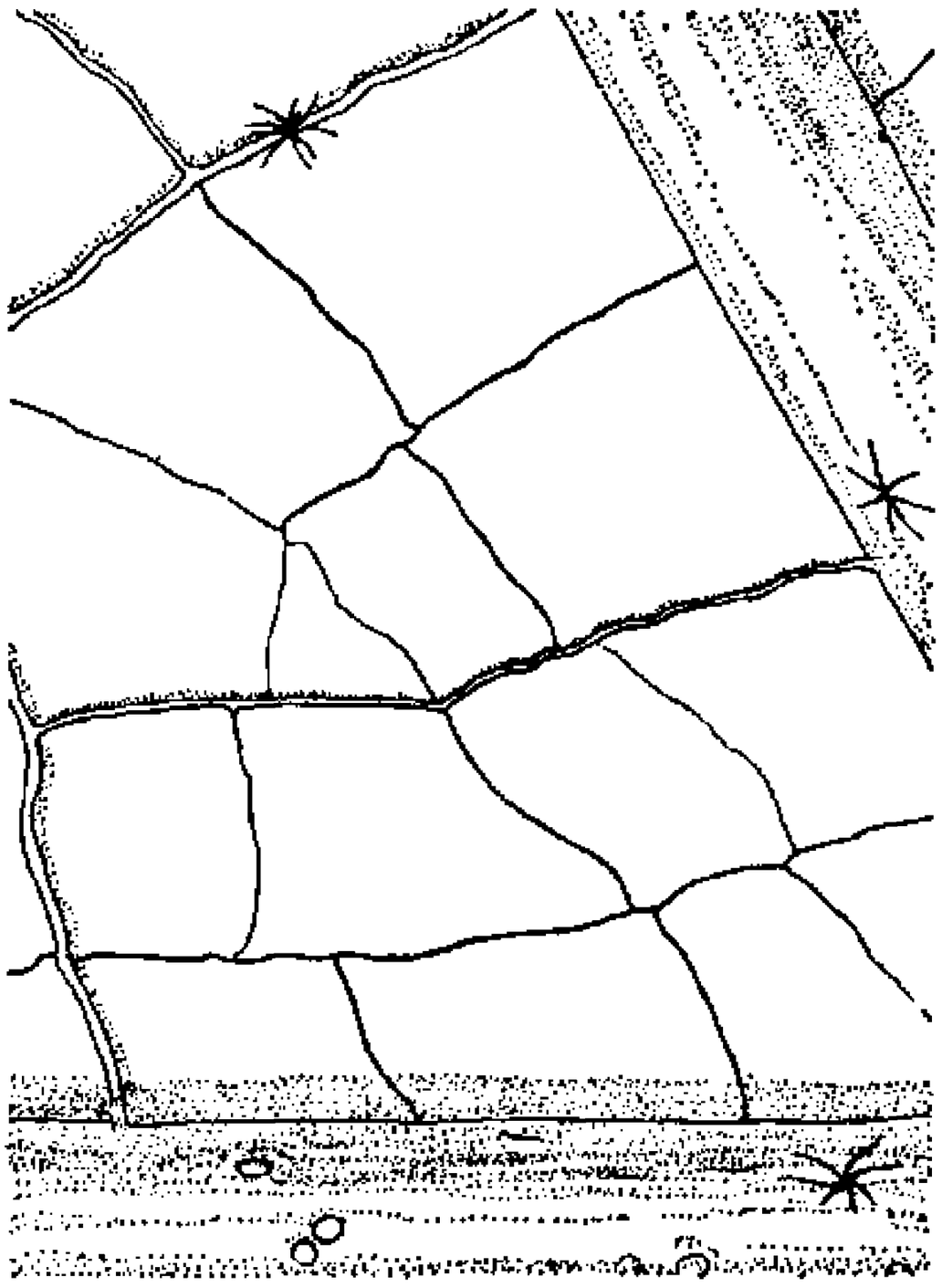


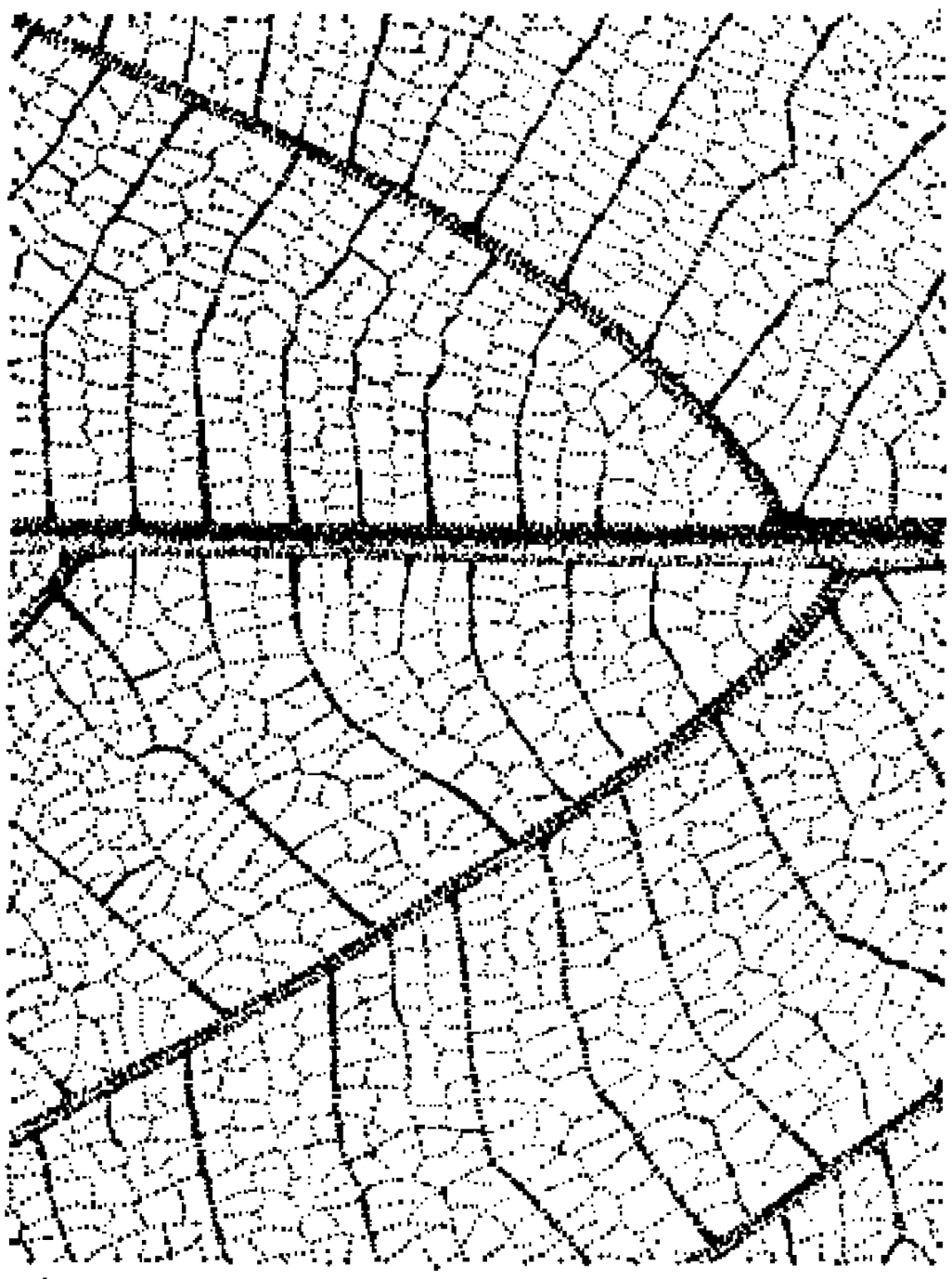
FIGURE 28.—*Theobroma gileri* (Giler 162, 168): A, leaf, × 1; B, young, ribbed fruit, × ½; C, transection of same; D, mature fruit, × ½; E, long. section of same; F, two seeds stripped from pulp, × ½; G, seed with its pulp, × ½.

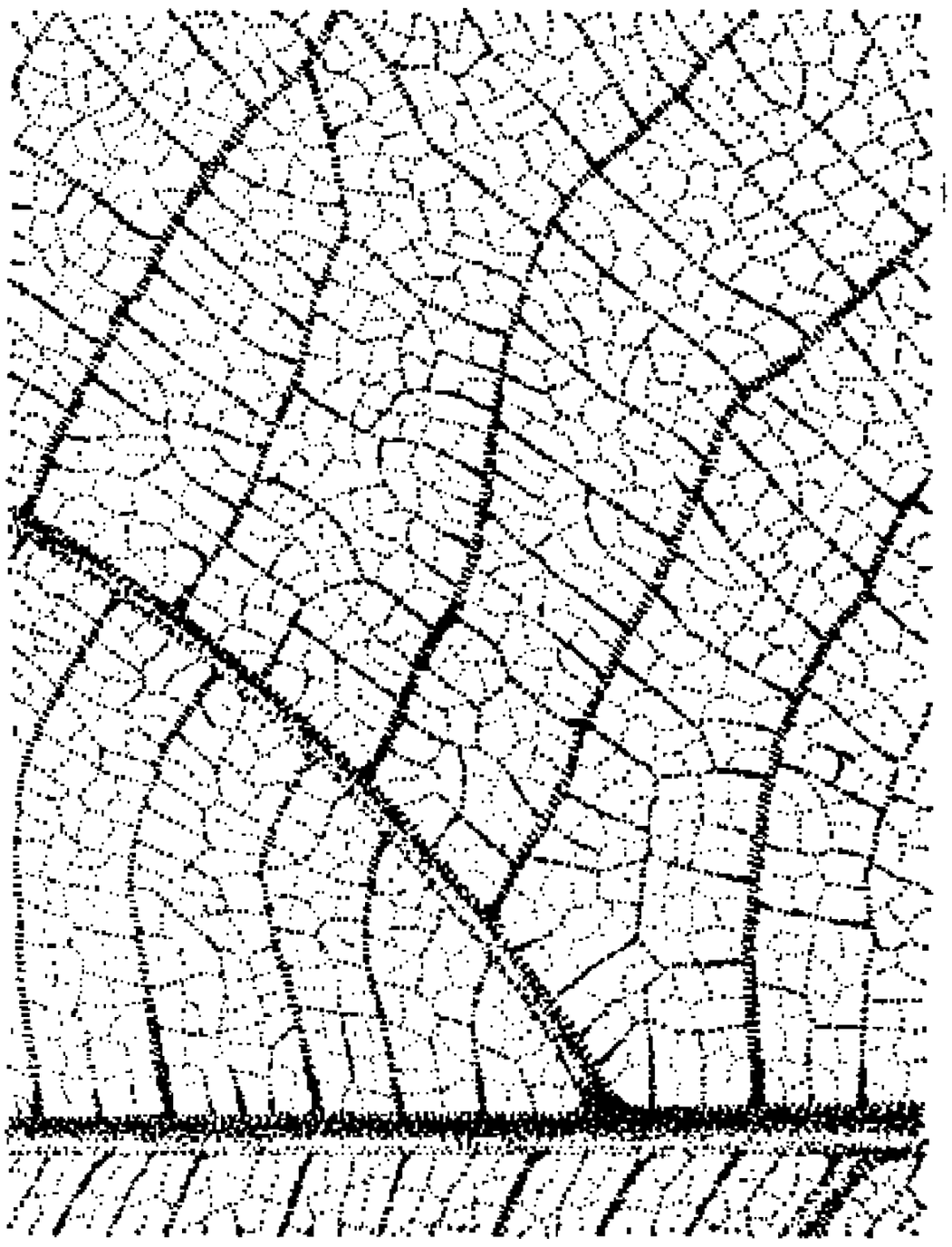




A

B





C

D

FIGURE 29.—A, B, Detail of indument on the underside of the leaf in: A, *Theobroma gileri* (Giler 162); B, *T. microcarpum* (Krukoff 1644). C, D, detail of nervation at the underside of the leaf in: C, *T. angustifolium* (Allen 6259); D, *T. subincanum* (Cuatr. 7277). A × 35, B × 25, C and D × 2.

cotyledons white, when fresh condition.[1] The juvenile fruits are ellipsoid or oblong-ellipsoid, with 5 very strong, protuberant ribs and 5 less prominent ribs, these sometimes becoming covered by the fleshy mesocarp at maturity, but often mature fruits are strongly 10-ribbed; fruiting peduncle 2–3 cm. long, about 6 mm. in diameter; germination hypogeous.

The fruits of *T. gileri* are conspicuously larger than those of *T. microcarpum*, its Amazonian vicariant; they are more oblong-ellipsoid or more oblong in shape. The young fruits have 10 very prominent and thick ribs, 5 of them much stronger than the alternate, and a coarse reticulum between the ribs. In a perfect, healthy, mature fruit, the surface becomes slightly 5-ribbed and shallowly reticulate-lacunose, the fleshy tissue of the mesocarp having filled up the spaces between the ribs, as is shown in *fig. 28*. But often mature fruits keep the 10-ribbed, strongly reticulate shape of the young stage, looking very similar then to the fruits of *T. bicolor*. Both kinds and different sizes of fruits are usually seen on the same tree. The trees are commonly 8–10 m. high in heavy rain forests. The growth is pseudo-terminal, that is to say, by shoots produced above the terminal whorl of branches or jorquette. The branching is normally verticillate (ternate) but often *T. gileri* develops adventitious, upright shoots which give irregularity to the branching. Fungus diseases may have some influence in this. Already in 1953 Patiño wrote: "Unfortunately, in spite of the abundance of trees, this species does not seem to offer much commercial prospects, because almost all fruits we found were diseased. I sent specimens to Quito to identify the responsible fungi," and he says further: "Almost all fruits we saw suffer a disease which hardens the mucilaginous tissue making it compact and hardening the seeds, many are covered by a mashy down, partly or the whole." I have seen myself the same, very recently near Villa Arteaga. Baker et al. wrote: "Seeds of this species were sent to Trinidad but arrived in a decomposed condition. The fungus *Monilia roreri* Ciferri was found infecting fruit of this species."

COMMON NAMES.—Chocolate de monte.

USES.—Natives used to chew or eat the pulp, which is sweet and aromatic. They prepare also a chocolate which is said to have a good taste (Patiño).

DISTRIBUTION.—Restricted to the rain forests of western Colombia and northwestern Ecuador.

COLOMBIA: ANTIOQUIA: Villa Arteaga; tree 10–12 m., 15–18 cm. in diameter at base, flowers not seen but borne in cushions on trunk and main branches, fruit about 9 x 7 cm., ridged and reticulate, said to be yellow at maturity, jorquette

[1] Holdridge reports them purplish when cut.

symmetrical, 22 VII 1953, *Holliday & Bartley* T./163 (TRIN, US). Ibidem; tree about 10 m., dry fruit 0–9.5 x 7–7.5 cm., no flowers, 24 VII 1923, *Holliday & Bartley* T/167 (TRIN, US). Mutatá, in virgin forest on slope above Villa Arteaga, 250 m. alt.; small tree, 8 m. tall, 18 cm. DBH, cauliflorous and ramiflorous, sepals greenbacked but reddish inside, petals dark blood red, base of central column reddish, fruit 10-furrowed, elliptical in long section, about 15 cm. long, seeds purplish inside when cut, 23 IX 1959, *Holdridge* 5133 (US). Ibidem, about 150 feet alt.; tree 12 m. tall, 6–20 II 1953, *Schultes & Cabrera* 18695 (US). Villa Arteaga, Las Caucheras, Villa Agraria, rain forest, 200 m. alt.; tree 15 m. tall, stem 8 cm. in diam., crown narrow, primary branches ternate, abundant inflorescence-cushions (now dry, woody) on the trunk and oldest branches, many old fruits on trunk and fallen, and some green ones, hanging, leaves chartaceous, firm, fruits 10 x 7 cm., 10 x 6.5, 11 x 7.5, 11 x 8 cm., 2 X 1961, *Cuatrecasas & Willard* 26167 (COL, US).

ECUADOR: Esmeraldas: Río Mira, Guadual, near Piguambí camp, 27 VII 1953, *Giler* 162 (holotype, F, 1423965; isotypes, F, US). Ibidem (fruits), *Giler* 168 (paratype, F). Ibidem, *Giler & Patiño* 164, 165, 166 (H. Cuatr.). Probably at Río Mira; fruit collected by *Acosta Solis & Giler* 12392, 12423 (F). Santo Domingo de los Colorados, cultivated from seeds brought from Lita, 27 IX 1957, *Jorge León* 4832 (TURRI).

9. **Theobroma microcarpum** Mart. Figures 26, 27, 29, 35; Map 7

Theobroma microcarpum Mart. in Buchn. Repert. **35**: 24. 1830; Linnaea, Litt. Bericht. 32. 1831; Bernoulli (1869) 11, *pl. 5;* Schumann in Mart. (1886) 75; Jumelle (1899) 32, *fig. 17;* De Wildeman (1902) 95; Huber (1906a) 273; Ducke (1925) 131; (1940) 271, *pl. 1, fig. 4;* (1953) 14; Chevalier (1946) 277; Addison & Tavares (1951) 25, *pl. 9, 12, fig. 5;* Baker, Cope & al. (1954) 12, *fig. 11*; León (1960) 316, 321, *fig.*

Type.—Brazil, Rio Negro, *Martius.*

Small tree up to 10–20 m. high; stem 20–30 cm. in diameter; growth pseudoapical; crown small; branches much ramose, ternate at least when young, brownish rugulose; branchlets thin, the hornotinous appressed stellate-tomentose, cinereous or pale ochraceous, becoming glabrous in age; stipules narrow, subulate, pubescent, 2.5–4 mm. long, soon deciduous.

Leaves chartaceous, light green; petioles mediocre, subterete, appressed tomentose, when older transversely wrinkled, 4–8 mm. long (in very young specimens longer, up to 15 mm.); blades triplinerved, elliptic-oblong or obovate-oblong, attenuate near the base, rounded or shortly attenuate at apex, abruptly long-acuminate, asymmetrically rounded at base or sometimes rounded one side, the other cuneate, rarely symmetrically cuneate, 6–18.5 cm. long, 2–7 cm. broad, including the acumen, this 0.7–2.5 cm. long, the margin entire, with scattered minute, simple and stellate hairs above and pubescent costa or glabrous throughout, the main nerves filiform, conspicuous, the loose reticulum almost obsolete, with sparse, minute, stellate hairs beneath or subglabrous, the principal nerves more or less minutely tomentellous or glabrate, the costa and the lower pair of lateral ascending nerves

prominent, the other 2–4 secondary nerves each side thin but prominent, ascending, curved near the margin, anastomosing, the slender, transverse tertiary nerves prominulous and the minor reticulate veins less prominulous, but conspicuous.

Inflorescences axillary or extra-axillary on young leafy branchlets, the cymose clusters extremely small, bearing 1–3 flowers, the woody primary branches short, knotty, bearing ovate, amplectant bracts, 0.6 mm. long and wide; peduncles rather thick, 0.5–1 mm. long, tomentulose, with 3 subulate, deciduous bracteoles at apex, these 0.6–1 mm. long; pedicels 0.5–1 mm. long, moderately thick, tomentulose; buds ovoid, acute, 4.5 mm. long, 3 mm. broad, with 5 whitish, minutely tomentulose lines and scattered, minute stellate hairs.

Sepals thick-membranaceous, lanceolate, acute, united about 1 mm. at base, 5–6 mm. long, 2 mm. broad, with scattered, minute, stellate hairs outside, minutely, whitish tomentulose at margin, with conspicuous midrib and sparse, mediocre, flexuous, glandular hairs inside; petal-hoods pale brown, thick-membranaceous, glabrous, oblong-obovate, rounded-cucullate and acuminate at apex, the acumen triangular, shortly bidentate, exappendiculate, the 5 nerves rather thick, prominent and minutely papillose inside, often confluent into pairs near the base; androecium red or reddish, the tube about 1.5 mm. high, 10-furrowed, minutely pilose; staminodes minutely pilose with a rather thick, oblong-ovate concave base, this 2.5 mm. long and 1 mm. broad with fine flexuose hairs inside, topped by a subulate, flexuose tail 4–5 mm. long; filaments rather thick, 1 mm. long, shortly 3-furcate, triantheriferous; cells of anthers ellipsoid, about 0.4 mm. long; ovary 1.5–1.8 mm. long, pyriform, glabrous or sparsely, minutely stellate-pilose, sharply 10-furrowed-costate; styles 5, united in the lower fourth, rather thick, acute, glabrous.

Young fruit ellipsoid (±3 cm. long), strongly 10-ribbed, with 5 very thick and prominent, dorsal, shortly pinnate costae, and 5 smaller, commissural ones; mature fruit 6.5–7 (–9) cm. long, 5.5–6.5 cm. broad, green yellowish, puberulous, ellipsoid-globose, conspicuously 10-ribbed, the surface between the ribs shallowly alveolate, the exocarp thick, carnose, padding the hollows between the lignose underlayer, when dry the ribs and the lignose reticulum become extremely marked and prominent; seeds more or less compressed, ovoid, 12–14 mm. long, 18–20 mm. broad, and 11–12 mm. thick; fruiting peduncle thick, robust, 4–8 mm. long and broad; cotyledons hypogeous at germination.

COMMON NAMES.—Cacauí, cacaurana, cacao rana, cacau bravo, cabeça de urubú (Brazil). Cacao de monte (Colombia). Me-tró-ree-moo-ee (*Karihona*, Upper Apaporis); bóo-e (*Mirana*, Caquetá River) (Angl-Col. Cocoa Exp., Baker, 1952).

USES.—None recorded on the use of its sweet scentless pulp or the seeds.

DISTRIBUTION.—In the southern and western upper Amazon Brasilian region Rios Solimoes, Yapurá, Purús, Madeira, Tapajós, and western Colombia on Caquetá River. (Baker & Cope.) The eastern known limit according to Ducke is Rio Tapajós. The specimens around Belém are cultivated. It is frequent in its area and may become abundant in some places as a significant element of the shadowy under layer of rain forests on elevated ground and in moderately inundatable alluvial lands.

COLOMBIA: AMAZONAS: Río Caquetá, La Pedrera, river level; tall tree 15–20 m., 30 cm. in diam. at base, extensive branch system, jorquettes of seedlings 3-branched, growth continuing from above, flowers small, petals without ligules, fruit abnormal due to attack by *Marasmius perniciosus*, 5 X 1952, *Baker & Cope* 28 (COL, K, TRIN, US). Ibidem; tall tree 15–20 m., native in forest on the riverbank, 7 X 1952, *Baker & Cope* 29 (COL, F, K, TRIN, US). Ibidem; tree 30 feet, 9 inches in diameter, on floodbank, 5 X 1952, *Schultes & I. Cabrera* 17780 (AMES, US). Río Caquetá, Remolino; leaves only from small seedling tree 2.5 m., typical *Theobroma* habit, jorquettes arising symmetrically, 2 V 1953, *Cope & Holliday* T/125 (COL, TRIN, US).

BRAZIL: AMAZONAS: In sylvis ad Costa de Ubicuna et de Camarocoari, fluv. Solimoes, prov. Rio Negro ("Dr. Martius Iter Brasiliensis, 321"), *Martius* Observ. 2890, [884] (M, lectotype, photo F. M. 19643). Ibidem, *Martius* Observ. 2890, [885, 886] (M, isotypes). Lower Rio Yapurá, Jubará matta, 15 IX 1904, *Ducke* 6773 (BM, MG). Basin of Rio Solimoes, Municipality São Paulo de Olivença, near Palmares; tree 60 ft. high, trunk 7 inches in diam., terra firma, high land, 11 IX–26 X 1936, *Krukoff* 8280 (A, BM, F, G, GB, K, LE, MICH, MO, P, S, U, US, USDA). Ibidem; mata, caatinga, "cacau bravo," arvore pequeña, 19 IV 1945, *Frões* 20750 (IAN, USDA), 34814 (IAN). Basin Rio Madeira, Municipality Humayta, near Livramento, on Rio Livramento on varzea land; tree 50 feet high, "cabeça de Urubú," 12 X–6 XI 1934, *Krukoff* 6592 (A, BM, F, G, K, LE, MICH, MO, S, U, US, USDA, WU). Ibidem, Municipality Humayta, near Tres Casas, on restinga alta; tree 60 ft. high, 14 IX–11 X 1934, *Krukoff* 6203 (A, F, G, K, LE, MO, S, U, US, USDA, Y). Rio Purus, Bom Lugar; "cacao rana," II 1904, *Goeldi* 4228 (BM, G, MG). Camatian; high forest lowland, border of creek; tree 7 m. high, 25 cm diam., 24 I 1949, *Frões* 23963 (IAN, US).

GUAPORE: Porto velho, Entrada de Redagan, Km. 8, Viana, mata derrumbada, terra firme; arvore pequena, 31 V 1952, *Black, Cordeiro, & Francisco* 52–14649 (IAN, UC).

MATO GROSSO: Machado River region, source of the Jatuarana River; tree 3 feet high in terra firma, "cabeca de urubu," XII 1931, *Krukoff* 1644 (A, BM, F, G, K, MICH, MO, P, S, U, UC).

PARÁ: Belém, Jardim Botanico do Museu Goeldi; medium tree, cultivated, 11 VIII 1942, *Archer* 7551 (F, IAN, K, USDA). Belém, Horto Botanico Pará (cultum proven. Rio Purus, Bom Lugar anno 1904), 25 V 1906, *Huber* 7081 (G, MG). Ibidem; arbor parva floribus rubescentibus, 4 II 1926, *Ducke* 21045 (G, GH, K, S, U, US). Ibidem; arbor parva, floribus pallide brunnescentibus, "cacaohy," IX 1936, *Ducke* 283 (A, F, K, MO, S, US). Ibidem, 21 VII 1944, *F. C. Camargo* 8 (IAN). Ibidem, 23 XI 1945, *Pires & Black* 742 (IAN). Rio Guama, near Belém, "cacao bravo," IV 1929, *Dahlgren & Sella* 10 (F, GH). Rio Tapajos, Cachoeira do Mangabal, beira de assahyzal, 7 IX 1916, *Ducke* 16466 (BM, G, MG, P, US).

COSTA RICA: (cult.) Limon, La Lola, experimental station IICA; tree 4 m. tall, narrow crown, eight years old, first flowers this year, 7 XI 1961, *Cuatrecasas & Paredes* 26538 (US).

Section 5. Glossopetalum

Theobroma sectio *Glossopetalum* Bernoulli, Uebers. Art. Theobroma 11. 1869

FIGURES 1, 3, 4; MAP 2

Sect. *Bubroma* Schum. in Engl. & Prantl. Nat. Pflanzenfam. **3**(6):89. 1890.

Sect. *Bubroma* subsect. *Glossopetalum* (Bernoulli) Pittier, Rev. Bot. Appl. **10** (110):779. 1930.

Petal-laminas obovate, spatulate or trapezoid, stipitate. Petal-hoods 7-nerved. Staminodes laminar, petaloid, obovate or broadly lanceolate, curved-reflexed covering the hoods in aestivation, erect or reflexed in anthesis. Filaments 3-antheriferous. Fruit ellipsoid or oblong, smooth or more or less angulate or tuberculate, the epicarp hard, woody, with a tomentose epidermis. Cotyledons hypogeous at germination. Leaves beneath reticulate-nerved, stellate-tomentose. Inflorescences on the main trunk or on the branches. Main axis sympodial with pseudoapical growth; orthotropic shoots from axillary buds of the terminal jorquette. Primary branching ternate.

TYPE SPECIES.—*Theobroma grandiflorum* Schumann.

10. **Theobroma angustifolium** Moçiño & Sessé

FIGURES 6, 25, 29, 30, 31, 37; MAP 8

Theobroma angustifolium Moçiño et Sessé ex DC. Prodr. 1: 484. 1824; Icon. Fl. Mexicana ex DC. *pl. 112;* Bernoulli (1869) 12, *pl. 6;* Schumann in Mart. (1886) 77; Donn. Smith in Pittier, Prim. Fl. Costar. 96. 1898; Preuss (1901) 255, *pl. 2,6;*De Wildeman (1902) 96, *figs. 12,13;* Standley (1923) 808; Standley (1937) 687; Chevalier (1946) 282; Standley & Steyermark (1949) 421; Holdridge (1950a) 3; Allen (1956) 342, *pl. 26;* León (1960) 318, 315, *fig.*

TYPE.—*Sessé et Moçiño*, Plantae Novae Hispaniae, Herbarium Florae Mexicanae.

Tree 8–26 m. high; trunk up to 30 cm. in diameter, with smooth bark and whitish wood; growth pseudoapical; primary branches ternate; lower branches horizontal, the higher ascending; branchlets when young green ochraceous, densely and moderately appressed tomentose, with very minute, fine, translucid-white stellate hairs intermixed with other mediocre, fulvous or ochraceous, somewhat thicker, stellate hairs, when older more or less glabrate, grayish, rugulose; stipules lanceolate-subulate, acute, broadened at base, above sparsely, below densely stellate-tomentose, 5–7 (–15) mm. long, about 1 (–2) mm. broad, deciduous.

Leaves distichous, thin-coriaceous, rather flexible; petioles moderately thick, densely subappressed tomentose, 6–10 mm. long; blades subobovate-oblong, elliptic-oblong, or oblanceolate, slightly narrowed

Map 8.—Geographical distribution of *Theobroma angustifolium* ● and *T. simiarum* ○.

to the obtuse and slightly asymmetrical base, attenuate and acuminate at apex, entire or at the upper part slightly sinuate-dentate, 9–25 cm. long and 3–9 cm. broad, including the 1–2 cm. long and 3–5 mm. wide acumen, green above, when adult smooth, glabrous or with few hairs scattered on the costa, this depressed, filiform, the secondary and tertiary nerves little conspicuous, light greenish or cinereous beneath, appressed tomentose, heteortrichous, the surface covered with a dense layer of white, minute, stellate hairs, and additional, more or less copious, larger, ochraceous, stellate hairs with longer rays on the main nerves, the costa very prominent, the 6–8 secondary nerves on each side thinner and prominent, ascending, near the margin decurrent, becoming slender, vanishing, the transverse tertiary nerves, thin, prominulous, 2–5 mm. from each other, the minute reticulum conspicuous.

Inflorescences usually abundant on the branchlets, axillary or extra-axillary, the cymes strongly reduced to a few extremely short 1–3-flowered branchlets; peduncles 0.4–1mm. long, 3-bracteolate; pedicels erect, rigid, mediocre, densely ochraceous or ferruginous, ebracteate, 5–10 mm. long; bracteoles very minute (1–0.5 mm. long), linear, deciduous; buds globose, 7–8 mm. broad, densely ochraceous tomentose; calyx 8–9 mm. long, reflexed in anthesis, all the sepals united to 3–4 mm. into a cupular base, in the upper part two united

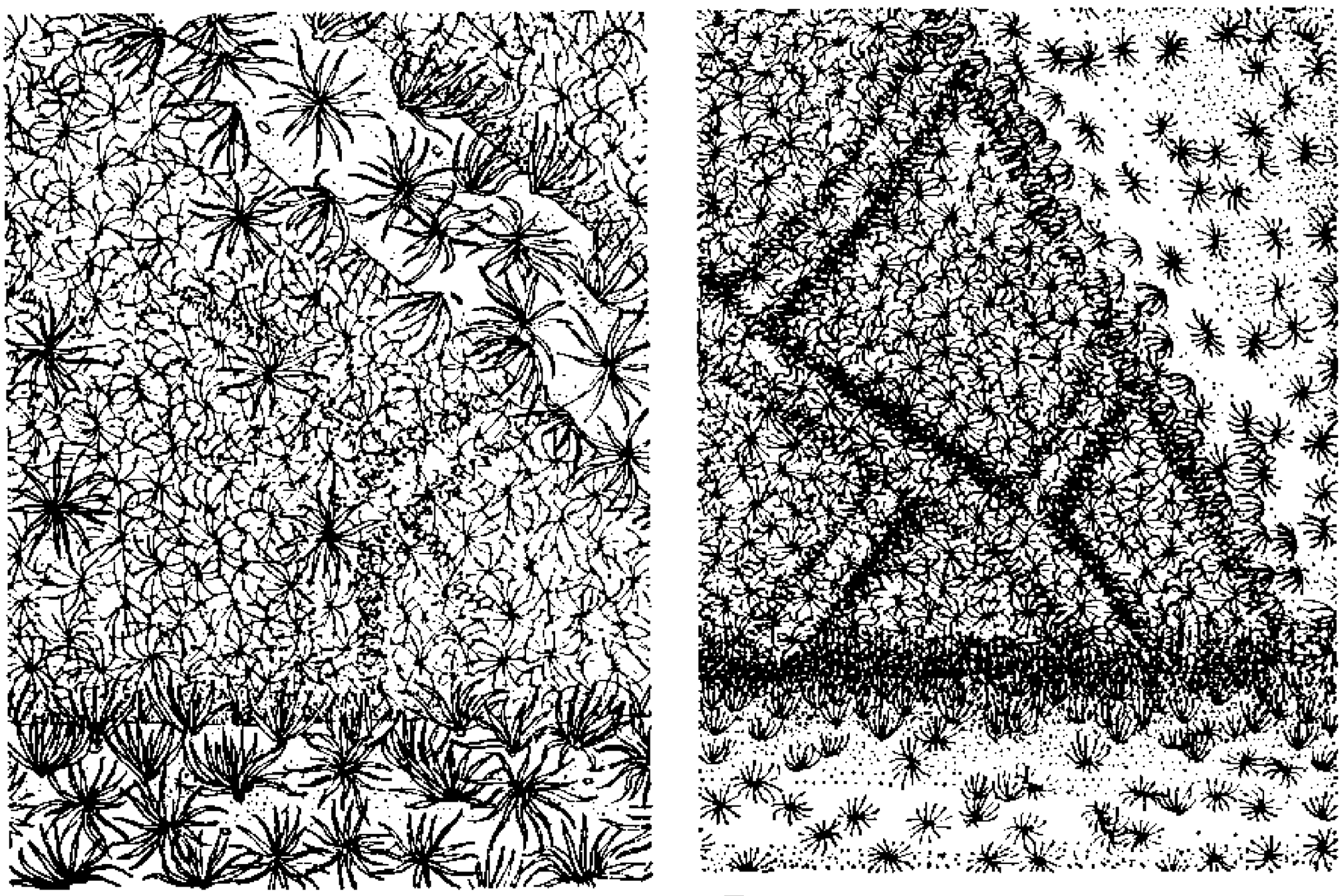
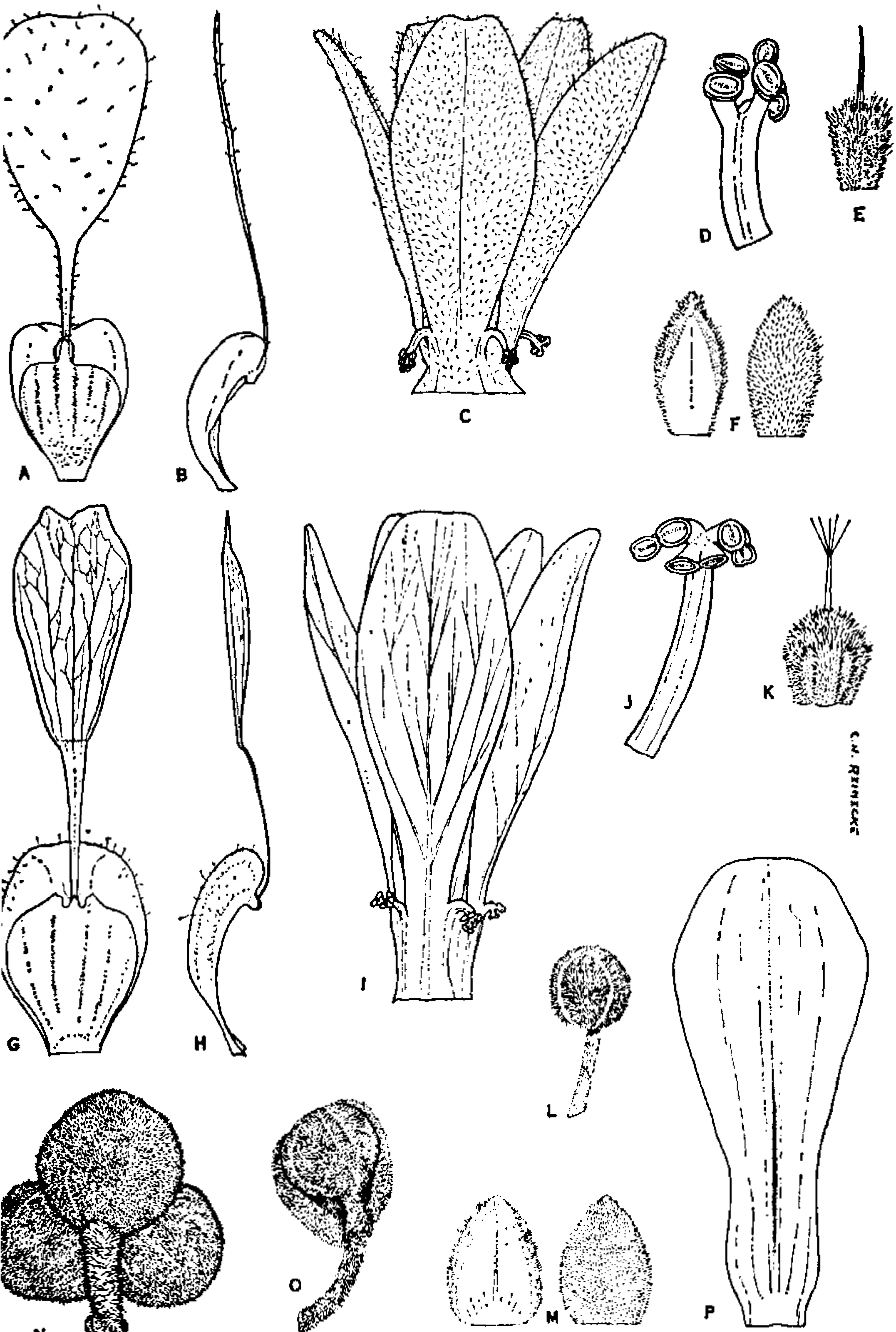


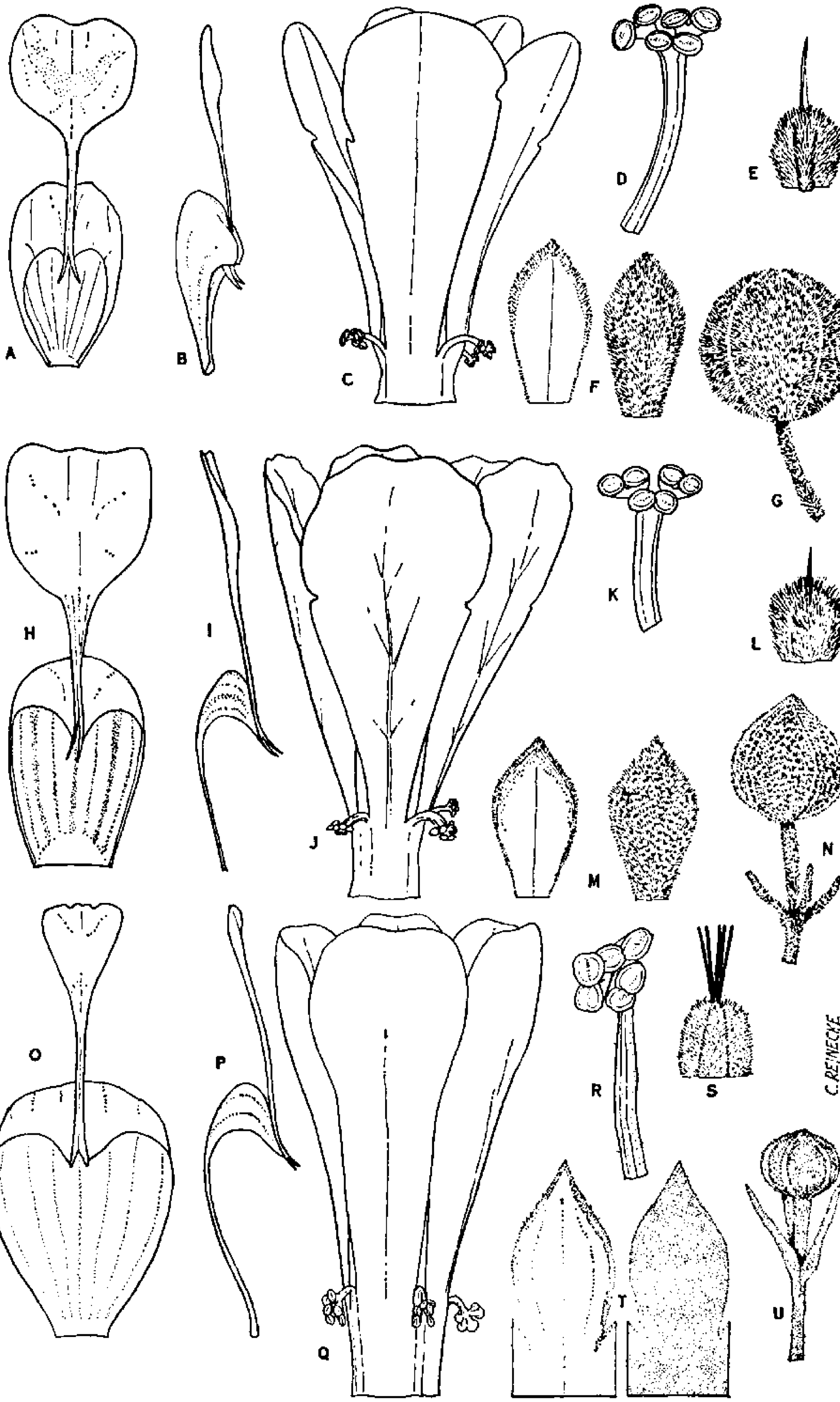
FIGURE 30.—Detail of indument on the underside of leaf in: A, *T. angustifolium* (Allen 6259); B, *T. cirmolinae* (Cuatr. 14897); C, detail of venation in *T. stipulatum* (Cuatr. 21339); D, indument in *T. stipulatum* (Cuatr. 21339). A, B, and D × 30, C × 2.

FIGURE 31.—A–F, *Theobroma nemorale* (Patiño 116): A, B, petal from inside and laterally, × 5; C, androecium, × 5; D, stamen, × 10; E, gynoecium, × 5; F, sepal from inside and outside, × 2. G–M, *T. angustifolium* (Allen 6341): G, H, petal from inside and laterally, × 5; I, androecium, × 5; J, stamen, × 10; K, gynoecium, × 5; L, bud, × 2;



[FIGURE 31]

M, sepal from inside and outside, × 2. N, O, *T. nemorale* (Cuatr. 26007): N, the three bracteoles covering the opening flower, × 2; O, pedicelled bud surrounded by a bracteole, the other two removed. P, *T. chocoense*, staminode, × 5 (Cuatr. 26074).



[FIGURE 32]

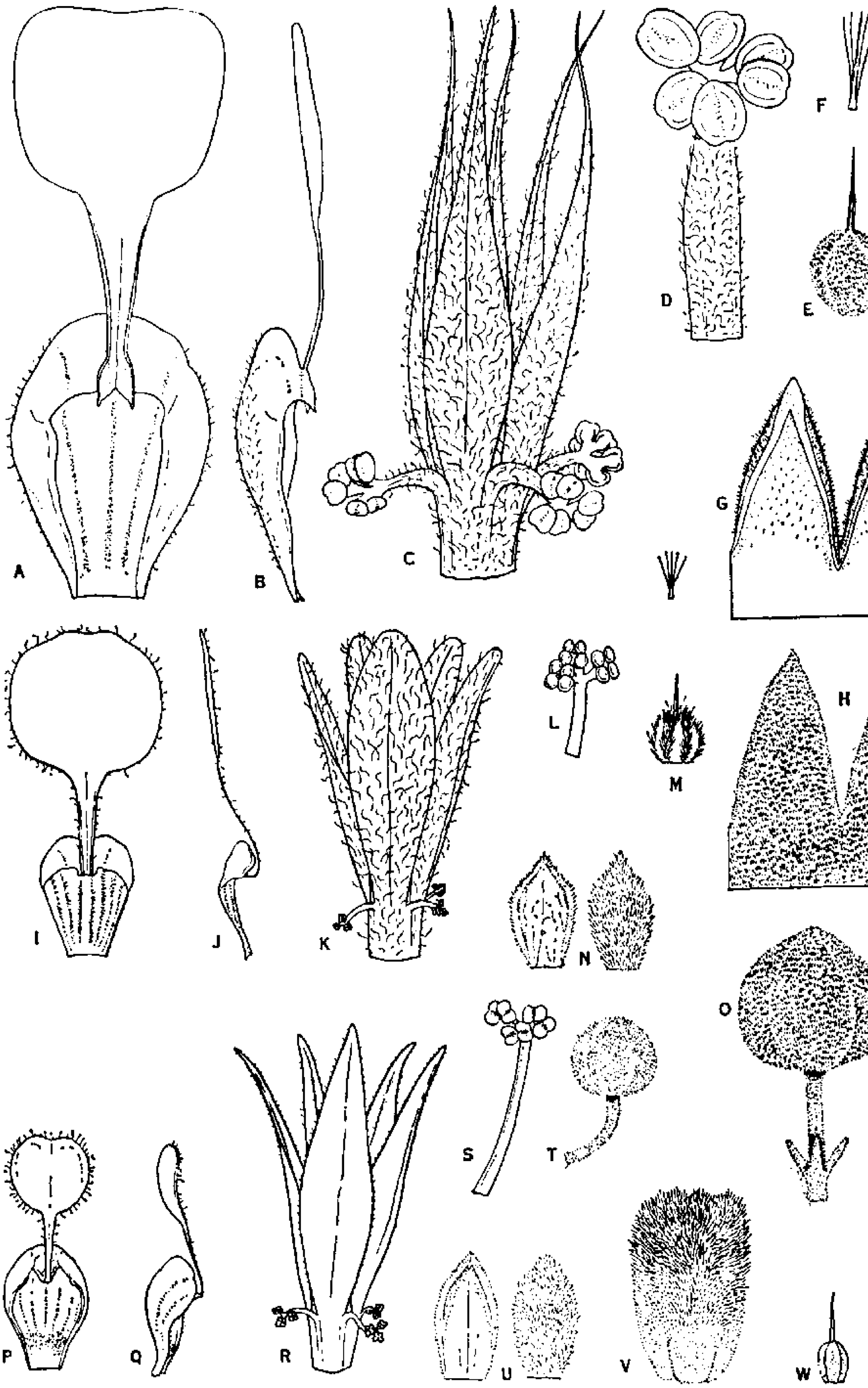
by pairs forming 3 unequal lobes, two of the lobes twice as broad as the third, ovate, rather obtuse, scarcely puberulous and with minute, thick, oblong glandular hairs at the base inside, tomentose, greenish ochraceous or ferruginous outside, each single sepal 4–5 mm. wide.

Petal-hoods thick-membranaceous, yellowish, broadly obovate, rounded-cucullate at apex, 7-nerved with very sparse, thin hairs outside, about 5 mm. long, 4 mm. broad; petal-lamina pedicellate, yellow, thick-membranaceous, 5-nerved and finely veined, subobovate-spatulate, emarginate at apex with 2 ovate or rounded lobes, attenuate towards the base, glabrous, about 5.5 mm. long, 3 mm. broad, the pedicel linear, 3-nerved, attenuate downward, about 4–5 mm. long, 1 mm. wide; androecium tube 2.5–3 mm. long, thick; staminodes laminar, thick-membranaceous, sulphur yellow, glabrous, oblong-obovate, rounded or subspatulate at apex, with marked venation, 8–11 mm. long, 4.2–5 mm. broad, at base 1.2 mm. broad, when in bud curved-reflexed, in anthesis erect; filaments glabrous, thick, curved, 2 mm. long, enlarged and shortly 3-furcate, 3-antheriferous; anther cells globose; ovary obovoid-oblong, about 1.5 mm. long, 5-sulcate, densely stellate-tomentose; styles 2.5 mm. long, united in a rigid erect column 1.5 mm. long, ending in 5 slender branches 1 mm. long.

Fruit unequally oblong-ellipsoid or ovoid-ellipsoid, more or less pentagonal, slightly attenuate at apex, umbilicate and 5-costate at base, very irregularly tuberculate-rugose, densely brown tomentose, the epicarp hard, ligneous, about 1.5 mm. thick, the mesocarp plus endocarp carnose 5–6 mm. thick, the pulp enveloping the seeds thick, juicy, aromatic, edible, 10–18 cm. long, 6–9 cm. broad; seeds 5–7 in each fruit compartment, compressed oblong-ovoid, 26–32 mm. long, 16–19 mm. broad, and 14–16 mm. thick, the cotyledons white; germination hypogeous.

The leaves of *T. angustifolium* are similar to those of *T. nemorale*, but they are narrower, rather lanceolate, and the larger hairs of the double indument beneath are longer with much finer, longer rays than those of *T. nemorale*. Paul Allen (1956) writes about this tree: "The young branches, petioles, and veins of the lower leaf surface are covered with a rather scurfy pale-tan tomentum. The relatively

FIGURE 32.—A–G, *Theobroma stipulatum* (Cuatr. 21339): A, B, petal from inside and laterally, × 5; C, androecium, × 5; D, stamen, × 10; E, gynoecium, × 5; F, sepal from inside and outside, × 2; G, bud, × 2. H–N, *T. simiarum* (Tonduz 7313): H, I, petal from inside and laterally, × 5; J, androecium, × 5; K, stamen, × 10; L, gynoecium, × 5; M, sepal from inside and outside, × 2; N, bud supported by pedicel and 3-bracteolate peduncle, × 2. O–U, *T. cirmolinae* (Cuatr. 14897): O, P, petal from inside and laterally, × 5; Q, androecium, × 5; R, stamen, × 10; S, gynoecium, × 5; T, sepal from inside and outside, × 2; U, pedunculate bud, × 2.



[FIGURE 33]

large, bright-orange flowers are produced in great profusion in several successive flowerings from November until February from the axils of the slender, younger branches, and are followed in August and September by the large, woody, brown-tomentose, cacaolike pendulous pods which are from 4″ to about 7″ in length."

COMMON NAMES.—Cacao de mico, cacao silvestre (Costa Rica), cushta, cacao de la India (Salvador), cacao silvestre (Mexico). Cacao de mico, cacao meco, coca mono (Nicaragua), soró (*Bribi* indians).

USES.—It was stated by Standley (1923) that *T. angustifolium* was much planted in southern Mexico, especially in Chiapas as a source of commercial cacao and that the famous Soconusco cacao was from this species. This statement is very doubtful, for the seeds of *T. angustifolium* are considered at present in that area as of inferior quality without commercial value.

DISTRIBUTION.—This species is often planted in Central America and southern Mexico. It is certainly native in the lowland forests of the Pacific range of Costa Rica (Allen) and nearby Central American countries (Holdridge). Standley and Steyermark (1949, 422) say that the native region of this cacao is unknown, but Tonduz already in 1891 cited it from the forests of Terraba; León (No. 937) writes: "Important tree in the regional forests," and Allen says that "it is locally frequent in lowland forests throughout the area [Golfo Dulce]."

MEXICO: Direción de Estudios Biológicos, Ord. 34–G823 (MEXU). Herbarium Sessé & Moçiño in M, "18–1, Theobroma Simiarum N. Ic," *Sessé, Moçiño, Castillo, & Maldonado* 3618 (holotype, MA; isotype, F, Photo F. M. 48411). *Sessé & Moçiño* s.n. (BM, probable isotype). Copy of the Sessé & Moçiño drawing at G (Negative F. M. 30527), plate 112 of the DC. published series.

GUATEMALA (cult.): Retaluleu, April, 1877, *Bernoulli & Cario* 3188 (GOET, K, S). Mazatenango, III 1865, cult., *Bernoulli* 95 (NY, BR). Region of Platanares, between Taxisco and Guazacapán (Dept. Santa Rosa), 220 m. alt., wet forested quebrada; small tree escaped here, 3 XII 1940, *Standley* 79068 (F, US).

SALVADOR (cult.): Sonsonate, "cushta," 1922, *Calderón* 630 (GH, NY, US). Vicinity of Sonsonate, 220–300 m. alt.; tree 20–30 feet, very dense and narrow crown, flowers on branches, fruit brown, the pulp edible with very aromatic odor, seeds give chocolate, grown here only in finca, "cushta," "cacao de la India," *Standley* 22317 (GH, MO, NY, US).

FIGURE 33.—A–H, *Theobroma grandiflorum* (Ducke 598): A, B, petal from inside and laterally, × 5; C, androecium, × 5; D, stamen, × 10; E, gynoecium, × 5; F, styles, × 5; G, sepals from inside, × 2; H, sepals from outside, × 2. I–O, *T. obovatum* (Ducke 265): I, J, petal from inside and laterally, × 5; K, androecium, × 5; L, stamen, × 10; M, gynoecium, × 5; N, sepal from inside and outside, × 2; O, bud supported by bracteolate peduncle and pedicel, × 2. P–W, *T. subincanum* (Baker & Cope 32 and Holliday 43): P, Q, petal, from inside and laterally, × 5; R, androecium, × 5; S, stamen, × 10; T, bud, × 2; U, sepal from inside and outside, × 2; V, initiation of fruit, × 5; W, ovary, × 5.

NICARAGUA: Quezalguaque, Dept. of León, *Baker* 2102 (A, AMES, C, GH, G, K, L, MICH, MO, NY, U, UC, US, WU). Chichigalpa, "cacao de mico," II 1900, *Preuss* 1381 (UC). Belén, "cacao meco," "coca mono," or "monkey cocoa," 28 VI 1893, *Hart* 5381 (K, NY, U).

COSTA RICA: GUANACASTE: Upper portion of cañón of Río San José, 460–480 m., 12, 13 II 1930, *Dodge & Thomas* 6399 (F, GH, MICH, MO, UC, US). Nicoya, 300 m. alt., VI 1949, *Lopez* s.n. (F, TURRI). Ibidem, *Pittier* s.n. (US). Hojancha de Nicoya, 20 m. árbol importante en la selva de la región, "cacao de mico," 29 I 1942, *León* 937 (F). Perico, Nicoya, 100 m., I 1954, *León* 4267 (TURRI). Borde du Río Zurquín, 3 1894, *Pittier & Durand* 8536 (P).

LIMON: Cienaguita, near Puerto Limón, 10 m. alt.; small tree with appressed crown, flowers sulphur yellow, VII 1901, *Pittier* 16142 (G, US, WU). La Lola, I.I.A.C.A. experimental station, about 20 m. alt.; tree erect, trunk about 25 cm. diam. at base; pseudoapical growth; primary branches ternate, spreading, persistent; leaves thin-coriaceous but firm, light green and somewhat glaucous and cinereous beneath; young fruits thickly tomentose, axillary flowers abundant, now dry, 6 XI 1961, *J. Cuatrecasas & Paredes* 26537 (US).

PUNTARENAS: Dans le forêt à Terraba, 260 m. alt., II 1891, *Tonduz* 4074 (US). Ibidem; "cacao de mico," II 1891, *Pittier & Tonduz* 4074 (BR, G). Boruca, Diquis Valley, 1891, *Pittier* s.n. (US). Tinoco Station, fairly frequent in swampy forest; tree 80 ft., fruits pendulous, produced from the ends of branches, "cacao de mico," 13 VII 1951, *Allen* 6259 (BH, MO, US). Lowland forest near Palmar Norte; tree 45 feet, flowers bright orange, *Allen* 6341 (BH, F, MO, US). Llanuras de Corredor (Golfo Dulce), III 1897, *Pittier* 11112 (G).

PANAMA: Progreso (Chiriquí); small tree 30 feet, 6 inches in diam., with a fruit like wild cacao except that the husk is smooth like a potato skin, big seeds with white meat inside, 1927, *Cooper & Slater* 242 (F, GH, NY, US, Y). Comarca del Barú, Puerto Armuelles, United Fruit Company farms between Canasco and Cocos, mostly cutover land with some of the original trees still standing, about 100 feet alt.; tree, fruit resembling a cacao pod; leaves pale bluish, green, beneath, 17 VI 1957, *Stern & Chambers* 140 (MO, US, Y).

TRINIDAD: Royal Botanic Gardens, Port-of-Spain, *L. H. Bailey*, s.n. (BH). Ibidem; small tree, flowers orange colour, 8 IX 1918 (originally from Guatemala), *Broadway* 8935 (BM, BR, MO, S). Ibidem; tree 8 m., flowers orange yellow, 10 VII 1953, *R. E. D. Baker* s.n. (TRIN). Government House Gardens, 12 III 1929, *Williams* 12121 (TRIN). St. Augustine, Imperial College of Tropical Agriculture; tree 3–4 m. alt., lower branches horizontal, upper ones ascending, bark granulose, lenticellate, more or less cleft, yellowish brown, abundant, hanging, very rugose dried fruits, 1 IX 1961, *Cuatrecasas & Cope* 25789 (US). Ibidem; tree about 8 m. (9 years old), trunk 20 cm. in diam. at base, primary branches ternate from near the base, leaves thin-coriaceous, yellowish green, shining above, greenish cinereous beneath, 1 IX 1961, *Cuatrecasas & Cope* 27591 (US).

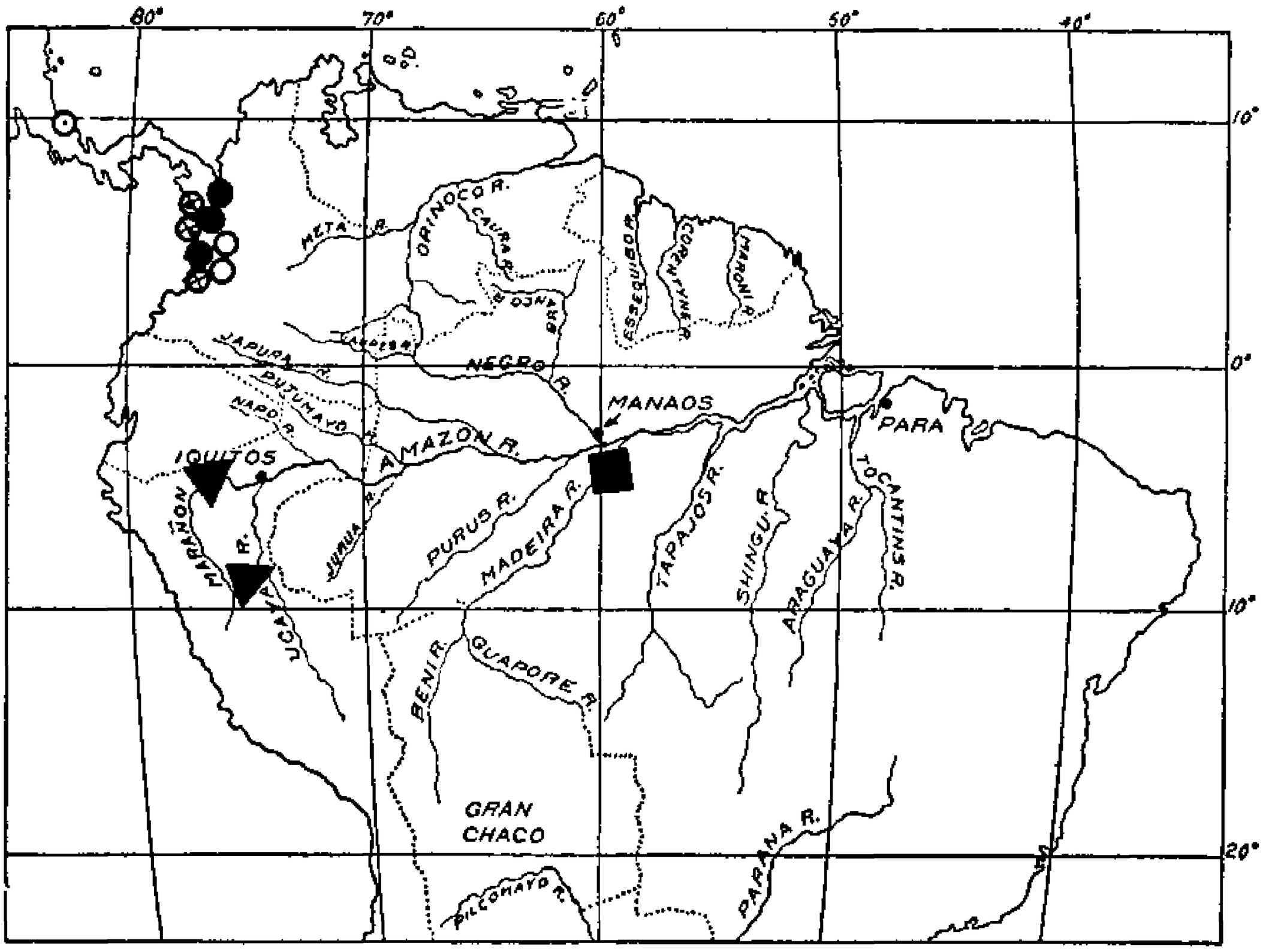
11. **Theobroma cirmolinae** Cuatr.

FIGURES 3, 4, 30, 32, 34, 36, 37; MAP 9; PLATE 7

Theobroma cirmolinae Cuatr. Notas Fl. Colomb. VI: 5, *fig. 1–5.* 1944; Rev. Acad. Colomb. Cienc. 6:32, *fig. 1–5.* 1944; Llano (1947) 34, *pl. 14;* Baker, Cope & al. (1954) 13, *fig. 22;* León (1960) 320, 317, *fig.*

TYPE.—El Valle, Colombia, *Cuatrecasas* 14897

Medium-sized or large tree up to 20 m. high; growth pseudoapical; trunk up to 40 cm. in diameter, branched in the upper third, the bark dark grayish, somewhat rimose-scaly, under the periderm brown or



MAP 9.—Geographical distribution of *Theobroma stipulatum* ●, *T. cirmolinae* ○, *T. chocoense* ⊕, *T. mammosum* ⊙, *T. sinuosum* ▲, and *T. canumanense* ■.

rufous, the wood ochraceous, the hardwood ochraceous reddish, very hard; branches gray or brownish gray, the primary ternate, the terminal leafy branchlets tawny or ferruginous, appressed stellate-tomentose; gum resin flowing easily from bark and wood; stipules large, persistent, subcoriaceous, oblong-lanceolate, subacute, ochraceous-tomentose, 12–22 mm. long, 3–5 mm. broad at base.

Leaves of the young branchlets (smaller than in adult) thin-chartaceous, green-ochraceous with scattered stellate hairs above, green ochraceous or grayish green, appressed stellate-tomentose beneath; adult leaves large, thick-coriaceous, rigid, shortly petiolate; petioles very strong, thick, subterete, appressed ochraceous-tomentose, 1–2 cm. long, 6–8 mm. broad; blades oblong-elliptic or ovate-elliptic, slightly asymmetrical, rounded, cordate, or sharply emarginate at base, little attenuate, rounded or very obtuse and shortly acuminate at apex, entire or very slightly sinuate and flat at margin, 26–54 cm. long, 14–30 cm. broad, ochraceous green above, pale brown when dry, apparently glabrous but with scattered, appressed stellate hairs, these more copious on the main nerves, the costa and the secondary nerves filiform and depressed, the minor venation less noticeable, velvety-tomentose beneath, the surface rosy-glaucous, the veins somewhat more ferruginous or rufescent, the costa very thick and prominent, the 12–14 secondary nerves on each side very

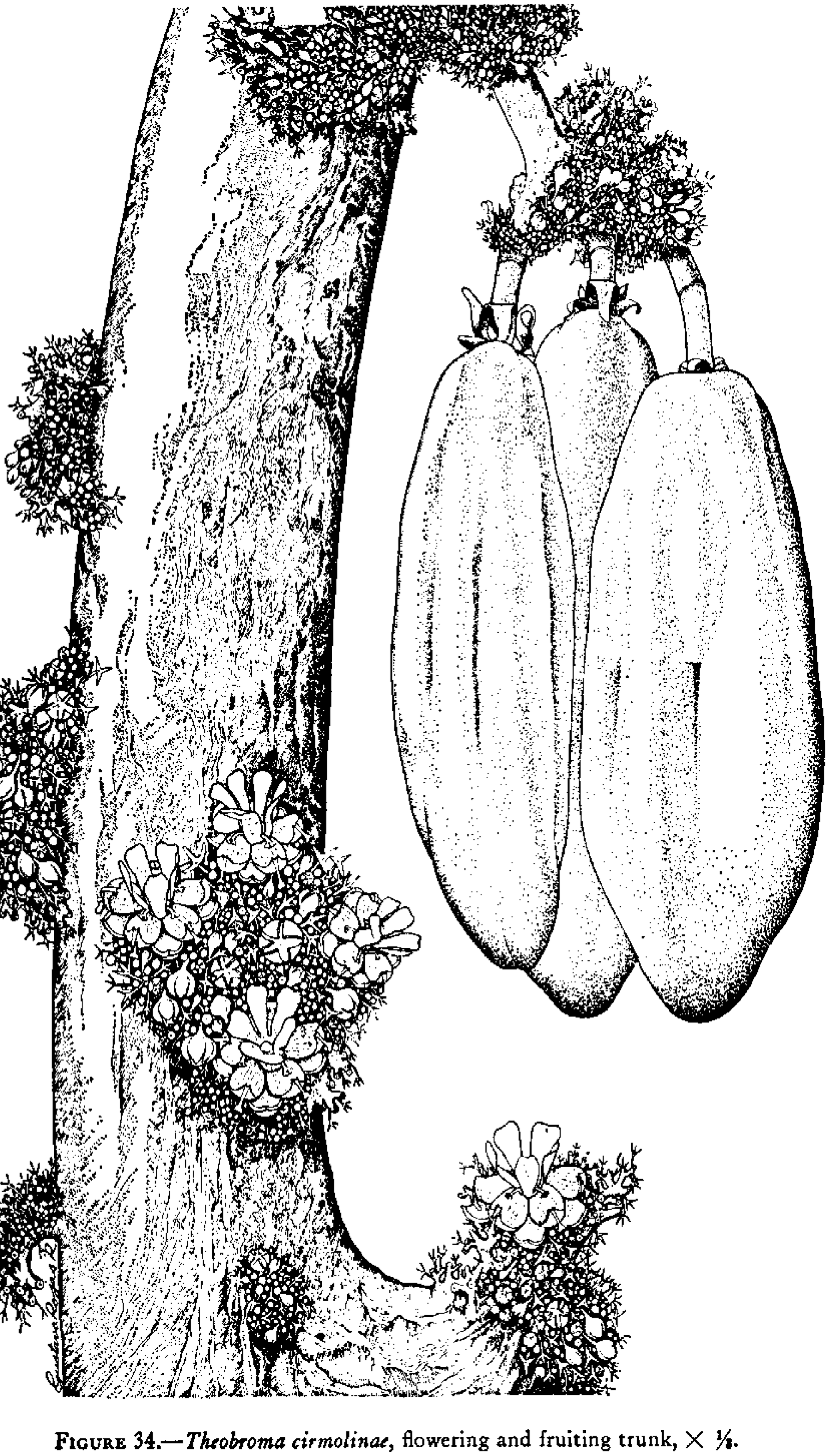


FIGURE 34.—*Theobroma cirmolinae*, flowering and fruiting trunk, × ⅛.

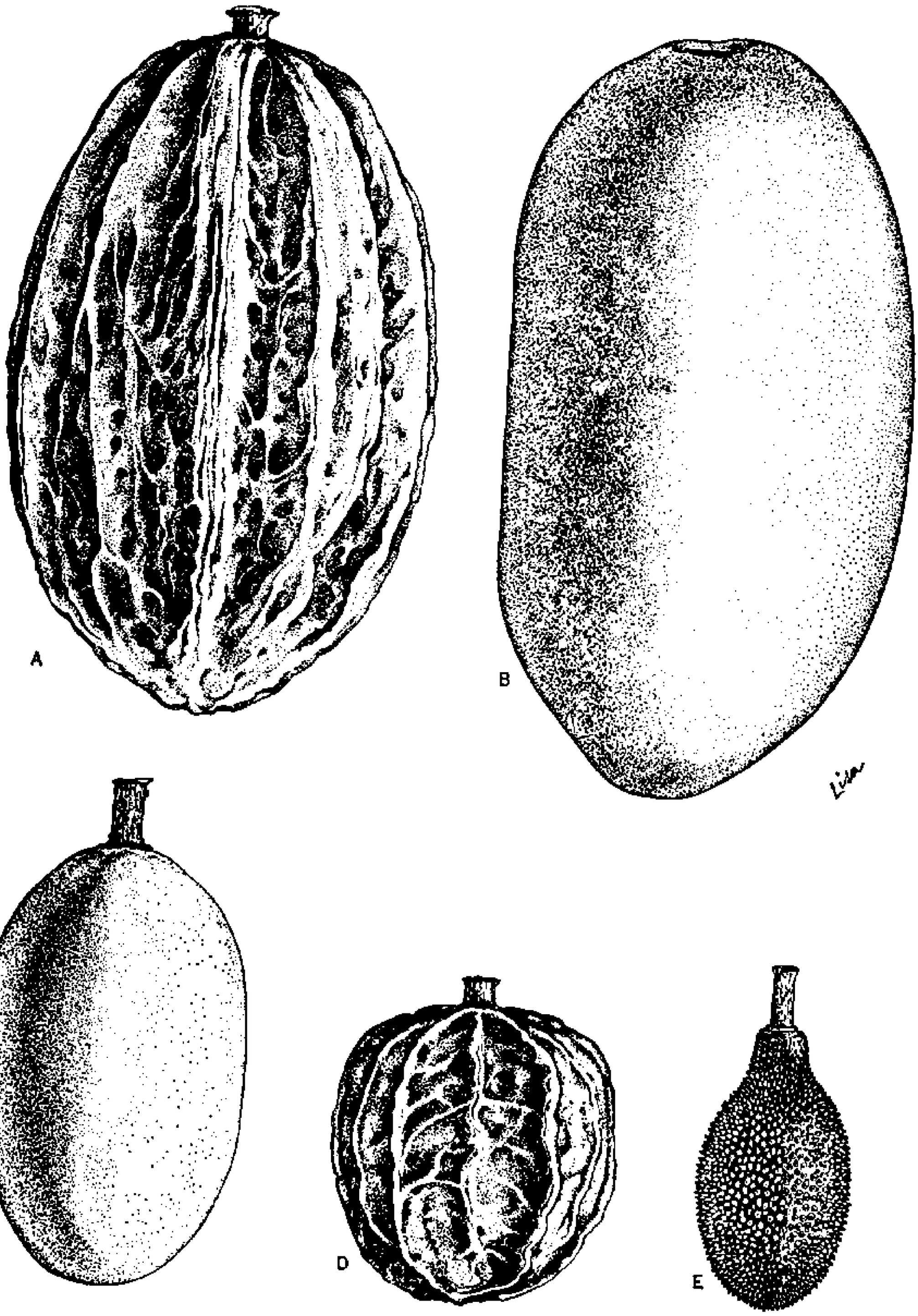


FIGURE 35.—Fruits of *Theobroma*, × ½: A, *bicolor* (Llano s.n.); B, *stipulatum* (Cuatr. 21339); C, *subincanum* (Little 9544); D, *microcarpum* (Archer 1551); E, *obovatum* (Klug 2983).

prominent, subspreading, near the margin arched, decurrent, anastomosing, the transverse tertiary nerves prominent, those of the fourth rank also prominent, reticulate-anastomosing, the lesser veins forming a minute, prominulous reticulum, the minor reticulum and areoles covered by a dense tomentum of intricate, white, sericeous, minute

stellate hairs, the major nerves with only scattered minute, slightly larger hairs and abundant, minute reddish, callose warts; base of lamina 7-nerved, the 4 lower nerves small, of lower degree.

Fertile branches perennial on main trunk and big branches, short, ligneous, tuberculate, prolific in flowering, the short, intricate, cin-

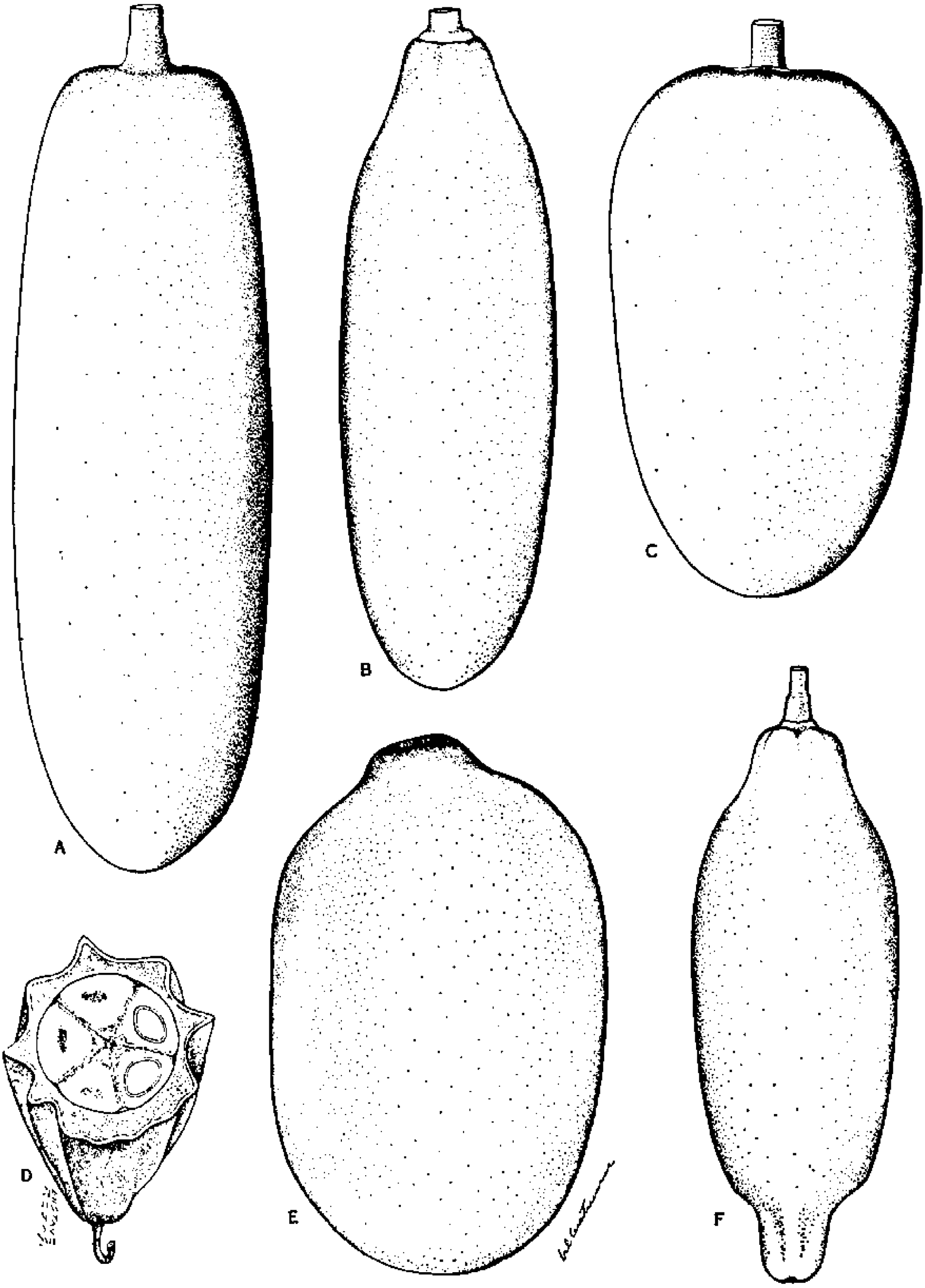


FIGURE 36.—Fruits of *Theobroma*, × ½: A, *simiarum* (Cuatr. 26515A); B, *simiarum* (Cuatr. 26536); C, *chocoense* (Patiño 115); D, *cirmolinae* (Cuatr. 15336); E, *grandiflorum* (Cuatr. 25780T); F, *mammosum* (Cuatr. 26535).

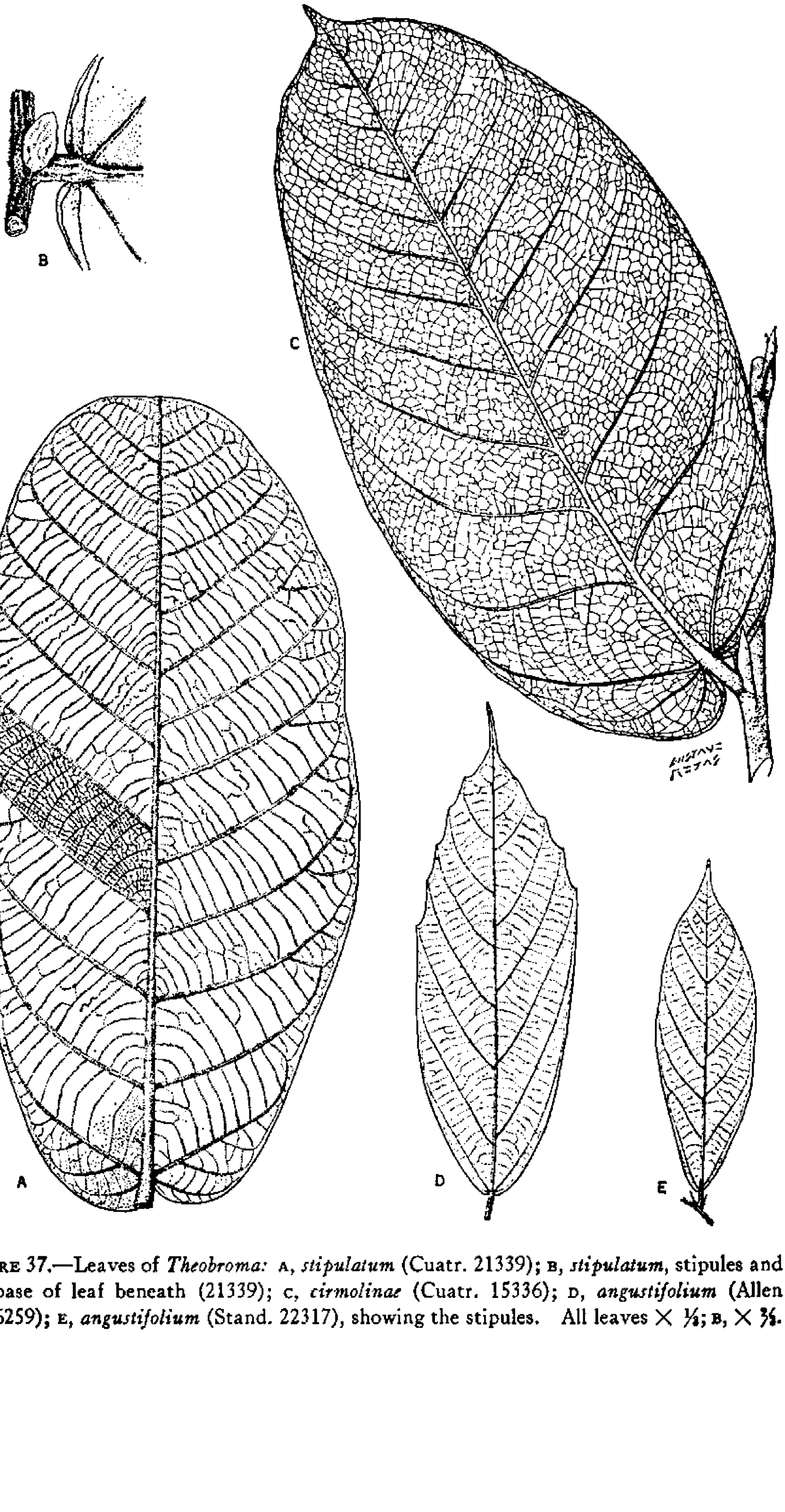


FIGURE 37.—Leaves of *Theobroma:* A, *stipulatum* (Cuatr. 21339); B, *stipulatum*, stipules and base of leaf beneath (21339); C, *cirmolinae* (Cuatr. 15336); D, *angustifolium* (Allen 6259); E, *angustifolium* (Stand. 22317), showing the stipules. All leaves × ½; B, × ⅔.

cinnate branches forming cushions up to 12 cm. broad on the trunk; sympodial branchlets angulate, ramose, bracteolate, forming crowded panicles up to 8 cm. long, appressed stellate-tomentose or glabrate when old; bracts 1.5–3 mm. long, 1.5–2.5 mm. broad, subcoriaceous, persistent, subamplectant, triangular-ovate, tomentose; peduncles elongate in anthesis, erect, rather thin, ferruginous tomentose, 5–8 mm. long, 3-bracteolate at apex; bracteoles linear, subacute, 3–6 mm. long, 1–1.5 mm. wide; pedicels in anthesis 15–20 mm. long, thin, erect, tomentose, ebracteate; buds globose, with 5 commissural ribs, densely ferruginous tomentose.

Sepals thick, carnose, ovate-triangular, acute, united in the lower third or fourth, soon umbilicate-reflexed, with the five free lobes spreading, 10–15 mm. long, 6–7 mm. broad, pale yellow inside, glabrous, except for the base, with minute, oblong, glandular hairs at their insertion, yellowish, thick-tomentose outside with ochraceous or tawny stellate hairs, the margin minutely cinereous-tomentose.

Petal-hoods yellow, thick-membranaceous, elliptic-obovate, rounded-cucullate at apex, glabrous, with 7 prominent nerves inside, 6–7 mm. long, 4-5 mm. broad; petal-laminae thick, carnose, glabrous, sub-triangular-spatulate, slightly 3-undulate or emarginate at apex, about 3.5 mm. long, 2.2 mm. broad, tapering to a pedicel at base; pedicel about 4 mm. long, 0.6 mm. wide, bidentate at the joint.

Androecium tube thick, 2–2.2 mm. high; staminodes laminar, rather thick, oblong-spatulate, slightly broadened towards the end, retuse at apex, erect, glabrous, sulphur yellow, often somewhat reddish near the base, 10–11 mm. long, 4–5 mm. broad, at base 1.5 mm. wide; filaments robust, glabrous, 2.2–3 mm. long, shortly 3-furcate, 3-antheriferous, rarely 4-furcate, 4-antheriferous; ovary ovoid, 1.6–2 mm. long, 1.8 mm. broad, 5-costate, tomentose; styles 2 mm. long, connivent, free up to near the base.

Fruiting peduncle robust, 3–4 cm. long, 8–10 mm. thick, articulate; young fruits large, fusiform, prismatic with 5 obtuse, prominent ribs corresponding to the loculi and 5 others, more or less marked, alternate commissural ones, the base umbilicate, the apex attenuate and obtuse; ripe fruit 25–35 cm. long, 10–12 cm. wide, ellipsoid-oblong or obovoid-oblong, very little narrowed to the umbilicate base, attenuate to the obtuse apex, the surface obtusely pentagonal, with rounded ridges, brown or ferruginous, stellate-tomentose; pericarp about 1–1.5 cm. thick; epicarp 2 mm. thick, very hard, ligneous, the mesocarp and endocarp carnose, becoming hard and coriaceous when dry; covering of the seeds fibrous, pulpy, yellowish white and flavorous; seeds striped from the more or less compressed pulp, ovoid, the testa brown, the outer tegument light brown, the inner one dark brown, the cotyle-

dons reddish, 20–24 mm. long, 15–19 mm. broad, and 9–16 mm. thick; germination hypogeous.

COMMON NAMES.—Bacao, cacao de monte, cacao indio.

USES.—No special uses known besides occasional preparation of chocolate by the natives. This species is the one which grows at the highest altitudes; it should be tried as a grafting base, especially in the coldest zone of cacao production.

DISTRIBUTION.—Only known from the Pacific slopes of the Andes in Colombia in the Department of El Valle, between 800 and 1300 meters altitude.

COLOMBIA: EL VALLE: Western slope of western Cordillera, valley of Río Dígua, Piedra de Moler, rain forests, 900–1180 m. alt.; tree 20 m., trunk 40 em. in diam., adult leaves thick-coriaceous, green above, yellowish green beneath, sepals ferruginous-green, petals yellow, staminodes bright yellow, their bases reddish, bark and central wood with resine, "bacao," 19 VIII 1943, *Cuatrecasas* 14897 (holotype VALLE; isotypes, F, Y). Valley of Río Dígua, La Elsa, forests 1000–1200 m. alt.; tree 12 m., branched in the upper part, bark dark gray, almost smooth, flowers yellow, 9 XI 1943, *Cuatrecasas* 15336 (F, VALLE, Y, paratypes). La Elsa, about 800 m. alt.; tree 12–15 m., 30–35 cm. in diam. at base, jorquettes arising symmetrically, flowers (yellow) and fruit on trunk and main branches, mature fruiting peduncle 4 cm. long, 1 cm. thick, pod 26–28 x 10–11 cm., bluntly ridged, 23 VI 1953, *Holliday* 140 (COL, TRIN, US). La Elsa; tree 9–12 m., 30 cm. in diam. at base, jorquettes arising symmetrically, flowers yellow, fruit on trunk and main branches, 23 VI 1953, *Holliday* 139 (TRIN, US). Hoya del Río Sanquininí, left side, La Laguna, forests 1250–1400 m. alt.; tree 20 m. alt., yellow flowers, fruits large, brown tomentose, "cacao indio," 20 XII 1943, *Cuatrecasas* 15700 (F, VALLE, Y).

12. Theobroma stipulatum Cuatr. FIGURES 30, 32, 35, 37; MAP 9

Theobroma stipulatum Cuatr. Fieldiana Bot. 27(1):84, *fig.7*. 1950; Baker, Cope, et al. (1954) 14, line 15 (as *Theobroma sp.*); León (1960) 322, 315, *fig.*

TYPE.—*Cuatrecasas* 21339, Colombia, Chocó.

Large tree to about 30 m. high; growth pseudoapical; trunk about 45 cm. in diameter, somewhat triangular at base, the bark rugose, granulate, reddish brown, the wood dark ochraceous, hard; branches grayish, rugose-squamulose, glabrate, the primary ternate; terminal branchlets pale ferruginous tomentose, densely covered by stellate or fasciculate hairs; stipules coriaceous, densely tomentose, pale ferruginous, ovate or ovate-oblong, obtuse, persistent, 8–12 mm. long, 5–9 mm. broad, the terminal up to 25 x 11 mm.

Leaves large, strongly coriaceous; petioles robust, very thick, short, densely ferruginous tomentose, 5–10 mm. long; blades ovate-elliptic or elliptic, more or less oblong, rounded, truncate or obtuse at apex, the usually slightly asymmetrical base emarginate-cordate, entire or slightly sinuate and flat at margin, 23–45 cm. long, 11–17 cm. broad, green above, when dry brown or pale brown, slightly rugose or

almost smooth, with scattered, minute, stellate hairs, the costa and secondary nerves linear, tomentose, depressed, greenish ochraceous beneath or when dry ochraceous brown or pale brownish, tomentose, covered with minute, whitish, intricate, stellate hairs, and other mediocre, thicker, ferruginous, stellate hairs copiously covering the veins, the costa very robust and prominent, the secondary nerves about 12 on each side, very prominent, subascending, near the margin curved, decurrent, and anastomosing, the transverse tertiary nerves prominent, parallel, 5–15 mm. distant from each other, the minor veins prominously reticulate.

Inflorescences cauline, on trunk or main branches, the fertile branches perennial originating from tubercles; ligneous branches short, tortuous, intricate, furcate-ramose (dichasial and cincinnate), bracteate, tomentose, up to 1–3 cm. long; bracts ovate, subcoriaceous, tomentulose, minute; peduncles solitary, 5–12 mm. long, thin, stellate-tomentose, 3 bracteolate and 1-flowered at apex; bracteoles linear, acute, 2–3 mm. long; pedicels erect, thin, densely tomentose, 10–22 mm. long; buds globose, 10–14 mm. in diameter, sublanate-tomentose; sepals thick, ovate-triangular, glabrous and ochraceous inside, except for the minute, thick, oblong, glandular hairs at base, densely stellate-tomentose or sublanate outside, 10–15 mm. long, united in the lower third, reflexed at anthesis, umbilicate at base; petals yellow, glabrous, the hoods obovate elliptic, 7-nerved-sulcate, involute at margin, round-cucullate at apex, about 5 mm. long and 3–4 mm. broad; petal-laminae yellow, thick, 3–3.5 mm. long, ca. 3–3.5 mm. broad, suborbicular or subspatulate, slightly retuse at apex, attenuate into a narrowly linear pedicel at base, this 3.5–4 mm. long.

Androecium tube 1.5–2 mm. long, glabrous; staminodes petaloid, yellow, thick, glabrous obovate-oblong, subspatulate, rounded at apex 1-toothed on each side, 10–11 mm. long, 4.5–5 mm. broad, at base 1.5 mm. broad; filaments rather thick, glabrous, 1.8–2 mm. long, curved, shortly 3-furcate, 3-antheriferous; anther lobes ellipsoid; ovary ovoid-oblong, 5-furrowed, densely tomentose-hirsute, about 2 mm. high; styles filiform, glabrous, coherent, about 2 mm. long.

Fruit 17–22 cm. long, 9–11 cm. broad, ovoid-ellipsoid or ellipsoid and oblong, rounded at base, slightly attenuate, obtuse or rounded at apex; pericarp hard-coriaceous, rigid, smooth, appressed brown tomentose, the epicarp woody, about 1.5 mm. thick, the mesocarp and endocarp carnose, creamy, about 1 cm. thick; seeds compressed about 20–55, surrounded with pale, yellowish white, soft, scented pulp, more or less amygdaliform, 20–25 mm. long, 18–21 mm. wide, and 7–10 mm. thick, the testa subcoriaceous about 0.5 mm. thick; cotyledons white; germination hypogeous; fruiting peduncles robust, 1–3 cm. long, about 1 cm. thick.

COMMON NAMES.—Chocolate de monte, cacao de monte.

USES.—The seeds are said to yield a good chocolate but they are only occasionally used by the natives.

DISTRIBUTION.—Restricted to the rain-forested basins of the rivers San Juan and Atrato (Chocó region) and perhaps Río Sequión (Nariño) in western Colombia, where it is of rare occurrence.

COLOMBIA: ANTIOQUIA: Villa Arteaga, about 100 m. alt.; tree 12 m., 20 cm., diameter base, flowers borne on trunk and main branches, pedicel from base to bracts 1.6 cm., from bracts to flower 2.2 cm., bracts 3, one usually larger, abscission layer near bracts, sepals joined about ⅓ way from base, reflexed when flower opens, all parts of flower yellow, 7 ridges on inside of petal, staminodes spatulate, 14 mm. long, 6 mm. wide, 22 VII 1953 *Holliday & Bartley T*/165 (TRIN, US). Ibidem, and same tree; *Cope* Ant. 2 (specimens lost), field annotations by Cope: "A branched tree, showing the branching of the *subincanum* group, new growth from above jorquette; 3 branches." "Interior parts of bud examined were creamy white; sepals reflexed in opened flower, 7 mm. long x 4 mm. wide, elliptic, pointed, apparently rather soft and spongy, truncate margins, free almost to base, inner surface glabrous; petals 5, free, with cup-shaped base and ligule, base 4 x 4 mm., ligule and strap 5 mm. long, expanded portion spatula-shaped, staminodes 5, reflexed, oblanceolate, 10 mm. x 3 mm., fruit somewhat ovate in outline, in cross section, slightly flattened on 5 side, no ridges or furrows, densely covered with medium brown, stellate hairs, which impart a mealiness to surface, 18 cm. long x 10 cm. diameter, wall with woody outer layer about 1.5 mm. thick, inner surface very soft, creamy, about 1 cm. thick, 55 seeds embedded in soft, cream-colored tissue, beans flattened, up to 1 cm. thick, somewhat triangular in outline, up to 25 mm. long x 21 mm. wide, testa chocolate brown in color, about 0.5 mm. thick, rather leathery, cotyledons pure white, markedly convoluted, pulp has smell of green bananas."

CHOCÓ: Río San Juan, right margin of river on low hill near Palestina, about 30 m. altitude; tree 32 m. tall; trunk triangular at base, 45 cm. diam., branchless up to 25 m. height, bark rugate-granulate reddish brown, wood rather dark ochraceous, leaves coriaceous, rigid, green above, ochraceous green beneath, when very young light yellowish green above, young branchlets and stipules pale ferruginous, fruits oblong-ellipsoid or oblong-subovoid, obtuse, dark brown tomentose, 17–22 cm. long by 9–10 cm. broad, pericarp rigid woody, "chocolate de monte," 28 V 1946, *Cuatrecasas* 21339 (holotype, F; isotypes, US, VALLE, Y). Río Atrato, Lloró; young tree 3 m., sterile, jorquette of three branches, 4 VIII 1953, *Holliday & Bartley* 175 (TRIN, US).

NARIÑO: Iscuandé, Río Sequión, 100 m. alt.; tree 18 m., bark reddish and smooth, wood cream colored, "chocolate," 23 XI 55, *Romero Castañeda* 5500 (COL). (A sterile specimen, the identification is doubtful; flowers and fruits necessary.)

13. Theobroma chocoense Cuatr., sp. nov. FIGURES 3, 31, 36, 38; MAP 9

Arbor 8–15 m., trunco erecto pseudoapicale crescente, cortice sublaevi, ramis ternatis robustis patulis superioribus ascendentibus ramulis alternis juvenilibus dense crasseque lanuginoso-tomentosis viridi-ochraceis vel viridi-ferrugineis, pilis stellatis intricatis mediocribus ochraceis densis et pilis fasciculatis longioribus pallidis sparsis tectis, denique glabratis brunneis nitidis angulosis cicatricosis; stipulae coriaceae persistentes petiolis longiores ovatae obtusiusculae longi-

tudinaliter striato-nervatae primum ochraceo-tomentosae, pilis ferrugineis mediocribus stellatis, deinde cinereae, pilis stellatis minutis albidis adpressis munitae, intus glabrae 12–22 mm. longae, 10–15 mm. latae, in ramis valde juvenilibus ovato-lanceolatae 2–25 mm. longae, 8–9 mm. latae.

Folia alterna rigide coriacea; petiolus brevis crassus robustus viridi-ochraceus vel viridi-ferrugineus dense lanuginoso-tomentosus, pilis mediocribus stellatis densis et pilis fasciculatis longissimis (ad 2 mm. longis) pallidis sparsis, 7–14 mm. longus, 8–10 mm. crassus; lamina oblongo-elliptica vel subovato-elliptica, integra vel levissime undulata, basi ampla leviter attenuata subsymmetrica rotundata cordato-emarginata, apicem versus paulo attenuata apice obtusa subite acuteque acuminata 18–42 cm. longa, 9–20 cm. lata, acumine 1–1.5 cm. longo, supra juventute ochraceo-stellato-tomentosa deinde glabra vel sparsissimis pilis stellatis mediocribus munita, plus minusve venoso-rugosa, nervis secundariis filiformibus impressis, nervulis venulisque plus minusve impressis, superficie lutescenti-viridi in sicco brunnescente, subtus valde nervosa viridi-cinerea in sicco ochraceo-ferruginea, costa crassa valde eminente, nervis secundariis valde prominentibus 12 vel 13 utroque latere paulo ascendentibus ad marginem arcuatis, nervis tertiaris transversis parallelis prominentibus 3–10 mm. inter se distantibus nervulis minoribus venulisque bene prominentibus reticulatis, indumento heterotricho-tomentoso, superficie alveolorum venulisque reticuli pilis-stellatis minutissimis tenuibus albidis intricatis dense tectis, nervis alteris copiosis punctis callosis rubris et copiosis, pilis stellatis majoribus ferrugineis radiis patulis munitis, in foliis vetustis nervis majoribus saepe glabratis, in prole foliis tenuioribus subtus albo-cinereis, pilis minutissimis stellatis albis dense tecta, in nervulis sparsis in petiolo costa nervisque principalibus densis pilis stellatis ochraceis radiis patulis gracilibus 1–1.5 mm. longis basi calloso-rubescente praedita.

Folia prolis orthotropae tenuia petiolata late ovata vel rhomboideo-ovata sursum crenato-dentata apice acuminata, circa 8 nervis secundariis utroque latere; lamina 12–20 cm. longa, 8.5–12 cm. lata, petiolo 3.5–4 cm. longo, vel latiore; stipulae anguste lanceolatae.

Inflorescentiae in trunco et in ramis majoribus copiosae, tuberculis lignosis persistentibus orientes, ramulis brevissimis cymosis tomentosis densos glomerulos floriferos formantibus; bracteae lineares circa 5 mm. longae ferrugineo-tomentosae; pedunculi ad 1 cm. longi tomentosi apice 3-bracteolati; bracteolae anguste lineares 2–2.5 mm. longae tomentellae; pedicelli 9–14 mm. longi erecti mediocres stellato-tomentosi viridi-ochracei; alabastra ellipsoideo-(globoso)-depressa 9–10 mm. lata, 7–8 mm. longa, in commissuris 5-costata, minute ochraceo-tomentosa; calyx basi cupularis, intus basi ad marginem insertionis

annulo pilis densis crassis glandulosis praeditus, in anthesin reflexus; sepala 5 crassuiscula ovato-acuta, 10–11 mm. longa, circa 7 mm. lata, basi 2.5–3 mm. longe in tubum coalita, extus minute ochraceo-stellato-tomentosa, margine minutissime albo-tomentosa, intus glabra superne parce pilosula excepta.

Petala glabra, cucullo crassiusculo pallido obovato-suborbiculato circa 6 mm. longo et lato, basi amplo apice subrotundato depresso apiculo bidenticulato, venulis 7 extus paulo conspicuis intus prominentibus; lamina crassa rigida rubra obovato-deltoidea apice subtruncata, 5–6 mm. longa, 5–6.5 mm. lata, basi attenuata et cum pediculo circa 3.5 mm. longo articulata.

Androecii tubus crassiusculus glaber circa 1.5 mm. altus; staminodia petaloidea crassiuscula glabra in anthesin erecta obovato-oblonga apice rotundata margine integra basim versus gradatim attenuata, 13–15 mm. longa, 5–7 mm. lata, basi 3–3.2 mm. lata; stamina filamentis crassiusculis circa 2 mm. longis recurvatis glabris, antheris 3, lobis bilocularibus loculis ellipsoideis circa 0.6 mm. longis; ovarium globosum 2.5 mm. diam. dense hirsuto-tomentosum; styli circa 2 mm. longi.

Fructus laevis ellipsoideo-ovoideus basi late rotundatus apice paulo attenuatus obtusus, 19–20 cm. longus, 10–11.5 cm. latus, pericarpio crasso duro, extus crasse brunneo-tomentosus, epicarpio circa 2 mm. crasso lignoso; semina ovoidea vel triangulari-ovoidea compressa, 20–23 mm. longa, 16–18 mm. lata, 11–12 mm. crassa.

Type in the U.S. National Herbarium, No. 2402158, collected on the grounds of the Experimental Station "Agroforestal del Calima," Bajo Río Calima, at about 35 m. altitude, in the Department El Valle, Colombia, September 25, 1961, by J. Cuatrecasas and L. Willard (No. 26074). Flowers from the same tree collected by H. Guerrero A. (No. 26074) December, 1961. Paratype collected at the same place with a dry mature fruit by *V. M. Patiño* (No. 115).

COMMON NAMES.—Cacao de monte, cacao grande de monte, bacao de monte.

DISTRIBUTION.—Restricted to the Chocó region, in the heavy forested valleys of the rivers San Juan and Atrato in western Colombia. The records of *T. simiarum* from the Calima River by Baker, Cope & al. (1954, 14) refer to this species.

Theobroma chocoense is closely related to *T. simiarum*, from which it differs in its broadly ovoid or ellipsoid pods, in its elliptic or ovate leaves (instead obovate), in the indument of the lower side of the leaves, which is composed of two kinds of hairs (minute, entangled, white, stellate hairs covering the surface and larger ones with long, spreading rays on the nerves), by the short, ovate, obtuse stipules, and shorter bracteoles. All these features indicate that Chocoan

species is distinct from the Costa Rican species. Although the fruit of *T. chocoense* is very similar to that of *T. stipulatum*, the red color of the flower and the different indument of the leaves readily distinguish these two species.

COLOMBIA: El Valle: Baja Calima (Chocó region), Río Calima, Estación Agroforestal del Calima, 30–40 m. alt.; tree about 8 m. high, with apical growing trunk almost smooth with few fertile tubercles, primary branches ternate, abundantly inflorescence-tuberculate, leaves rigid, medium yellowish green above, cinereous green beneath, "cacao de monte," 25 IX 1961, *J. Cuatrecasas & L. Willard* 26074 (holotype, US; isotype, COL). Ibidem; flowers purple red, XII 1961, *Humberto Guerrero* 26074 (US). Ibidem; small tree (about 10 m.) on the edge of the small creek behind the Palmetum, dry fruit 19 x 11.5 cm., I 1953, *V. M. Patiño* 115. Ibidem; tree 12–15 m. in forest, fruit 16 x 11 and 20 x 10 cm., quite smooth, no flowers, 29 VI 1953, *Holliday* 144 (TRIN, US). Río Calima, Caño la Brea; young tree 2 m., in forest, sterile, 29 VI 1953, *Holliday* 143 (TRIN, US).

Chocó: Río San Juan, in front of Palestina, Quebrada de la Sierpe, 0–40 m. alt.; tree about 14 m. high, trunk 30 cm. diam., leaves rigid, rugose, coriaceous, deep green above, cinereous green beneath, strongly nerved, fruit ellipsoid, smooth, velvety tomentose, 20 cm. long, 10 cm. wide, the seeds acid, "bacao de monte," 13 III 1944, *J. Cuatrecasas* 16896 (F, VALLE, US).

13a. Theobroma chocoense var. **bullatum** Cuatr., var. nov.

A var. *chocoensi* foliis rugosis reticulato-bullatis differt. Lamina rigida elliptico-oblonga vel paulo obovato-oblonga, magna, usque ad 50 x 21 cm., basi rotundata, apice rotundata breviter subiteque cuspidata, juvenilis basim versus plus minusve attenuata apice magis angustato-acuminata; cucullum petalorum 5–6 mm. longum, 3–4 mm. latum, pediculo 3.5–4.5 mm. longo; lamina triangulari-spathulata, 2.5–4 mm. longa, 2.5–3 mm. lata; staminodia obovato-oblonga apice rotundata, circa 10 mm. longa, 4 mm. lata, basi 1.5 mm. lata; sepala extus tomentosa intus glabra, circa 12 mm. longa, 5 mm. lata, 3 mm. basi coalita.

Type in the U.S. National Herbarium, No. 2404636, collected in Quebrada Juan María, a small tributary of Río Juradó, at about 500 m. from its mouth, in the Municipality of Nuquí, Department of Chocó, Colombia, at 50–100 m. altitude, on a hill in a region having a dry season of about 4 months, 15 II 1955, *V. M. Patiño* 171.

Although at first sight the leaves of this variety look very different from typical *T. chocoense*, no other differences can be found on the basis of the available material. According to fragmentary data it seems that the fruit of the Juradó specimens are identical with those of *T. chocoense*. The leaves are strongly nerved, reticulate and rugose-bullate, but some specimens of typical *T. chocoense* also show rugosity in the leaves. V. M. Patiño writes about his specimens: "Tree 12–14 m. alt., the trunk straight, triangular on the lower half, with sides

about 30 cm. broad, tubercular, floral cushions copious on the whole trunk; the specimens are scattered; no other trees were seen in the vicinity; the "cuzumbies" like its fruits very much, for which reason it is difficult to find them unbroken; branches few, terminal; leaves 40–50 x 16–21 cm., petiole 1–1.5 cm., 6–11 mm. thick; leaves of very young specimens dentate in their upper half; fruits on trunk and branches; the 2 flowers collected were dry but a Choko Indian told that its natural color is red and that the seeds are purplish; the Choko name for the species is "cumajó" or "judromajó."

To this variety belong the sterile specimens from Río Atrato referred to by Baker, Cope and al. in their Report, page 14 as "*Theobroma* sp. (possibly new)." Additional flowering and fruiting collections of this plant are needed to complete our knowledge and to determine better its taxonomic rank.

COMMON NAMES.—Chocolate de monte, bacaíto de monte, cumajó (*Chokó*), judromajó (*Chokó*), according to Victor M. Patiño notes.

USES.—The pulp is acid and of pleasant taste, for which reason it is sought by animals and also by the Indians.

DISTRIBUTION.—Río Atrato and northwestern Pacific drainage, Chocó (Colombia).

COLOMBIA: CHOCO: Río Atrato, Lloró, about 50 m. alt.; tree 12 m., 4 VIII 1953 *Holliday & Bartley* T/176 (K, TRIN, US). Municipality Nuquí, Río Juradó, Quebrada Juan María, about 500 m. from mouth, 50–100 m. alt., 15 II 1955, *Patiño* 171 (US). Ibidem, seedling, *Patiño* 171A (US); first branches of a young plant, *Patiño* 171B (US).

14. Theobroma simiarum Donn. Smith. FIGURES 5, 6, 32, 36, 38, 40; MAP 8

Theobroma simiarum Donn. Smith in Pittier, Prim. Fl. Costar. 2: 52. 1898; Bot. Gaz. **25**: 145. 1898; DeWildeman (1902) 97; Standley (1937) 689; Chevalier (1946) 282; Holdridge (1950a) 2; Allen (1956) 343; León (1960) 322, 321, *fig.*

TYPE.—Turrialba, Costa Rica, *Tonduz* 8373 (= 7313 distributed J. Donnell Smith). Lectotype: US 1,382,332 [Photo F. M. 40723], US 471,873 [Photo F. M. 40722]. Syntypes: *Pittier & Tonduz* 3925, *Tonduz* 6852, *Cooper* 10244.

Medium to large tree up to 20 m. tall, with erect, thick trunk up to 60 cm. in diameter at the triangular base; growth pseudoapical; bark more or less rugose; branches spreading, the primary ternate, the upper ones ascending; young branchlets thick-tomentose, greenish ferruginous or brownish, covered by three kinds of hairs: 1) abundant minute squamose stellate hairs with thin rays, 2) mediocre stellate, longer hairs and 3) scattered large stellate or furcate hairs with very long white rays, when older glabrate, brownish or grayish; stipules persistent, longer than the petioles, subcoriaceous, firm, erect, lanceo-

late or linear, acute, 15–24 mm. long, 3–6 mm. broad, tomentose outside.

Leaves large, rigid, coriaceous; petiole robust, thick, somewhat striate, thick-tomentose-ferruginous, 5–12 mm. long, 6–10 mm. thick; blades obovate-oblong, rounded or very obtuse and abruptly cuspidate at apex, broad or slightly narrowed, rounded or slightly cordate and asymmetrical at base, entire or sinuate-dentate in the upper third, in very young plants obovate-rhomboid, long-acuminate, the upper half or third repand, acutely dentate, the adult 20–40 cm. long, 8–17 cm. broad, the acumen 0–1 cm. long, green above, when dry pale brown, smooth, glabrous or with scattered stellate hairs on the midrib, this and the secondary nerves filiform and depressed, the other veins usually obsolete, light green beneath, when dry cinereous or whitish but the nervation ferruginous, the costa thick, very prominent, the 9–11 secondary nerves on each side thick and prominent, spreading-ascending, the lower pair usually at a more acute angle, the transverse tertiary nerves prominent, separated 5–10 mm. from each other, the minor nerves and veins prominulous, reticulate; indument heterotrichous, the areolar surface and the small reticular veins covered by a dense tomentum of intricate, minute, white, stellate hairs, the thicker nerves with sparse mediocre, ferruginous, stellate hairs and reddish callous scars, the costa densely ferruginous by more or less copious mediocre hairs and other ochraceous, long ones; in seedlings the under leaf surface whitish, covered with a white tomentum of extremely minute, white, stellate hairs, and on the nerves sparse and on the costa dense ferruginous stellate hairs with long (1 mm.), thin, patulous rays and red, callous bases.

Inflorescences borne on tubercular protuberances on the trunk; cymose branches usually cincinnate, ligneous, very short, forming dense, many-flowered glomerules; branchlets up to 4 cm. long, tortuous, rugose, glabrate, bracteate, the bracts coriaceous, ovate, subacute or acuminate, tomentulose outside, 1–2 mm. long, 1–1.5 mm. broad, persistent; hornotinous branchlets short, crowded, ferruginous-tomentose, covered by fertile, tomentose, imbricate bracts; peduncles axillary, mediocre, densely stellate-pilose-tomentose, 5–15 mm. long, 3-bracteolate at apex, the bracteoles narrow-linear, tomentose outside, 3–7 mm. long; pedicels up to 15 mm. long; buds globose, densely tomentose, above almost 5-angulate; calyx cupular at center, subglabrous, with a ring of minute, thick, oblong, glandular hairs at base and with very thin hairs above inside, densely and thickly stellate-tomentose and ochraceous green or ferruginous outside, the sepals ovate-acute, about 10–12 mm. long, 6 mm. broad, united about 2 mm. at base, reflexed at anthesis; petals red, thick, glabrous; hood yellowish white, obovate-oblong, with 7 prominent nerves inside,

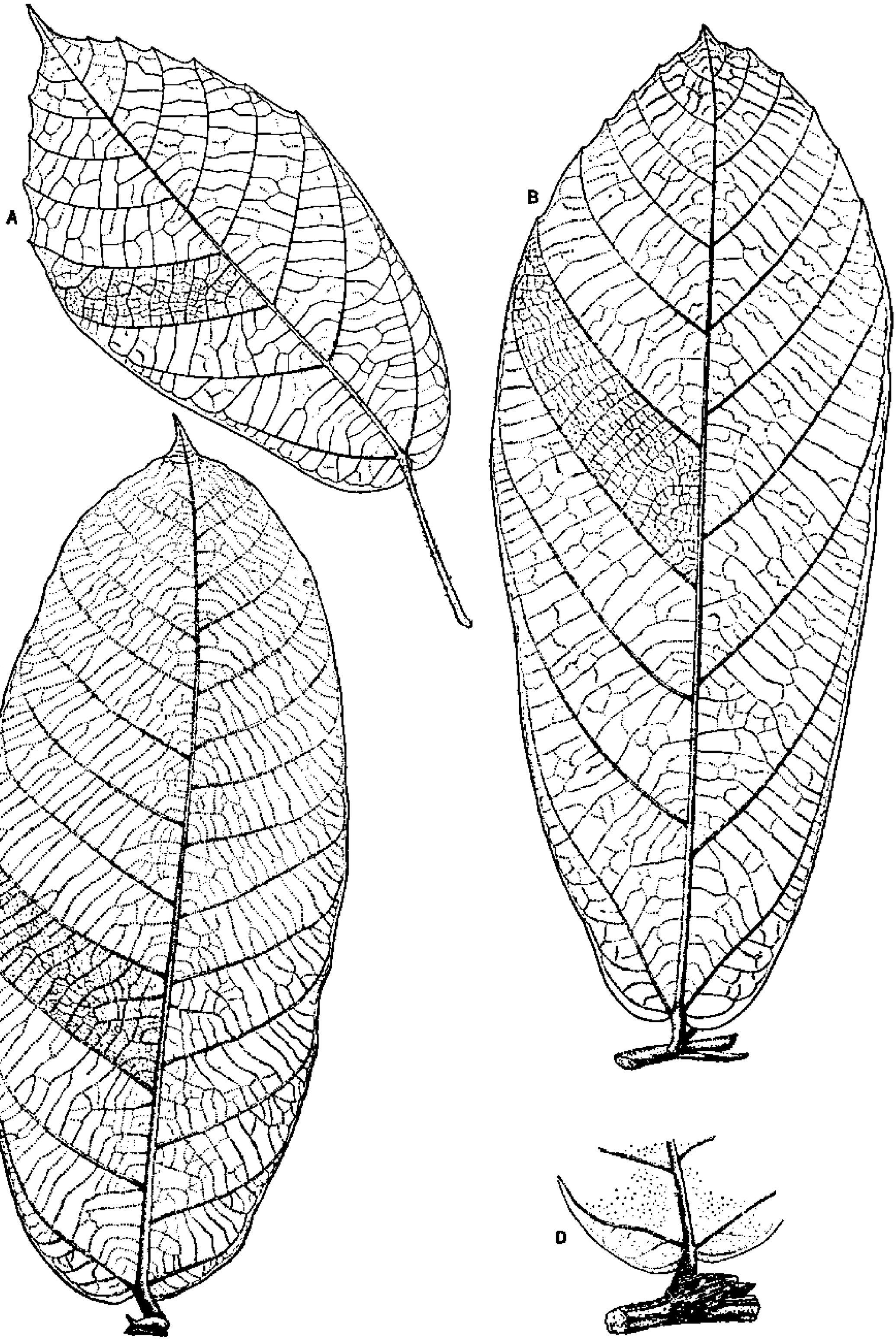


FIGURE 38.—Leaves of *Theobroma:* A, *simiarum*, from orthotropic stem (Stand. 37377); B, *simiarum*, from normal lateral branches (Cooper 10244); C, *chocoense* (Cuatr. 26074); D, leaf base and stipules of *T. chocoense* (Cuatr. 26074). All leaves × ⅓; D, × ⅔.

narrowed-unguiculate, and inside reddish at base, 6–8 mm. long, 4–5 mm. wide, rounded-cucullate, inflexed-apiculate at apex, the apiculum bifid, articulate to the pedicellate lamina; petal-lamina obtrapezoid, carnose, red, subtruncate at apex, cuneate at base, 3.5–4.6 mm. long, 3.5–5 mm. wide, reflexed in bud, erect in anthesis; pedicel linear, 4–5 mm. long, 1 mm. broad; androecium tube about 2 mm. long, rather thick, glabrous; staminodes petaloid red, glabrous, obovate-oblong, rounded at apex, slightly sinuate-dentate in the upper third or subentire, 11–13 mm. long, 5–7 mm. broad, 1–2 mm. wide at base, reflexed in bud, erect at anthesis; filaments rather thick, glabrous, curved, 2 mm. long, shortly 3-furcate, 3-antheriferous; anther lobes ellipsoid, 0.6–0.7 mm. long; ovary obovate, densely hirsute-tomentose, about 1.2 mm. high; styles about 1.2 mm. long, thin, acute, united at base.

Fruiting peduncle short, thick, usually 1–1.5 cm. long; fruit ellipsoid-oblong, smooth, truncate or very blunt, rarely narrowed at base, rounded, very obtuse or slightly attenuate at apex, 16–35 cm. long, 6–10 cm. broad, covered by dense and thick, ferruginous or brown tomentum; pericarp 11–15 mm. thick with: 1) epicarp woody, 1.5–2 mm. thick, with a tomentose epidermis, 2) mesocarp 5–10 mm. thick, firmly carnose, pale ochraceous whitish, and 3) endocarp 2–5 mm. thick, softer carnose; seeds 36–60, distributed in 5 more or less double rows, each one covered by a thick, fibrose, white or rosy-white, aromatic pulp irregularly ovoid, 20–21 mm. long, 18–17 mm. broad, and 13–15 mm. thick; cotyledons white; germination hypogeous.

COMMON NAMES.—Cacao de mico, cacao de mono, teta negra. Indian names: Kráaku (*Guatuso*), Nunísup (*Rama*), Uirub (*Bribrí*), Dzug-mang-uá (*Brunka*), Ku-gín, Bik (*Térraba*), according to Standley, loc. cit., Uir-ub (*Bribrí*) according Pittier.

USES.—The seeds are said to give a cacao of good quality. They are occasionally used.

DISTRIBUTION.—Limited to Costa Rica. Infrequently found in preserved or remnant forests in both Atlantic and Pacific lowlands, from sea level to 600 m., and exceptionally in higher altitudes up to 900 m.; recorded from the provinces of Limón, Heredia, Puntarenas, and Cartago. It may extend to Nicaragua and northern Panama, but no records from these two countries exist at present in herbaria.

In its natural habitat *T. simiarum* attains a considerable height and thickness. The trunk is erect and branchless up to several meters. The inflorescences may appear on the trunk but they are more abundant on the big branches. The fruit is very characteristic because of its terete, sausage shape. From the closely related Colombian species *T. stipulatum* and *T. chocoense* it can be distinguished by the elongate

shape of the pod; in the two other species the fruit is ovoid or broadly ellipsoid. From *T. stipulatum* it differs also by its red flowers, longer lanceolate stipules, longer bracteoles, and by the indument of the leaves. From *T. chocoense* it differs also by its narrower and longer stipules, the obovate form of the leaves, by the leaves having beneath usually three kinds of hairs, and by its longer bracteoles.

COSTA RICA: CARTAGO: Turrialba, grassland, 570–600 m. alt., XI 1893, *Tonduz* 8373 (distributed by Donn. Smith under number 7313) lectotype US; isolectotypes BR, G, GH, K; Photos F. M. 30722, 40723, 40743. Turrialba, forest at margin of Río Reventazón, about 600 m. alt.; tall tree with unbranched trunk in the lower half, 60 cm. diam. near the subtriangular base, abundant tuberculate inflorescences on the upper part and big ternate branches, few sausage-shaped pods, 6 XI 1961, *J. Cuatrecasas & León* 26515A (US). Turrialba, Instituto Interamericano C.A., 600 m. alt.; flowers bright red, cult., 4 XI 61, *J. Cuatrecasas & J. León* 26515 (US). Turrialba, I.I.C.A., 600 m. alt., cult., 14 III 51, *J. León* 3189 (TURRI). Tuis, forests, 670 m. alt., "cacao de mico," XI 1900, *Pittier* 14016 (*Donn. Smith* 7731) (GH, K, US). Tucurrique, grassland and forests around Las Vueltas, about 635 m. alt.; large tree, fruits brown, oval-elongated 30–40 cm. long, XI 1898, *Tonduz* 12822 (BM, G, LE, P, US), 18222 (M) [erroneous number].

LIMON: La Colombiana Farm of the United Fruit Company, about 70 m., wet forest; tree 60 feet or more tall with trunk 2 ft. thick, small crown, flowers bright red in bunches on trunk, fruit sausage-shaped, hairy, 1 foot long or more, said to be rare here, seeds give good cacao, 6, 7 III 1924, *Standley* 36822 (US). 28 miles on the railroad from Puerto Limón, towards Río Barbilla, in marginal forest, about 60 m. alt.; tall tree, flowers flame red, 12 V 1930, *Cufodontis* 599 (WU). Along Río Reventazón, below farmhouse Finca Castilla, 30 m. alt., in *Gynerium sagittatum* thickets, 27 VII 1936, *Dodge & Goerger* 9420 (MO). Palm swamp between Río Reventazón and Río Parismina, on Castilla Farm, 2 IV 1930, *Dodge & Nevermann* 7164 (MO). La Lola, farm of the I.I.C.A., about 40 m. alt., cult.; trees about 10 m. high, trunk 20–30 cm. diam., triangular at base, flowers scarlet, fruits oblong 15.5 x 7 cm., 18 x 8.7, 19.5 x 8.5, 22.7 x 7.7, 23.3 x 8.4, 25.7 x 9.3 cm., with thick brown tomentum, 6 XI 1961, *Cuatrecasas & Paredes* 26536 (US). Vicinity of Guápiles, 300–500 m., seedling, III 1924, *Standley* 37377 (US).

HEREDIA: La Concepción, Llanuras de Santa Clara, 250 m. alt., "cacao de mico," II 1896, *Donn. Smith* 6457 (BM, US). Santa Clara; 6–7 m. high tree, "cacao de mono," IX 1896, *Cooper* 10244 (syntype, US) (Photo F. M. 40724).

PUNTARENAS: Terraba, 260 m. alt., forests; caulinar flowers, large cylindrical fruits (30–35 by 10 cm.), "cacao de mico," II 1891, *Pittier & Tonduz* 3925 (syntype, BR). Boruca, forests 466 m. alt., III 1892, *Tonduz* 6852 (syntype, US).

TRINIDAD (cult.): Imperial College of Tropical Agriculture, *Cuatrecasas & Cope* 25792 (US), 25794 (US).

SURINAM (cult.): Paramaribo, culture garden; tree 10 m., 15 cm. diam., almost horizontal branches, flowers bursting in dense clusters from the trunk and old branches, calyx rusty brown, ligula and staminodes shining lacquer red, 8 IV 1954, *Lindeman* 5725 (U). Ibidem; seeds round, cotyledons white, germination hypogaeic, VIII 1956, *van Suchtelen*, s.n. (US).

BRASIL (cult.): Pará, cultivated and said to be introduced from Venezuela; small tree with purplish flowers, II V 1957, *Pires* 6575 (IAN).

15. Theobroma grandiflorum (Willd. ex Spreng.) Schum.

FIGURES 3, 5, 6, 7, 33, 36, 39, 40; MAP 10; PLATE 8

Theobroma grandiflorum (Willd. ex Spreng.) Schum. in Mart. Fl. Bras. **12**(3):76, *pl. 8*, 1886; Jumelle (1899) 28, *figs. 14, 15;* DeWildeman (1902) 95; Ducke (1925) 131; Ducke (1940) 272, *pl. 4, fig. 2;* Chevalier (1946) 281; Addison & Tavares (1951) 25, *pl. 1, fig. 1, pl. 2, fig. A, pl. 14, fig. 10;* Ducke (1953) 11; Baker, Cope & al. (1954) 13, *fig. 14;* Cuatrecasas (1956) 656; León (1960) 320, 319, *fig.*

Bubroma grandiflorum Willd. ex Spreng. Syst. Veg. 3:332. 1826.

Guazuma grandiflora (Spreng.) Don, Hist. Dichl. 1:523. 1831.

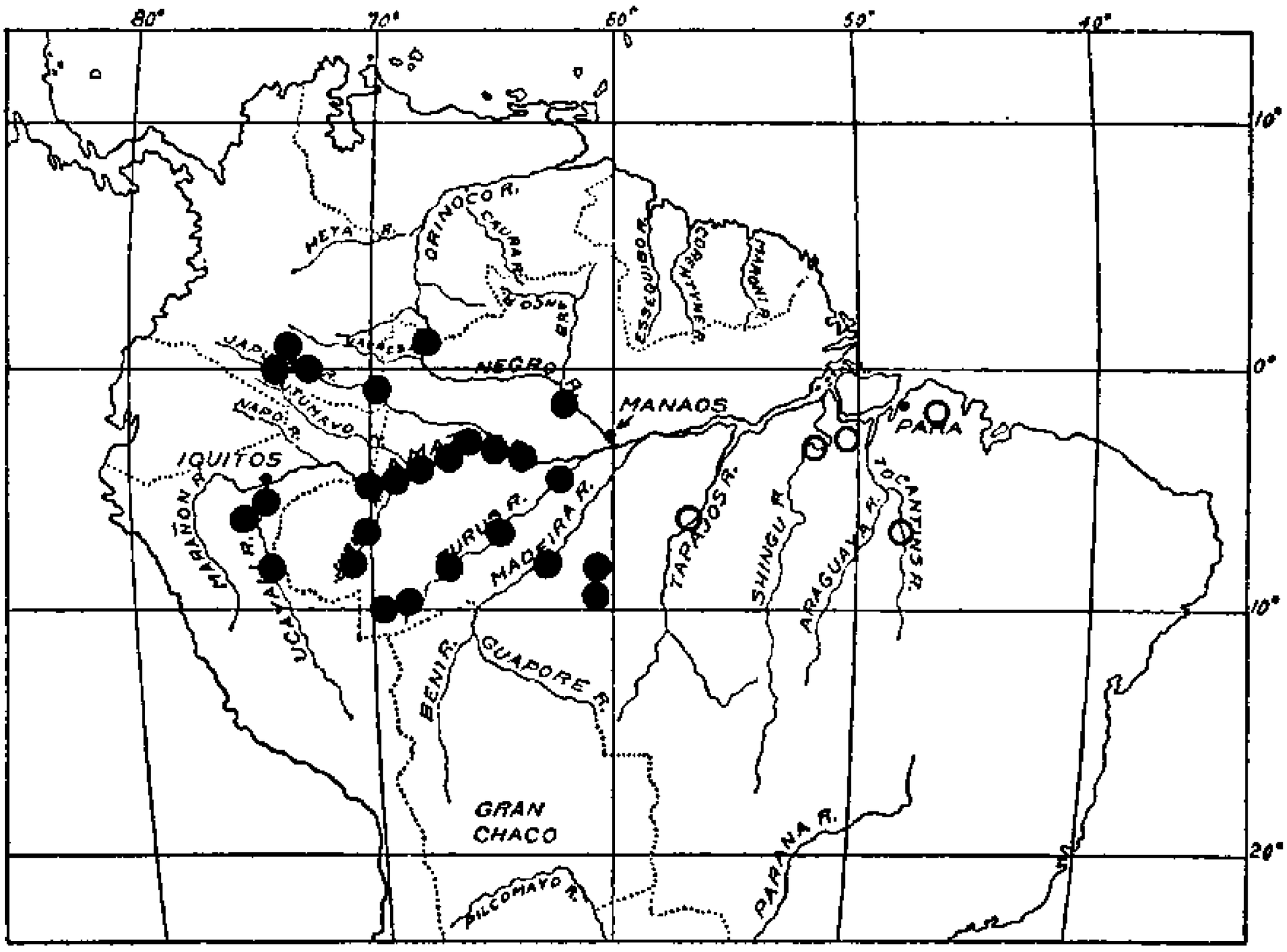
Theobroma speciosum Willd.?, sensu Mart. in Buchn. Repert. Pharm. 35:24. 1830; Linnaea Litt. Bericht 32. 1831, non Willd.

Theobroma macrantha Bernoulli, Uebers. Art. Theobroma 11. 1869.

Theobroma silvestre Spruce ex Schum. in Mart. Fl. Bras. 12(3):76. 1886, as synonym.

TYPE.—*Siber* 4, "Hoffmannseg" in Herbarium Willdenow No. 14352 (B). *Spruce* 1822 (syntype of *T. macrantha* Bernoulli and neotype of *B. grandiflorum* Willd.).

Medium-sized tree, usually 6–10 m. high, reaching up to 18 m.; growth pseudoapical; trunk up to 25–30 cm. in diameter, the bark grayish, granulose, more or less wrinkled, internally rosy or reddish, the wood pale; branches robust, spreading, the superior ascending, the primary ternate; branchlets terete, the terminal rather thick, densely and abundantly lanate-tomentose, the indument ferruginous, floccose,



MAP 10.—Geographical distribution of *Theobroma obovatum* ● and *T. grandiflorum* ○.

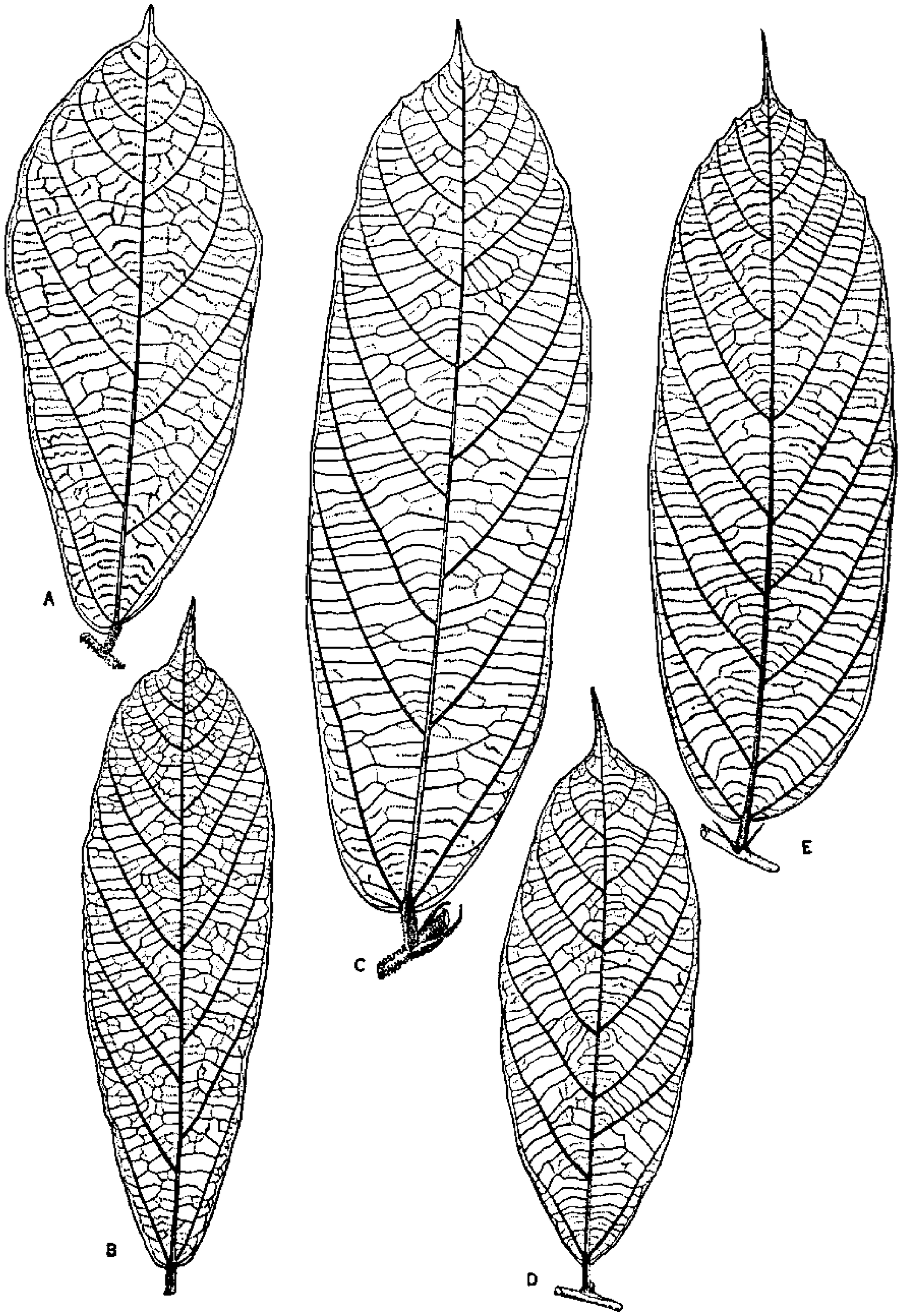


FIGURE 39.—Leaves of *Theobroma*, × ⅓: A, *obovatum* (Poeppig s.n.); B, *grandiflorum* (Cuatr. 25780T); C, *grandiflorum* (Killip & Smith 30011); D, *hylaeum* (Araque & Barkley 18C745); E, *subincanum* (Baker 38).

more or less deciduous, the hairs stellate or fasciculate with long, intricate rays, caducous, the surface fulvous, with exfoliating rhytidome, becoming gray, glabrous, and reticulate-rimose; stipules subcoriaceous, rigid, oblong or lanceolate-oblong, obtuse or subacute, nervate-striate, abundantly lanate-tomentose, the tomentum more or less deciduous, 10–20 mm. long, 3–6 mm. broad, persistent.

Leaves firmly coriaceous, medium sized or large; petiole thick, terete, with a dense, thick, ferruginous, lanate tomentum, 7–14 mm. long, 2–5 mm. thick; blades oblong, subobovate-oblong or subelliptic-oblong, more or less attenuate toward the base, this obtuse, rounded, usually emarginate, or subcordate and slightly irregular, abruptly attenuate and acutely acuminate at apex, the margin entire or slightly dentate-sinuate toward the apex, 20–35 (15–60) cm. long, 6–11 (5–16) cm. broad, the acumen 1–2.5 cm. long, glabrous above, green, more or less shining, brownish olivaceous or tabacine when dry, the midrib and secondary nerves filiform, depressed, the tertiary ones slightly marked or obsolete, greenish cinereous, glaucescent, or pale rosy beneath, the costa very prominent, the 9 or 10 pairs of parallel secondary nerves prominent, subascending, near the margin thinner, curved, anastomosing, the lowest pair usually forming a more acute angle and more distally separated from the next, the filiform tertiary nerves prominent, transverse, parallel, the minor nerves and veins forming a fine prominulous reticulum, the costa, secondary, and tertiary nerves glabrous, nitidous, with sparse reddish, callose dots, the reticulum and areoles minutely tomentose, covered by white, minute, intricate, dense, stellate hairs.

Inflorescences small, axillary and extra-axillary on leafy branches, the short cymes reduced to 3–5 flowers or fewer, the branchlets extremely short, ferruginous tomentose, the peduncles robust, 2–5 mm. long, 3-bracteolate at apex, the bracteoles narrowly linear, tomentose, 3–4 mm. long; pedicels robust, rather thick, tomentose, ebracteate, 5–20 mm. long.

Calyx subcymbiform; sepals firm, thick, carnose, ovate-oblong, subacute, about 14–15 mm. long, 6–8 mm. broad, 1.5 mm. thick, united in the lower third, but often the five separated to near the base in two pairs and one free (2S+2S+S), the margin involute, the apex minutely inflexed, thickly stellate-tomentose outside, ochraceous green or ferruginous, rosy or reddish inside, shining, minutely, sparsely, whitish pubescent, at base with minute, thick glandular trichomes, the margin densely and minutely whitish tomentose.

Petal-hoods thick, carnose, whitish or yellowish, often with red lines, obovate, rounded-cucullate at apex, 7-nerved, rugulose without, pubescent, glabrous within, near the base reddish, 6–7 mm. long, 4–6 mm. broad; petal-lamina dark red or crimson, pedicellate, thick,

carnose-coriaceous, trapezoid-elliptical, more or less truncate or slightly retuse, obcordate, minutely puberulous, 4–9 mm. long, 4.5–8.5 mm. wide, abruptly contracted at base into a 4.5–7 mm. long, 1.5 mm. broad pedicel.

Androecium tube 2.5 mm. high, sparsely pilose; staminodes reflexed in bud, spreading in anthesis, crimson, dark red or purplish red, lanceolate, very acute, thick, but somewhat flattened with a marked midrib, 9–15 mm. long, 2–2.5 mm. broad throughout, pilose, especially outside, the abundant hairs rather long, thin, flexuous; filaments 1.7–2 mm. long, thick, pilosulous, very shortly 3-furcate, 3-antheriferous; lobes of the anthers broadly elliptic, 1 mm. long; ovary pentagonous-obovate, densely whitish hirsute-tomentose; styles 2 mm. long, connivent, free to the base.

Fruits falling from tree at maturity, without peduncle, densely covered with a brown tomentum, large, smooth, ellipsoid or obovoid-ellipsoid, rounded at both ends or, rarely, slightly attenuate at apex, umbilicate and conically excavate at base, 16x10–25x12 cm.; pericarp about 1 cm. thick, with: 1) epicarp hard, woody, about 2 mm. thick, covered with a thin, tomentose epidermis, 2) mesoendocarp about 7 mm. thick, softly carnose at maturity with a thin, but firm, inner pellicle limiting the seed cavity; seeds about 50, 5-seriate, each surrounded by a yellowish, acidulous and distinctively scented, fibrous pulp, the inner tegument a delicate pellicle, the testa subcoriaceous, light brown, striped from the remains of the pulp, ovoid, or ellipsoid-ovoid, more or less flattened, 20–30 mm. long, 20–25 mm. broad, 10–12 mm. thick; embryo white marbled, 19–23 mm. long, 16–20 mm. broad, 9–12 mm. thick; cotyledons white; germination hypogeous.

The type of *Bubroma grandiflorum* Willd. ex Sprengel is the specimen No. 14352 of the Willdenow Herbarium in Berlin, received from the Hoffmannsegg Herbarium, collected in Brazil by Siber. This species was transferred to *Guazuma* by G. Don who probably did not see the plant, his description being taken from Sprengel. Schumann found out that *B. grandiflorum* is synonymous with *T. macranthum* described by Bernoulli many years later. The short diagnosis given by Sprengel agrees with *T. macranthum* and the description of the leaves ("amplis oblongis abrupte acuminatis integerrimis") disagrees with any known species of *Guazuma*, which always have serrate leaves. Freitag, who listed *Bubroma grandiflorum* as synonym of *Guazuma ulmifolia* (p. 216), did not see the type. In 1952, Dr. Mildbraed of the Berlin Herbarium wrote me about this type specimen: "Im Herbar Willdenow fehlte unerklärlicherweise der Bogen 14352 mit *Bubroma grandiflorum.*" Schumann had seen the type in the Willdenow Herbarium, for which reason I accept his judgment as final regarding the synonymy established by him. Accordingly, I propose *Spruce* 1822 as a neotype

of *B. grandiflorum* Willd. ex Spreng., as it is the first collection cited by Schumann and likewise a syntype of *T. macranthum* Bernoulli.

COMMON NAMES.—Cupassú, with some variations in the spelling or pronunciation throughout its area of cultivation, cupuaçú, cupú-assú, copuassú, cupai-açú. Ducke quoted cupú do matto for wild specimens in the middle Tapajoz River. The Anglo Colombian Cocoa Expedition recorded the following indigenous names (Baker, 1952): Win-cheék-chóo-ai (*Puinave*), Inírida-Guaviare; bawk-pom (*Maku*), Piraparaná, Tarraira; maga (*Barasana*), Upper Piraparaná; ñee-aw (*Tanimuka*), Guacaya; cupu-uassú (Brazil-Portug.); ba-dja-na-hoo (*Makuna*), Lower Piraparaná.

USES.—The natives like to eat the acid and agreeably scented pulp which covers the seeds, for which reason cupuassú is very much cultivated or planted in the state of Pará and the eastern section of Amazonas. This pulp is used to prepare soft drinks (vinho do cupuassú) and different kinds of preserves and candy which are exported from Pará and Maranhão. The taste of the pulp is *sui generis*. L. Williams compares it with that of guanábana. Patiño found the odor of it similar to that of the "mate" (*Crescentia cujete*) when beginning its fermentation. The fruits are very much liked by animals, especially by monkeys (macacos), which very often empty the pods to sip the pulp, contributing to the dissemination of the seeds.

DISTRIBUTION.—The known natural area of *T. grandiflorum* is the southern half of state of Pará, Brazil, and adjacent Amazonian Maranhão. It has been found wild only in the rain-forest, on elevated ground in the middle Tapajóz River region (waterfalls of Mangabal and of Itapacurá, *Ducke*), Tocantins River (railroad of Alcobaca, *Ducke*), Guamá River between Ourem and Bragança (*Huber*), Xingú River between Victoria and Altamira (*Ducke*), and Anapú River (*LeCointe*). The tree is always scarce in its natural area.

This medium-sized tree with large leaves, the largest flowers in the genus, and the largest pods among the Brazilian cacaos, is frequently planted or cultivated throughout the states of Pará, Maranhão, and the eastern part of Amazonas to Manaos. It is also occasionally planted outside Brazil in warm lowlands of other tropical American countries, such as Colombia, Venezuela, Ecuador, and Costa Rica. It is found also in tropical botanical and agricultural gardens.

MARTINIQUE: From seeds from Cayenne, *L. C. Richard*, s.n. (P).

BRITISH GUIANA: "Herbarium Benthamianum," *Schomburgk*, s.n. (K).

VENEZUELA: AMAZONAS: Capihuara, Alto Casiquiare, 120 m. alt.; cultivated, small tree up to 8–10 m., subrounded crown, trunk 25 cm. diam., gray bark, inner rose or reddish, wood pale, pulp of fruit used to prepare beverages with similar taste to the guanábana, "cupuasú," 28 V 1942, *Ll. Williams* 15615 (F, US, VEN).

COLOMBIA: Vaupés: Monfort; tree 6 m., sepals fleshy, petals maroon, 23 IX 1943, *P. Allen* 3105 (COL, MO, US). Río Vaupés, opposite confluence with Río Papurí, Yavaraté, Salesian Mission São Miguel; tree about 3 years old, growing in full sunlight, beginning to flower, no fruit, 20 II 1952, *Bartley & Holliday* T–46 (COL, US). Río Piraparaná, near confluence with Río Apaporis, river level; young tree 3–4 m., cultivated in Indian garden, 24 VIII 1952, *Baker & Cope* 5 (TRIN).

Amazonas: Río Caquetá, La Pedrera, river level; cultivated tree, rather exposed, in the garden of the Orfanatorio, 19 IX 1952, *R. E. D. Baker* 16 (COL, F, TRIN, US). La Pedrera, cultivated, highland; bushy tree 12 ft. tall, petals purple red, calyx light golden brown, staminodes yellowish, 7 X 1952, *Schultes & Cabrera* 17781 (US). Río Ricapuya, tributary of Río Apaporis, river level; 2–3 years, young cultivated tree in Indian garden, 25 VIII 1952, *Baker & Cope* 6 (COL, F, TRIN, US). Leticia, 22 VIII 1946, *Black & Schultes* 46–61 (AMES, F, IAN, NY, U, VEN); tree 8 m., "cupu-assú," cult., 24 IX 1946, *Black & Schultes* 46–III (IAN). Trapecio Amazónico, Amazon River, Leticia, 100 m. alt.; cultivated, "cupuassú," IX 1946, *Schultes* 8178 (AMES, F, US).

BRAZIL: "Catal. Geogr. Pl. Bras. Trop.," *Burchell* 9467 (GH, K, P). Ibidem, *Burchell* 9375 (syntype of *Theobroma macrantha* Bernoulli, K). "Amazon region," *H. A. Wickham*, s.n. (K). "Brazil Cameta," Herb. *Hanbury* 9471 (K).

Amazonas: Rio Negro, São Gabriel; arvore 8 m., planta antiga dos sitios, "cupu-assu," 27 XII 1945, *Fróes* 21556 (IAN, K, NY, USDA). Upper Rio Negro basin, Mouth of Rio Xie, cultivated; small tree, staminodes and ligules deep red, rest of flower pink, "cupu-uassu," 29 XI–7 XII 1947, *Schultes & López* 9204 (AMES, F, IAN, US). Rio Negro, prope Barra; "shrub 12–15 ft., flowers only on ramuli, solitary normally ascendant, calyx pinkish within, petals crimson, cucullate, bases yellow white, coronal scales red"; the Munich specimen bears the number 83 on a mounting tape (F. M. Photo 40705), Oct. 1851, *Spruce* 1822 (neotype of *B. grandiflorum*, M; isosyntypes of *T. macrantha* Bernoulli, BM, E, G, GH, K, LE, LD, NY, OXF, P, WU). Manaos, Horto Experimental, 20 m., "cupai-açú," 19 XII 1923, *Luetzelburg* 22007 (M, NY, WU). Manaos, Agricultural Experiment Station, 25 m. alt., cultivated; tree 35–40 ft., inflorescences on main trunk, sepals green without, pink within, petals red, 13 X 1929, *Killip & Smith* 30011 (NY, US). Manaos, Estrada do Aleixo, firm land; tree 6 m., flower red, edible fruit, "cupuaçú," 16 IX 1955, *Francisco* (*INPA*) 1966 (IAN). Manaos, Hacienda Brasil, 15 m. alt., "cupu-açú," *Luetzelburg* 23287 (M). Manaos, VIII 1906, "cupu-assú," *Labroy*, (P). Three days upstream from Manaos, 300 ft. alt.; grown in semishade; flowers cream colored or dark crimson, growing out of the bark, faintly scented, *Sandeman* 2333 (K). Paraná de Matitins, Rio Putumayo, Içá, between Tarapacá and its mouth (Santo Antonio do Içá, 100 m. alt.); small treelet; calyx very fleshy, green yellow; staminodes white, laciniae flesh red turning brown on fertilization, "cupuassú," 11–18 IX 1946, *Schultes & Black* 8146 (F, IAN). Municipality of Mahacapuru, Solinos River region, terra firma, Lago do Italiano; tree 25 ft. high, 4 inches diam., "cupu-assú," *Krukoff* 1274 (A, BM, G, K, MICH, MO, NY, P, S). Tefé; tree 7 m., flower brownish rose, cult. "cupuaçú," *Black* 47–1502 (IAN).

Maranhão: Turyassu, Igapo-wald; Baum 6–15m., Krone gelblich, filaments rot-violett, 31 X 1923, *Snethlage* 300 (F, GH, US).

Acre (Territorio Federal): Brasilea, in a house in front of the Bolivian town Cobijia, 150 m. alt., "copuassú," cultivated, 5 IX 1954, *Patiño* 163 (GH).

Pará: Belém, northeast woods of the Instituto Agronómico do Norte; infected with witches broom, "cupu-assu," 30 X 1942, *Archer* 7734 (IAN, NY, US). Belém, Botanic Garden of the Museu Goeldi; native of the lower Amazon

country; the tree becomes much larger than the cacao and the top is relatively narrower; the fruit resembles the pod of cacao but is much larger and the pulp surrounding the seeds is most delicious; Dr. Huber speaks of it as the most important native fruit of Pará; "cupuaçú," 25 VI 1908, *C. F. Baker* 62 (A, C, E, GH, LE, MICH, MO, P, U, US, NY). Museu Goeldi, 23 XI 1945, *Pires & Black* 744 (IAN). Jardim Botánico do Museu Goeldi; large tree, calyx with red marks inside base, spatulate portion petal dark red, fruit edible, "cupuaçú," 11 VIII 1942, *Archer* 7549 (F, IAN, K, US). Ibidem; small tree, leaves gray both surfaces, flowers large, cauliflorous, calyx white yellow, staminodes deep red, petals pinkish, very showy, a profusion of flowers, cultivated, 15 VII 1946, *Schultes* 8065 (AMES, US). Horto Botánico do Pará, XI 1903, "cupuassú," *Huber* 4008 (BM, G). Ibidem, "cupuassú," XI 1903, *Siqueiros* 4008 (MG). Belém, "in urbe cultum; arbor parva floribus brunnescentibus centro albido," "cupuassú," 16 X 1940, *Ducke* 598 (F, IAN, MG, MO, NY, US). Ibidem, III V 1929, *Dahlgren & Sella* 438, 634 (F), "cupu-assu," *Dahlgren & Sella* 733, 739 (F, GH, US). Vicinity of Pará, 1 VII 1908, *C. F. Baker* 421 (BM, C, F, L, U, WU). In sylva prope Barba et alibi, VIII 1828, *Riedel* 1373 (A, LE, S, US). "Brasilia, Borbar," *Riedel,* s.n. (OXF). Bõa Vista, on the Tapajós River, Aramanahy River, "cupuassú," *Monteiro de Costa* 121 (F). Taperinha bei Santarem, kultiviert; aus dem Fructen wird Marmelade bereitet, kleiner Baum, "Cupu-assú," 18 IV 1927, *Ginzberger & Zerner* 800 (F, WU). "Habitat in sylvis udis umbrosis ad Para, Dr. Martius Iter Brasil. Jul. 323," *Martius* [874] (M). "Prov. Paraensis ad Para, Dr. Martius Iter Brasil. 323," *Martius* [875], [876] (M) (Photo F. M. 40706). Ibidem, Martius [873] (M) mixed with *T. guianense* in Photo F. M. 19641). Pará, "Bresil-Martius," *Martius* (G, P). Tapana, near Pará, woods; 30–40 ft. tall, appendages purplish red, clearing, fruit edible, 29 X 1929, *Killip & Smith* 30320 (NY, US). Forêt des collines du Mangabal, moyen Tapajós, Cachoeira do Mangabal, "cupú do matto," 5 IX 1916, *Ducke* 16458 (BM, G, MG, P).

RIO DE JANEIRO: Rio Janeiro, cultivated, "cupú assú," *Glaziou* 9643 (C, P).

PERU: LORETO: Caballo Cocha, on the Amazon River, "cupuassú," VIII 1929, *Ll. Williams* 2401 (F).

TRINIDAD: St. Augustine, Imperial College of Tropical Agriculture, River State Diego Martinez, Field 2; trunk 20 cm. diam. at base, leaves coriaceous dark green above, green beneath, fruits ellipsoid, densely tomentose, brown ferruginous, 11 x 17, 11.5 x 18.5, 11.5 x 16.5, 12 x 19, 12 x 19.5, 12.5 x 19 cm., with 47–50 seeds, pulp yellowish with special scent, cultivated, brought from Belém do Pará, 31 VIII 1961, *Cuatrecasas, Cope, & Bartley* 25780 T (US). Ibidem; tree with larger and slightly attenuate fruits at apex, 10.7 x 22, 11.1 x 21.5, 11.8 x 25 cm., 31 VIII 1961, *Cuatrecasas, Cope, & Bartley* 25781 T (US). Saman Plot, cultivated from seeds brought from Pará; trunk 30 cm. diam., the diameter reducing progressively upwards from one cluster of branches to the next, primary branching ternate, from the base, apical growth, bark greenish brown, granulate-lenticellate, minutely rimose, sepals 1.5–2 mm. thick, greenish ochraceous outside, whitish and pink at base inside, hoods white yellowish or dirty whitish, the margin and the base inside purplish, lamina carnose, dark red, later red brown, staminodes star-patulous, red purplish becoming red brownish, styles united whitish, ovary white, hirsute-tomentose, 2 IX 1961, *Cuatrecasas & Cope* 25801 (US).

16. Theobroma obovatum Klotzsch ex Bernoulli

FIGURES 33, 35, 39, 40; MAP 10

Theobroma obovatum Klotsch ex Bernoulli, Uebers. Art. Theobroma 14, *pl. 7, fig. 3.* 1869; Ducke (1935) 132; (1940) 271, *pl. 5, fig. 1;* Chevalier (1946) 280; Addison & Tavares (1951) 25, *pl. 1, fig. 2, pl. 2, fig. B, pl. 3, fig. 2, pl. 4, fig. B, pl. 11, fig. 1;* Ducke (1953) 10; Cuatrecasas (1956) 657; Baker, Cope & al. (1954) 12, *fig. 15;* León (1960) 322, 319, *fig.*

Theobroma sylvestre sensu Huber, Bull. Herb. Boiss. II, 6: 273. 1906, non Mart.

TYPE.—Maynas, Peru, *Poeppig.*

Rather small tree up to 15 m. high; growth pseudoapical; trunk 10–25 cm. in diameter; primary branches ternate, the inferior horizontal, the upper ascending; terminal branchlets slender, when young ochraceo-ferruginous, densely lanate-tomentose, the intricate, long, stellate hairs more or less floccose, deciduous, when older glabrate, pale brown or pale gray, the rhitidome somewhat scaly; stipules narrow-linear, subulate, acute, tomentose, 3–5 mm. long, 0.5–1 mm. wide, soon deciduous.

Leaves chartaceous, flexible, variable in size; petiole mediocre, subterete, transversely rimose, densely and thickly lanate-tomentose, ferruginous, when old the indument appressed, grayish, 4–15 mm. long; blades obovate-elliptic or obovate-oblong, more or less narrowed to the very asymmetrical and rounded base, more abruptly attenuate and cuspidate at apex, entire or slightly sinuate at margin, 7 x 3 to 38 x 13 cm., including the 0.5–3 cm. long acumen, varying very much in size on the same branch, when very young stellate-pilose above, then glabrous, pale olivaceous or pale brownish, shining, the main nerves depressed, filiform, the others obsolete, pale ochraceous or pale cinereous beneath, glaucescent, the costa very prominent, the 5–7 secondary nerves on each side prominent, curved-ascending, near the margin arched anastomosing, the lower pair usually forming an acute angle, ascending and more distally separated from the others, the transverse tertiary nerves thin but prominent, the minor veins forming a prominulous conspicuous reticulum, the costa and the principal lateral nerves covered when young, mainly towards the base, by a floccose deciduous indument of ochraceous, entangled, stellate hairs, in time becoming glabrous, shining, marked with minute callose, reddish, sparse dots, the tertiary nerves also glabrous, the minor veins, reticulum, and areoles covered by minute, white, stellate hairs forming an appressed, whitish tomentum.

Inflorescences very small, axillary or in exfoliated, thin branchlets, the axis and branchlets of the cymes very reduced, ochraceous-ferruginous, lanuginose-tomentose; peduncles 2–7 mm. long, 3-bracteolate at apex; pedicels 3–8 mm. long, somewhat thicker; bracteoles

linear, 1.5–2 mm. long; buds globose, also ochraceous-lanuginose and woolly-tomentose.

Sepals thick, ovate, subacute, slightly involute-marginate, about 6–7 mm. long, 3–4 mm. broad, united 1 mm. at base, rosy or reddish inside, subglabrous, glandular at base, 3–5 nerved, the margin minutely whitish tomentose, rather woolly outside, stellate-tomentose, spreading in anthesis; petal-hoods yellowish or reddish obovate, rounded cucullate and slightly retuse at apex, with 7 prominent nerves and copious, spreading, minute hairs inside, subglabrous with few, slender, flexuous hairs outside, 3–3.5 mm. long, 2.5 mm. broad; petal-lamina deep red, rather thick, suborbicular, often retuse at apex, abruptly contracted into a pedicel at base, pilose at margin, and with very sparse, flexuous, slender hairs on the inner side, 3.5 mm. long, 4 mm. broad; pedicel red, 0.6 mm. wide with sparse, slender hairs, 2.5 mm. long.

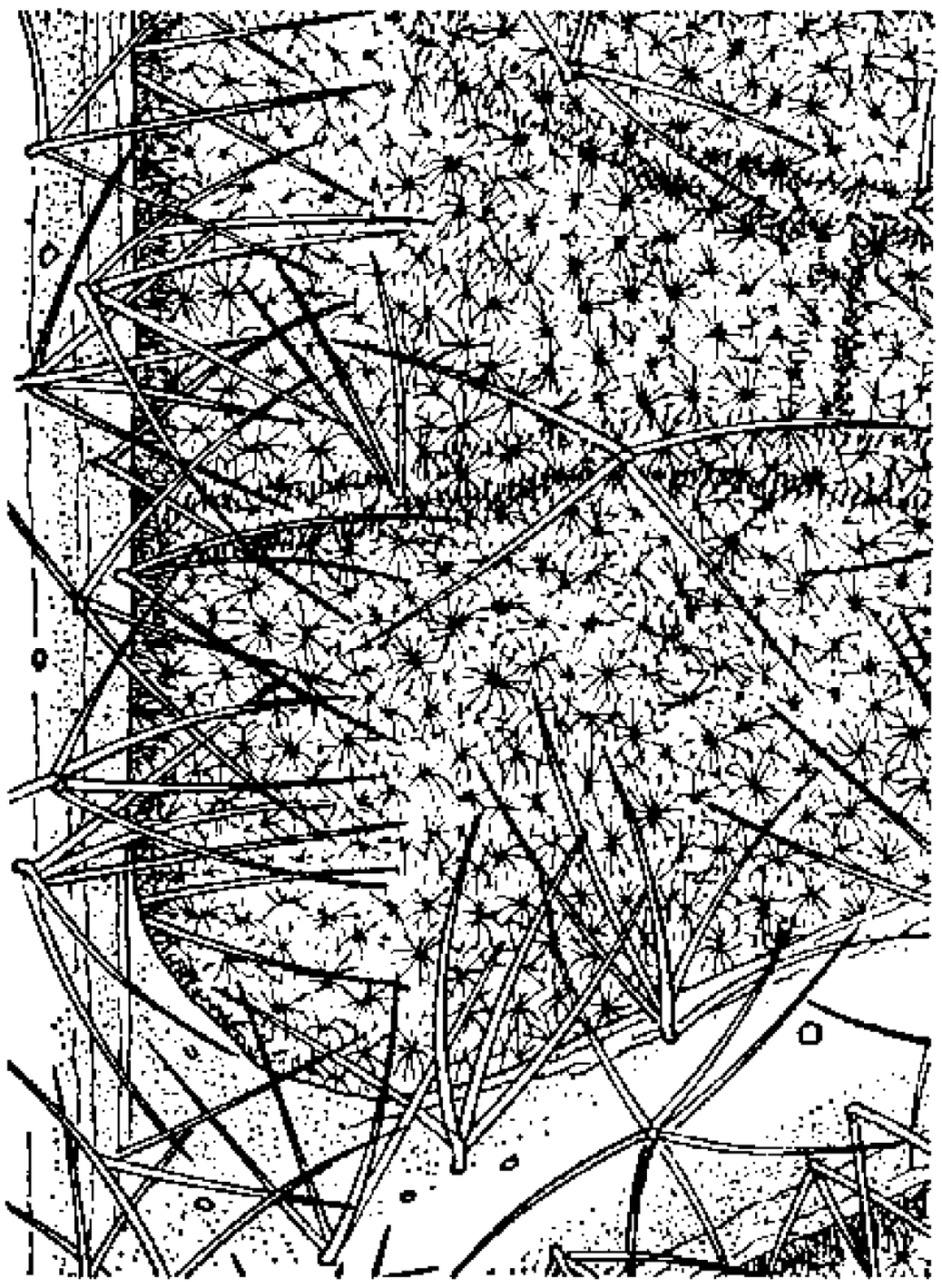
Androecium tube about 1.5 m. high, glabrous; staminodes laminar, thick-membranaceous, deep red, oblong-elliptic, rounded and often emarginate at apex, attenuate near the base, with a conspicuous medial nerve and thin, flexuous, subspreading hairs distributed throughout, especially on the margins, 5–6 mm. long, 2.5–3 mm. broad; filaments thick, glabrous, 1.5 mm. long, shortly 3-furcate, 3-antheriferous; anther lobes ellipsoid, 0.4–0.5 mm. long; ovary ovoid, 1.5 mm. long, densely tomentose-hirsute; styles glabrous, 5 mm. long, united only at base.

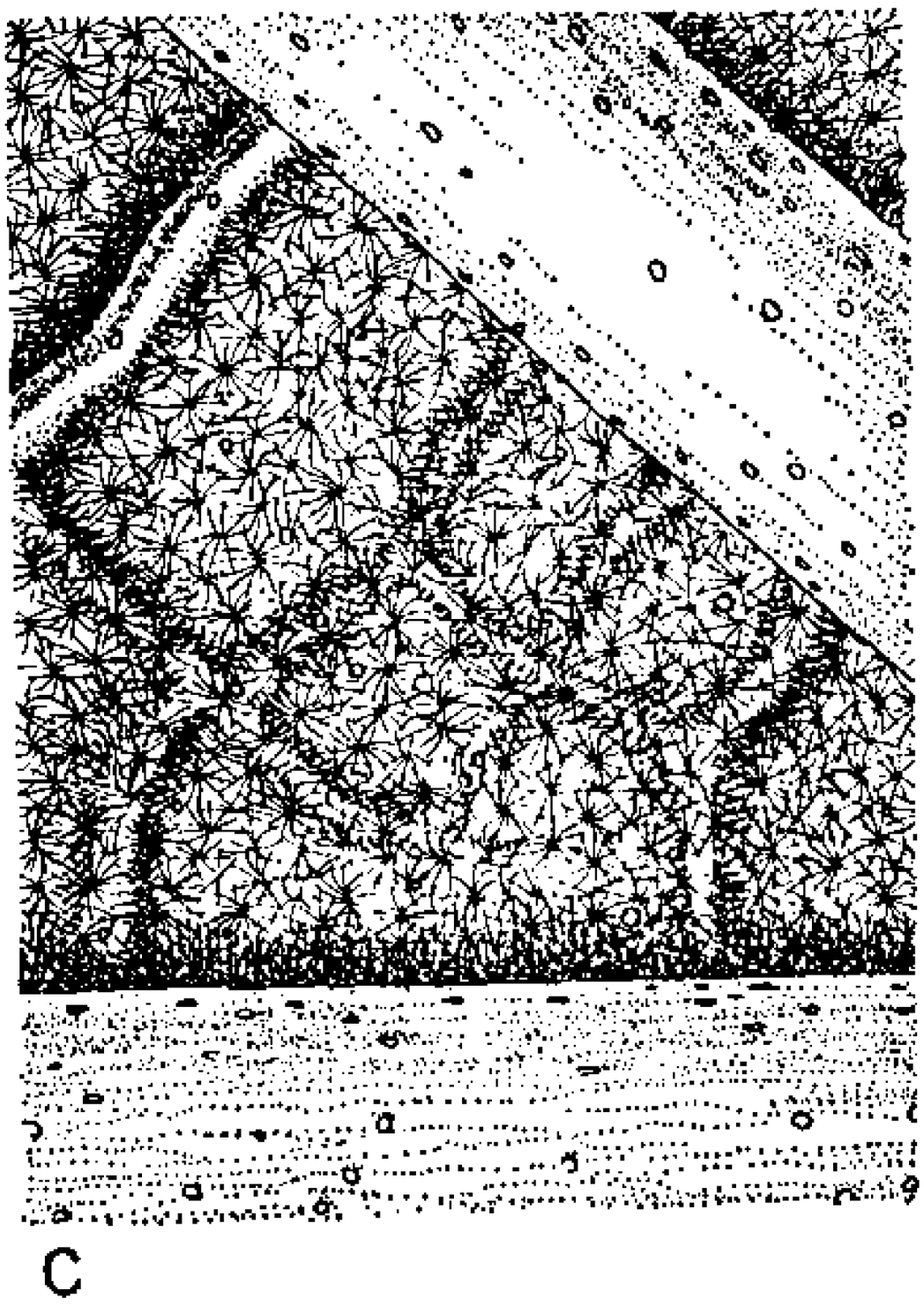
Fruit obovoid-ellipsoid, rounded at apex, contracted at base, greenish, when ripe brown yellowish, 5–7 cm. long, 3–4 cm. broad, the pericarp thin-coriaceous densely covered with acute, hard warts and sparse stellate hairs, when dry about 1.5 mm. thick; seeds 16 mm. long, 9 mm. broad; germination hypogeous.

COMMON NAMES.—Cabeça de urubú is the most common and widespread. Also, the following have been locally recorded: copu-ai, cupu-curúa, cupurana, cacao de macao, urubú-acain, cabeça de Umbú.

Win-cheék (*Puinave*), Inírida-Guaviare; ma-oo-hee-rée (*Kabuyarí*) (Rio Cananarí) (Angl. Col. Cocoa Exped., Baker 1952).

DISTRIBUTION.—Spread throughout the western part of the Amazon basin, on elevated ground and humid, fertile soil of rain forests. In Brazil it is frequent in the western half of Amazonia, the easternmost localities known being Teffé, on Rio Solimoes and Rio Jau, a tributary of the Rio Negro (*Ducke*). The Anglo-Colombian Cacao Expedition found it (although not abundantly) in the rivers Caguán, upper and lower Caquetá, and the Putumayo (Report, 1954, 12, 13). In Peru goes as far as the lower parts of Río Huallaga and Río Ucayali, Río Itaya, and also Putumayo.





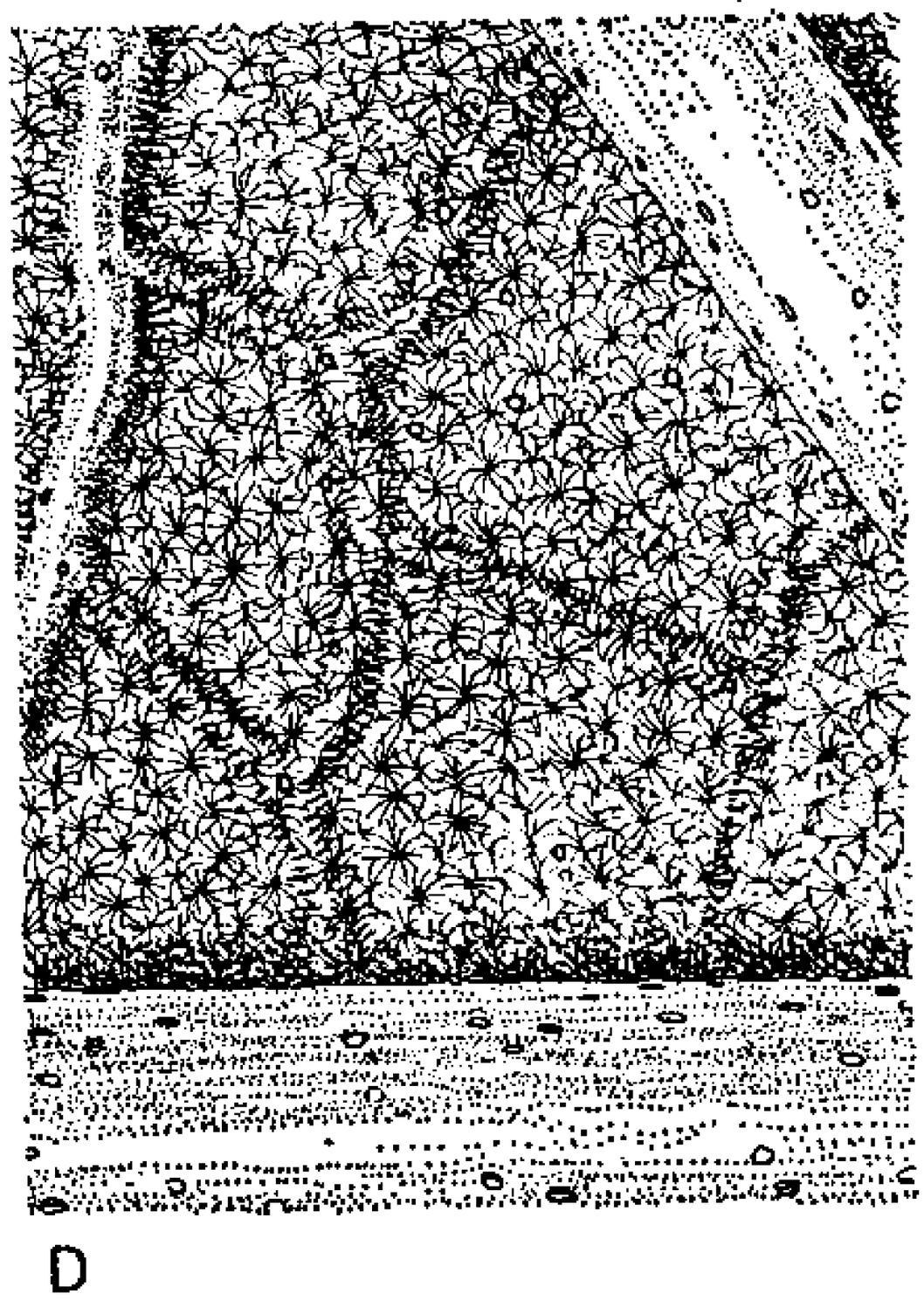


FIGURE 40.—Detail of indument on the underside of leaf in: A, *Theobroma simiarum* (Standley 37377) from seedlings; B, *T. simiarum* (Pittier 7731), from adult branches; C, *T. grandiflorum* (Killip & Smith 30011); D, *T. obovatum* (Ducke 265). A × 20, B × 30, C and D × 40.

Theobroma obovatum is a rather small tree with a crowded, leafy crown, easy to recognize by its small, ellipsoid-obovoid fruits constricted at the neck, with thin, fragile, granulate or verrucose pericarp, usually green but becoming brownish yellow when ripe. Also characteristic are its light, papery, asymmetrical, oblong-obovate leaves with a close, white or cinereous monotrichous tomentum beneath; when very young the upper side, the principal nerves as well as the petioles, stipules, and twigs, are covered with an ochraceous brown or orange, easily removed down, composed of long, deciduous, stellate hairs. The fruit when ripe separates from the pedicel and falls.

Schumann did not know the species, for it is lacking in his herbarium; he included the name *T. obovatum* as a synonym of *T. subincanum* in his treatment in the Flora Brasiliensis (p. 77).

Huber knew the species well, although he called it *T. sylvestre*, confusing and misinterpreting Aublets figure of *Cacao sylvestris*. Ducke also knew *T. obovatum* and its distribution very well, but he thought that *T. sylvestre* Mart. was a synonym.

COLOMBIA: Putumayo: Río Caucayá, Rio Leguízamo, Laguna Primavera; tree 15 m., 3 IV 1953, *Holliday & Cope* T/90 (COL, TRIN, US). Ibidem; tree 10 m., flowering, on elevated land above river, 5 IV 1953, *Holliday & Cope* T/95 (COL, TRIN, U, US).

Caqueta: Río Caguán, camp 4, 27 IV 1953, *Holliday & Cope* T/119 (COL, TRIN, US). Ibidem; found on sloping land, 30 ft., above river, tree 6 m., jorquettes arising symmetrically, 26 IV 1953, *Holliday & Cope* T/114 (COL, TRIN, US).

Amazonas: Río Caquetá, La Pedrera, river level; tree 10 m., native in forest on the riverbank, 7 X 1952, *Baker & Cope* 30 (COL, F, TRIN, US). Ibidem; tree 7–8 m. in forest river-bank, presumed native, jorquettes regularly of three branches growth continuing from above, young twigs and leaves with caducous fuzz, flowers pale crimson, 5 X 1952, *Baker & Cope* 27 (COL, F, TRIN, US). Ibidem; large tree 30 ft. high; calyx lobes light outside and pinkish inside, petals dark purplish red, diameter 9–10 inches, 5 X 1952, *Schultes & Cabrera* 17775 (US). Rio Caquetá, Remolino; tree 6–8 m., no flowers but had two ripe pods, 2 V 1953, *Holliday & Cope* T/123 (COL, TRIN, US). Trapecio Amazónico, Loretoyacu River, 100 m. alt., XI 1945, *Schultes* 6921 (F).

BRAZIL: Pará: Belém, Jardim Botánico do Museu Goeldi; small tree, "cacau cabeça de urubú," cultivated, 11 VIII 1942, *Archer* 7537 (USDA, IAN). Ibidem; arvore no. 482, 22 XII 1958, *Cavalcante* 339 (MG, US). Ibidem, *Pires & Black*, s.n. (BH), 743 (IAN). Ibidem (Río Purús, loco dicto Bom Logar oriuntur, J. Huber anno 1904 accedit); arbor parva floribus atrorubris, fructus maturitate flavidis, "cabeça de urubu," 4 II 1926, *Ducke* 21044 (G, K, P, U, US). Ibidem, *Ducke* 265 (A, F, K, MO, S, US). Belém, cultivado in Instituto Agronómico do Norte, "cabeça de urubú," *Pires, Nilo, & Silva* 4339 (IAN, UC, US).

Amazonas: San Antonio do Içа, matta, 27 IX 1906, *Ducke* 7704 (MG). On the Rio Negro, *Schomburgk* 870 p.p. (L). Municipality São Paulo de Olivenca, near Palmares; tree 35 ft. high, trunk 4 inches diam., terra firma highland, 11 IX–26 X 1936, *Krukoff* 8275 (A, BM, FE, F, G, K, MICH, MO, P, S, U, US, USDA, Y). Basin Rio Madeira, Municipality Humayta, near Tres Casas, on

varzea land, shrub 25 ft. high, "cabeça de umbú," 14 IX–11 X 1934, *Krukoff* 6263 (A, BM, F, GOET, K, LE, MICH, MO, S, U, US, Y). "Amazonas Ega," *Poeppig* 2746 p.p. (LE). "Brasilia in sylvis circum Ega, 1831," *Poeppig*, s.n. (WU). Amazonas; Bocca et Teffé, matta, "cabeça de urubú," 27 X 1904, *Ducke* 6823 (BM, G, MG, P, US). Teffé, matta virgen; tree, flower white, "copu-ai," 22IX 1947, *Black* 47–1496 (IAN). Igarapé Jandiatuba, lowland, border of the river, 14 I 1949, *Frões* 23926 (US, IAN). Arredodes de Fonte Bôa, terra firma alta; arvore media, "cupurana," "cupu-curua," 12 IV 1945, *Frões*, 20646 (F, K, IAN, USDA). Rio Juruá, Juruá Miry; Baum 3–9 m., Blumen dunkelpurpurn, VIII 1901, *Ule* 5637 (G, HBG, K, MG, L). Purús, Monte Verde, "cacao de macaco," II 1904, *Goeldi* 4226 (MG). Rio Acre: Antimari, matta, 31 III 1904, *Huber* 4295 (BM, G, MG, P, US). Upper Amazon, Paranary; low tree, petals purple, stamens yellowish, staminodia yellow, "urubú-acaim," 20 X 1924, *Traill* 61 (K, P).

ACRE: Basin Rio Purús, near mouth of Rio Macauhán (tributary of Rio Yaco), Lat. 9°20′ S, Long. 69° W, on terra firma; tree 35 ft. high, 9 VIII 1933, *Krukoff* 5388 (A, G, K, MICH, MO, S, U, US). Ibidem; shrub 40 feet high, 3 IX 1933, *Krukoff* 5759 (A, BM, F, G, K, MICH, MO, S, U, US).

MATO GROSSO: Machado River region, source of the Jatuarana River; tree 45 ft. high in terra firma, "cupuarana," XII 1931, *Krukoff* 1668 (A, BM, G, K, F, MICH, MO, S, U, UC).

GUAPORE: Porto Velho, km. 8, matta on elevated ground; small tree, 17 VI 1952, *Silva* 155 (IAN).

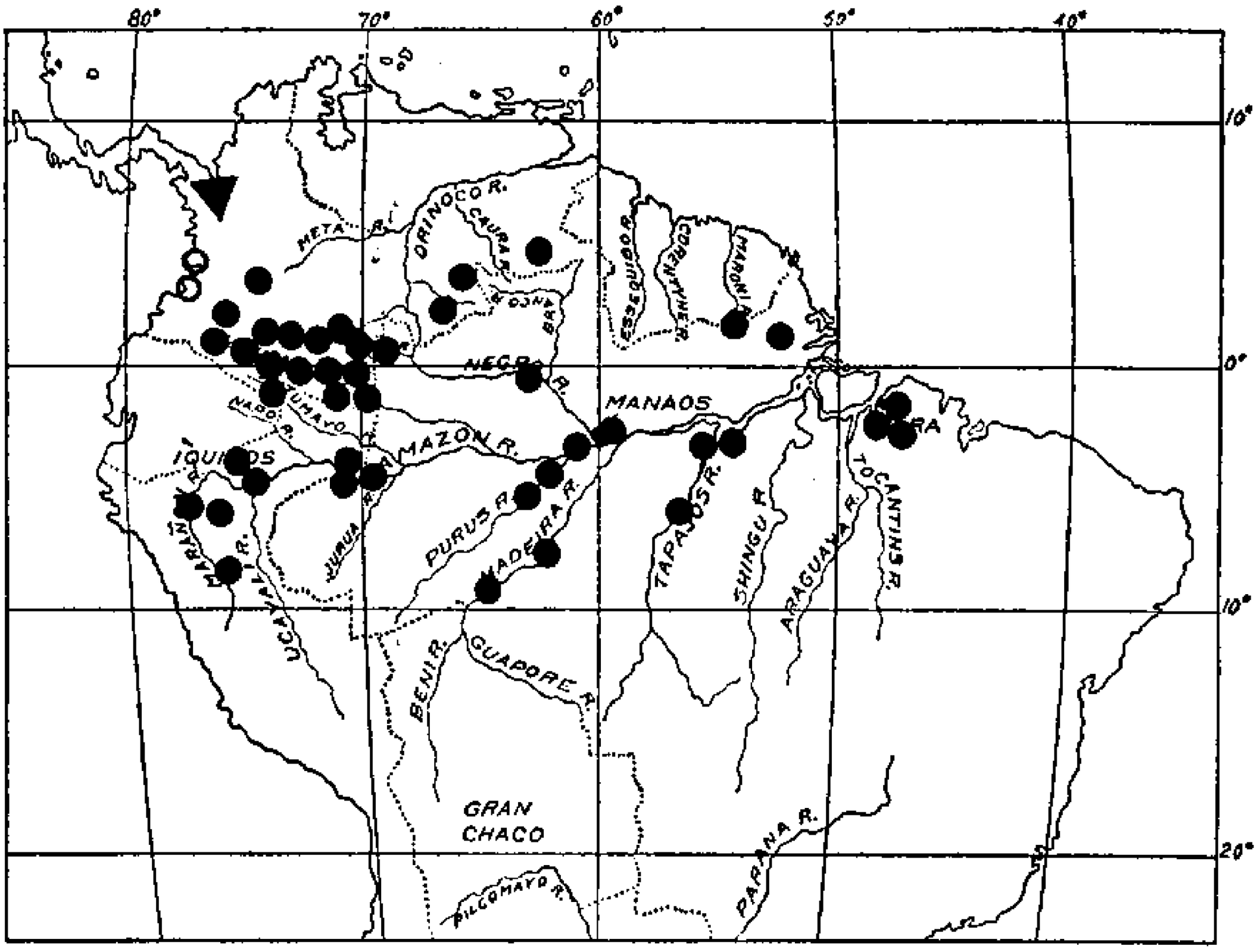
PERU: LORETO: Along Río Itaya, Río Masana, 8 V 1929, *Ll. Williams* 161 (F). Forest of Río Itaya, 3 V 1929, *Ll. Williams* 230 (F, US). Lower Río Huallaga, Puerto Arturo, Yurimaguas, 155–210 m., medium-sized tree, forest, 20 XI 1929, *Ll. Williams* 5268 (F, US). Balsa-puerto, 220 m., forest; tree 4 m., flowers wine red, IV 1933 *Klug* 2983 (A, BM, G, GH, K, F, MO, S, US). Maynas, in sylvis circum Yurimaguas, 1831, *Poeppig* 1845 (G). Maynas 1831, *Poeppig* 2352 p.p. (lectotype, WU; isosyntypes, F, GOET, G, LE, P). Stromgebiet des Ucayali, von 10° S bis zur Mündung, 1923, *Tessmann* 3433 (G, S). Rain forest of the Amazon basin, 230 m., 40 km. south of Pucallpa, 24 VII 1957, *Ellenberg* 2551 (L). Bank of Río Putumayo, opposite Puerto Leguizamo; sucker of large flowering tree, leaves rather large, 7 IV 53, *Holliday & Cope* T/98 (COL, TRIN, US).

TRINIDAD (cult.): Imperial College of Tropical Agriculture, River State Diego Martínez, Field 19; primary branching ternate; growing pseudoapical; branchlets and twigs ochraceous lanate-tomentose, leaves thin, flexible, very pale, with costa and secondary nerves yellow green, with woolly, floccose, deciduous tomentum beneath, green above, 31 VIII 1961, *Cuatrecasas, Cope, & Bartley* 25783T (US). Ibidem; trunk 15 cm., bark lenticellate-granulate; branching ternate; terminal branchlets light brown or brownish ochraceous, lanate-tomentose, crown very branched and leafy, the lower branches horizontal, the upper ones ascending, young, tender, terminal leaves hanging, light yellowish green, 1 IX 1961, *Cuatrecasas & Cope* 25788 (US).

17. **Theobroma subincanum** Mart.

FIGURES 29, 33, 35, 39, 41; MAP 11; PLATES 9, 10, 11

Theobroma subincanum Mart. in Buchner, Repert. Pharm. **35**:23. 1830; Linnaea Litt. Bericht, 32. 1831; Bernoulli (1869) 13; Schumann in Mart. (1886) 77; Jumelle (1899) 27 (in part); Huber (1906a) 274; Ducke (1925) 132; (1940) 272, *pl. 4, fig. 1;* Addison & Tavares (1951) 25, *pl. 3, fig. 1,*



MAP 11.—Geographical distribution of *Theobroma subincanum* ● and of its vicariants at the western side of the Andes, *T. hylaeum* ▲ and *T. nemorale* ○.

pl. 4, fig. A, pl. 11, fig. 3; Ducke (1953) 10; Cuatrecasas (1956) 699; Baker, Cope, & al. (1954) 12, *fig. 13.*

Cacao sylvestris Aubl. Pl. Guian. **2**:687, *pl. 276.* 1775.

Cacao guianensis Aubl. Pl. Guian. 2:684. 1775, pro parte (*tantum folia*).

Theobroma sylvestris (Aubl.) Don, Hist. Dichl. Pl. **1**:622. 1831, non Mart. 1830; Chevalier (1946) 279; Lemée (1952) 380; León, (1960) 322, 321, *fig.*

Theobroma ferruginea Bernoulli, Uebers. Art. Theobroma 13. 1869.

Theobroma alba Ruíz & Pavón, Fl. Peruv. Chil. 6, *pl. 68,* ined.

TYPES.—Amazonas, Brazil, *Martius.* French Guiana, *Aublet* (of *Cacao sylvestris*). Peru, *Ruíz & Pavón* (of *T. ferruginea*).

Medium-sized tree commonly 6–12 m. tall, at times up to 20 m. high, the trunk 15–20 (–30) cm. in diameter, with gray, almost smooth bark, older bark rugose-rimose, reddish within, the wood whitish, darker toward the center; growth pseudoapical; primary branches ternate, grayish, spreading; juvenile branchlets covered by a dense ferruginous tomentum of stellate hairs, when older glabrescent, pale brownish or brown, somewhat rugose, rimose-reticulate; stipules narrowly linear, densely ferruginous-tomentose, 5–7 mm. long, 1 mm. wide, soon deciduous.

Leaves firmly coriaceous, rather thick and large; petiole robust, subterete, densely and appressed ferruginous-tomentose, 8–15 mm. long; lamina elliptic-oblong or subobovate-elliptic-oblong, very little

attenuate to the base, slightly unequal, rounded or very obtuse, emarginate or rarely cordate at base, somewhat narrowed or rounded and abruptly acuminate at apex, sometimes blunt, entire, or near the apex dentate-sinuate, 16–40 cm. long, 5–20 cm. broad, the acumen acute, 1–3 cm. long, when very young ferruginous-tomentose throughout, but soon glabrescent above, when adult glabrous above, green, somewhat brownish olivaceous when dry, the costa and the lateral nerves depressed, filiform, the lesser veins obsolete, cinereous beneath, the veins more or less tawny or ferruginous, the costa thick, very prominent, the 9 or 10 pairs of secondary nerves very prominent, subascending, thinner near the margin, decurrent, the superior arched, anastomosing, the basal pair often straighter and forming a more acute angle, the transverse tertiary nerves prominent, the minor ones and small veins prominulous, minutely reticulate, the midrib, major nerves, and reticulum more or less densely covered by mediocre, reddish or tawny stellate hairs, the areoles between the veins with a dense whitish indument of very small, delicate, intricate, stellate hairs.

Inflorescence small, few-flowered, axillary or extra-axillary on leafy branches; cymes with 3–9 fasciculate branchlets, usually 1–3-flowered; peduncles 2–8 mm. long, with 3 bracteoles at apex, the bracteoles subulate, about 3 mm. long, deciduous; pedicels 3–6 mm. long, thicker than the peduncle; buds ovoid-globose; sepals thick, carnose, ovate, acute or subacute, densely stellate-tomentose outside, ferruginous, the margin minutely whitish tomentose, shining inside, purplish or red, subglabrous with minute, crowded, oblong-capitate, glandular hairs at base, near the margin slightly pubescent, 8–9 mm. long, 3–4 mm. broad, united at base for 2 mm., subpatulous.

Petal-hoods thick-membranaceous, pale yellow and red striate, obovate, rounded-cucullate at apex, slightly emarginate, 7-nerved, inside minutely hirtulous, glabrous outside except for the puberulous margin, 3–3.5 mm. long, 2–2.4 mm. broad; petal-lamina pedicellate, carnose, thick, rigid, red, suborbicular, 2–2.5 mm. long, 2.2–4 mm. broad, with slightly retuse apex, slightly pilose at margin, the hairs very slender, flexuous; pedicel 2 mm. long, compressed, pilose.

Androecium tube 1.5–1.7 mm. long, glabrous; staminodes laminar, red, lanceolate-oblong, acute or subacute, with marked midrib, subglabrous with sparse flexuous hairs at margin, 6–7.5 mm. long, 2 mm. broad; filaments rather thick, glabrous, about 1.5 mm. long, arched, very shortly 3-furcate, 3-antheriferous, the anther cells ellipsoid, about 0.5 mm. long; ovary ovoid-oblong, 1.3 mm. long, glabrous, with very sparse, minute, granulate dots; styles 1.5 mm. long, connivent.

Fruit ellipsoid, light green, tawny or orange at maturity, smooth, oblong-ellipsoid or obovate-ellipsoid, rounded at apex, often more or less narrowed at base, 7.5–11.5 cm. long, 5–6.6 cm. broad; pericarp

coriaceous, rigid, hard, 3–4 mm. thick, the woody epicarp 1–2 mm. thick, covered by a brown, thin, appressed, stellate-tomentose indument; seeds ellipsoid-oblong or ovate-ellipsoid, 1.8–2.3 cm. long, 12–16 mm. broad, 8–11 mm. thick, the surrounding pulp rather slightly sweet, scentless, white, becoming yellowish; cotyledons white; fruiting peduncle 1–1.5 cm. long, 0.5–1.0 cm. thick; germination hypogeous.

COMMON NAMES.—The commonest names in Brazilian Amazonia are cupuí and cupuaí. Other names or other ways of spelling and pronouncing the former are: copuí, copuaí, cupuhy, cupuahy, cupuy do Igapó, cupuarana, cupú do matta, cupú-assuy, cupú-assú-rana. In Colombia, Venezuela, and Peru this species is usually called cacao de monte or cacao silvestre, and also cacao rana (Orinoco valley), yurac-cacao (Yurimaguas), uchpa-cacao, cacao-ceniza (Peru), cacao blanco (Peru, *Ruíz & Pavón*). Indian names recorded are: abekará (*Makuna*, Vaupés, *García Barriga*), padama (*Arekuna*, Venezuela, cumalá (Peru). The Anglo-Colombian Cocoa Expedition (Baker, 1952) recorded the following indigenous names: Win-cheék (*Puinave*), Inírida-Guaviare; bawk (*Maku*), Piraparaná-Taraira; poo-hoo (*Barasana*), Upper Piraparaná; a-ba-ka-ra (*Makuna*), Lower Piraparaná Popeyaca; mah-we-re (*Yukuna*), Miritiparaná; no-tór-ree-ka (*Tanimuka*), Guacaya; too-soo (*Yauna*), Lower Piraparaná; ma-oo-hee-reé (*Kabuyarí*), Canarari; wa-kó (*Kubeo*), Cuduyarí; wah-pek-la (*Tukano*), Papurí; a-sö-ya-ee (*Piratapuya*), Papurí; wa-be-ga-ra (*Desano*), Papurí; wa-be-ka-ra (*Siriano*), Paca; ma-wé-roo-da (*Kuripaka*), Guainía.

USES.—Although this species gives an acceptable chocolate it is practically never used by the natives. The slightly sweet and scentless pulp is occasionally eaten or sucked; it is very much sought by animals, especially monkeys.

DISTRIBUTION.—Widespread throughout Amazonia from Pará to the most western tributaries of the Amazon River, the upper Orinoco range, and the Venezuelan and French Guayanas; frequent in the shade of the Hylaean rain forests, in noninundatable lowlands, often on rich and humiferous soil but ascending small hills on sandy grounds, along creeks and small rivers. *Theobroma subincanum* is the species of most frequent and abundant occurrence and with the broadest area of distribution, other than *T. cacao*.

COLOMBIA: META: Acacias, Canaima, farm 350 m. alt., cultivated, 18 XI 1951, *Patiño* 22 (F). Sierra de la Macarena, trail from Río Guéjar to Caño Guapayita, Caño Yerli, 500–600 m. alt.; tree about 35 ft. tall, flowers deep red, fruit ripening brown, leaves rusty beneath, 20–28 XII 1950, *Idrobo & Schultes* 776 (COL, IAN).

PUTUMAYO: Río Caucayá, Laguna Primavera on Río Leguízamo; tree 18 m., symmetrical jorquette, 3 IV 1953, *Holliday & Cope* T/91 (COL, TRIN, US).

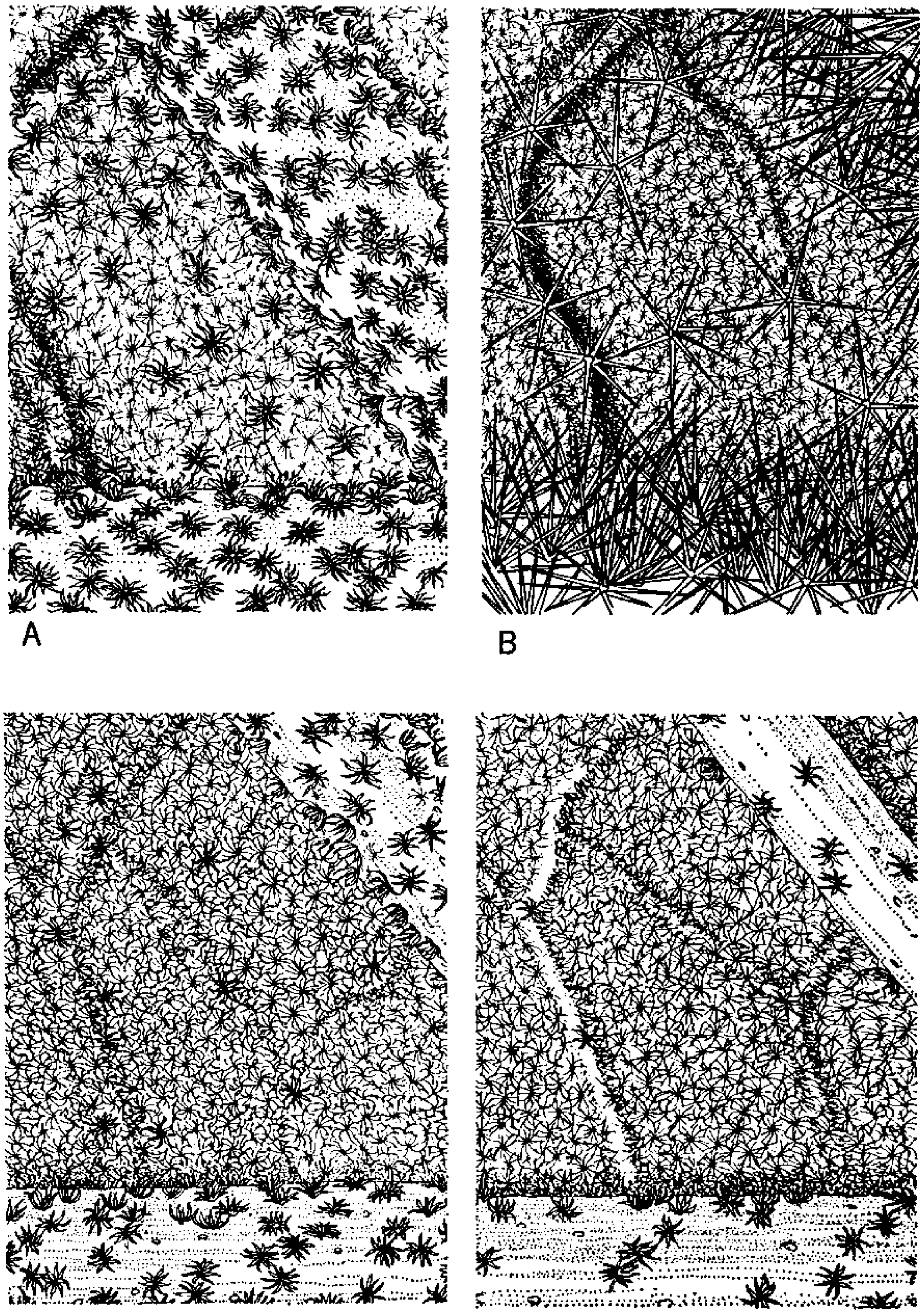


FIGURE 41.—Detail of indument on the underside of leaf in: A, *Theobroma subincanum* (Cuatr. 7277); B, *T. sinuosum* (Pavon, s.n.); C, *T. nemorale* (Cuatr. 21921); D, *T. mammosum* (Leon 1363). A, C, and D × 25, B × 10.

Vicinity of Mocoa; tree in forest, 15 m. high, no fruits or flowers, 17 III 1953, *Holliday & Cope* T/81 (COL, TRIN, US).

CAQUETÁ: Río Caguán, camp 4; tree 10 m., 26 IV 1953, *Holliday & Cope* T/116 (COL, TRIN, US). Upper Río Caguán; small trees, 10 IV 1953, *Holliday & Cope* T/101 (COL, TRIN, US), 13 IV 1953, *Holliday & Cope* T/103 (COL, TRIN, US). Solana, 8 km. SE. of Tres Esquinas, on Río Caquetá, below mouth of Río Ortegüaza, 200 m. alt., wet tropical forest; tree 15 m. high, 15 cm. thick, bark gray, smooth, with lichen patches and bryophyte patches, long, ellipsoidal orange-brown fruits 10 x 6-6.5 cm., edible, "cacao silvestre," 4 VI 1945, *Little & Little* 9544 (F, US) (fruit US No. 1096). Municipality of Florencia, site San Luis, right margin of Pescado River, "cacao silvestre" 5 VI 1942, *Ranghel* 195 (in part) (COL).

VAUPÉS: Caño Mayabo, near San Felipe, river level; only flowers and old fruits, no young or ripe fruit at this season, 27 X 1952, *Baker* 33 (COL, F, TRIN, US). Mitú: Caño Paraná-Midí, 200 m. alt.; tree 5 m., 19 X 1939, *Cuatrecasas* 7277 (F, US, COL). Cerro de Mitú, 380 m. alt.; small tree with bending, fruiting branches, fruits 9.3 × 6 cm., 17 IX 1939, *Cuatrecasas* 6890 (COL, F, US). Mitú and vicinity, 280 m. alt.; tree, cultivated, 22–30 VI 1958, *García Barriga, Schultes & Blohm* 16064 (COL). Ibidem; tree 5 m. with spreading branches, flowers red, 10–13 XI 1952, *García Barriga* 15139 (COL). Cerro de Circasia, 300 m. alt., base of hill 10 X 1939, fruiting tree, 10 X 1939, *Cuatrecasas* 7178A (COL, F, US). Río Barbas, river level, native in the forest, 28 X 1952, *Holliday* 43 (COL, F, TRIN, US). Río Cuduyarí, tributary of Rio Vaupés, Yacara, middle and lower course, highland, ±700–800 feet, 9 XI 1952, *Schultes, Baker, & Cabrera* 18552 (US). Río Cuduyarí, river level, showing jorquette of 3 branches, 16 X 1952, *Baker & Cope* 31 (F). Ibidem; young red flowers, *Baker, Bartley, & Holliday* 31 (COL, TRIN). Río Cuduyarí, Pakwativa Mission, river level, heavily infested with *Marasmius perniciosus*, 19 X 1952, *Baker & Cope* 32 (COL, F, TRIN, US). Ibidem; flowers distinctly paler in color, *Baker, Bartley, & Holliday* 32a (TRIN). Río Apaporis, Soratama, above mouth of Río Cananarí, Caño Surruco, 900 feet alt., highland; small tree, leaves rusty beneath, fruit rusty brown, ovoid, 30 I 1952, *Schultes & Cabrera* 15116 (US). Río Apaporis, Rio Jinogojé, river level; tree 40–50 ft., native in forest or river bank, 13 IX 1952, *Baker & Cope* 12 (TRIN). Jinogojé, growing just above flood level with numerous ellipsoid pods, *Baker & Cope* 7 (COL, TRIN). Ibidem; river level, tree 16 m., 20 cm. diam. at base, a long, tall thin pole, without obvious jorquettes, native in forest, 23 VIII 1952, *Baker & Cope* 3 (COL, F, TRIN, US). Ibidem, 250 m. alt.; tree 15 m., large, coriaceous leaves, brownish fruits 7.5 X 4.5 cm., 25, 26 VIII 1952, *García-Barriga* 14224 (COL, US). Río Piraparaná, cultivated tree, 21 VIII 1952, *Schultes & I. Cabrera* 17005 (AMES). Río Piraparaná, 250 m. alt.; tree 3 m., red petals, sepals red above, 22–26 VIII 1952, *García-Barriga* 14203 (COL, US), 14253 (COL). Río Piraparaná, near confluence with Río Apaporis, river level; small tree 3 m., in Indian garden, 24 VIII 1952, *Baker & Cope* 4 (COL, F, TRIN, US). Río Inírida, near Morichal, near the mouth of Río Papunaná, 200 m. alt.; tree 10 m., 14 II 1953, *Fernández* 2275 (COL, US). Río Inírida, Raudal, 300 m. alt., 3 II 1953, *Bartley & Holliday* T/71 (COL, TRIN, U, US). Río Inírida, Santa Rosa; tree 12 m., 25 I 1953, *Bartley & Holliday* T/68 (COL, TRIN, U, US). Río Inírida, right bank below Caño Caribe (5 hours above Morichal); tree about 10 m., no flowers, one small fruit, 22 I 1953, *Bartley & Holliday* T/65 (COL, E, TRIN). Río Inírida, Morichal, 30 m. alt., in forest, small fruits, no flowers now, 8 II 1953, *Bartley & Holliday* T/72 (COL, TRIN, US). Río Inírida, affluent Papunaná, 300 m., red leaf flush, nearly mature pod 11.5 X 6 cm., fruit pedicel 2 cm. long, fruit green with brown pubescence, pericarp woody, pulp white, cotyledons white, convolute, 18 II 1953, *Bartley & Holliday* T/75 (COL, TRIN, US).

AMAZONAS: Río Caquetá, La Pedrera, river level; tree 45–50 ft., native in forest, 29 IX 1952, *Baker & Cope* 25 (COL, F, TRIN, US). La Pedrera, river level, native tree in forest, 26 IX 1952, *Baker & Cope* 21 (TRIN). Río Caquetá, Remolino, leaves from young tree, 2 V 1953, *Holliday & Cope* T/124 (COL, TRIN, US). Río Apaporis, near mouth of Río Cananarí; tree 45 feet tall in forest, fruit rust colored, "cacao de monte," III 1951, *Schultes* 12104 (COL, US). Río Apaporis, between Río Pacoa and Río Cananarí, Soratama, 250 m. alt.; weak tree, leaves rusty beneath, flowers red, 26 IX 1951, *Schultes & Cabrera* 14140 (US). Río Miritiparaná, near varadero to Río Apaporis, river level; tree 50 ft., native in forest, 15 IX 1952, *Baker & Cope* 13 (COL, TRIN). Trapecio Amazónico, Loretoyacu River, 100 m. alt., IX 1946, *Schultes* 8385 (AMES, F). Leticia, 100 m. alt.; bark rough, cracked, light gray, flowers red, 20 IX 1945, *Schultes* 6536 (F). Leticia, forest; flowers pale red, tree 5 m., 22 VIII 1946, *Black & Schultes* 46–61 (USDA).

VENEZUELA: BOLIVAR: Mount Duida, 500 m. alt.; small tree, VIII 1928–IV 1929, *Tate* 944 (NY, US). Caroní, rain forests of the Icaburu valley, 440 m. alt.; tree 15 m., fruit large and tasty, "padamá" (Arekuna), XI 1947, *Cardona* 2379 (US, VEN).

AMAZONAS: Alto Río Orinoco, Tamaná, 121 m. alt.; medium-sized tree (10–12 m.) with few branches, flowers purplish or red on the branchlets, trunk bent, up to 40 cm. diam. with no branches in 2–5 m., bark gray, inside light brown, wood pale brownish; "cacao-rana," *Ll. Williams* 15204 (A, F, G, US, VEN). Río Guainía, Maroa, river level, with one ripe pod (wall mealy, smooth, thin and brittle), seeds extracted and sent to Trinidad, *Baker* 38 (COL, F, TRIN, US).

FRENCH GUIANA: *Aublet* s.n. (part of syntype of *Cacao guianensis* Aublet, BM, Photo, Mo. Bot. Gard. no. 4028). "Guyane Francaise," *Poiteau*, s.n. 1819–1821 (G). French Guiana, "*Cacao sylvestris* Aublet," *Aublet* (syntype, BM, Photo Mo. Bot. Gard. no. 4029).

BRAZIL: AMAZONAS: Rio Negro, Barcellos, "cupuhy," 25 VI 1905, *Ducke* 7200 (MG). Rio Negro, Rio Caure, Igarapé Miriti; tree 5 m., 15 cm. diam., red flowers, in rather lowland high forest, VII 1948, *Frões* 23343 (IAN, P). Rio Negro, Porto Cabary, "cupuhy," 4 XII 1945, *Frões* 21482 (IAN, NY, USDA). "Prov. Rio Negro Martius Iter. Brasilienses 325," *Martius* [898] (M) (Photo F. M. 19645). "Prov. Rio Negro, Martius Iter. Bras. 325," *Martius* [872, 873 p. p., 894, 895, 896, 897, 899, 900] (M). "Rio Negro Dr. Martius Iter Brasil. 325, *Theobroma subincanum*," *Martius* [893] (M) (Photo F. M. 40704). Rio Vaupés: Jauraté, inundatable forest, 17 X 1945, *Frões* 21162 (IAN, NY, USDA). San Antonio de Içá, forest; tree 10 m. "differt a *T. ferrugineo* Bern. foliis majoribus latioribus floribus majoribus," *Ducke* 7679 (MG, F) (Photo F. M. 7679). Municipality of Saõ Paulo de Olivença, near Palmares; tree 40 ft. high, trunk 5 inches diam., high land, "cupuarana," 11 IX–26 X 1936, *Krukoff* 8226 (A, BM, F, G, GB, K, LE, MO, NY, P, U, US). Basin of Rio Madeira, Municipality Humayta, near Livramento, on Rio Livramento, terra firma; tree 60 ft. high, "cupuarana," 12 X–6 XI 1934, *Krukoff* 7016 (A, F, G, K, MICH, MO, S, U, US, WU). Rio Madeira, Varadouro do Morcego, 31 VIII 23, *Kuhlman* 18110 (U). Manaos, mata; arvore, tree 30 m. alt., 15 cm. diam., "cupuhy," 17 II 1945, *Frões* 20518 (IAN, K, NY, USDA). Manaos, Mata do Aleixo, "cupuhy," 16 III 1945, *Frões* 20555 (F, IAN, USDA). Manaos Aurora Fazenda, 15 m., Urwald, "cupú do Matto," 28 VIII 1921, *von Luetzelburg* 22079 (M). Without locality *Spruce* 97 (K).

AMAPÁ: Rio Amaparí, Serra do Navio, slopes of Curuca Ore Body, down to Igarape Sentinela; occasional tree 6 m. tall; fruit brown, 9 XI 1954, *Cowan* 38186 (NY, US). Lower slopes of Observatorio Ore Body, heavily forested hills,

70–300 m. alt.; tree 10 m. tall, fruit brown, 8 XI 1954, *Cowan* 38164 (NY). Missao do Servico Florestal no T. Amapá, IX 1955, *Miranda Bastos* 68 (IAN).

PARÁ: Belém, "cupuahy," VI 1896, *Huber* 162 (BM, G, MG, P, (US). Belém, Bosques Rodriguez Alves, 1 VIII 1944, *A. Silva* 317 (IAN, USDA). Belém, Horto do Museo Goeldi; tree 481, small tree, flowers brown yellow, 22 XII 1958, *Cavalcante* 938 (MG, US). Belém, Bosque municipal; tree 30 feet high, sparsely branched, 4 VIII 1942, *Archer* 7517 (IAN, USDA). Belém, south forest of the Instituto Agronómico do Norte; large tree, contents of fruit eaten by birds, "cupu-assuy," 16 XI 1942, *Archer* 7820 (IAN, USDA). Belém, along roads on lands of Inst. Agr. do Norte; large tree, flowers rose color, "cupu-assu-rana," *A. Silva* 237 (IAN). E. F. Bragança, João Coelho; tree 8 m., 14 III 1947, *Pires & Black* 1414 (IAN). Region of Igarapé Pitoró; tree 10 m., flowers red, 19 IX 1958, *Fróes* 34663 (IAN). Taperinha, near Santarém, bushed river margins of Igarapé Assú, "cupuy do Igapó," 23 VIII 1927, *Ginzberger & Hagmann* 801 (F, WU). Rio Tapajóz, Cachoeira do Mangabal, "beira de assahyzal," "cupuy," 6 IX 1916, *Ducke* 16464 (BM, MG). Matta do Alto Ariramba, "cupuy" 7 X 1913, *Ducke* 14925 (MG). Rio Purús, Monte Verde, "cupuahy," II 1904, *Goeldi* 4225 (MG). Paranary, upper Amazon, "cupua-i," 20 X 1874, *Traill* 59 (K, P).

GUAPORÉ: Porto Velho, km. 8, in high forest on firm land; tree about 30 m., "cupuí," 17 VI 1952, *J. F. Silva* 143 (IAN).

RIO DE JANEIRO: Quinta de S. Christovao; small tree planted by Riedel probably originally from Amazon basin, "cupuaí," 16 II 1876, *Glaziou* 9633a (P).

PERU: LORETO: Mishuyaco, near Iquitos, 100 m. alt., forest; tree 6 m. high, flowers dark red, "wild cacao," X–IX 1929, *Klug* 87 (F, NY, US). Ibidem, II–III 1930; tree 8 m. high, flowers wine red on branches, *Klug* 857 (F, US). Alto Itaya, 145 m., in forest of Paraíso, "cumalá," 30 IX 1929, *Ll. Williams* 3254 (A, F, G, S, US). Upper Río Nanay, Santa Ana, "uchpa-cacao," 7 VII 1929, *Ll. Williams* 1233 (F, S, US). Río Nanay, Tierra Doble, deep forest, "Campamento balatero Lira Dabu," 8 VI 1929, *Ll. Williams* 1076 (US, F, S). "Peru," *Ruiz & Pavón*, "Theobroma alba R. & P." (ined.), "*Theobroma ferruginea* Bern." (K, BM). Ibidem, Herb. *Pavón* 201 (G). "*Theobroma alba*," *Rivero* 1836 (P). *Tessmann*, s.n., NY–3717; probably the same as the *Tessmann* 4115, cited by Mildbraed (Notizbl. 11:139. 1931) as *T. ferrugineum* and collected near Pongo de Manseriche, 160 m. alt., tree 19 m. tall, 21 cm. diam., "pako-kakao" (Dunkel Kakao), 23 IX 1924.

HUÁNUCO: Prov. Huánuco, Tingo-María, forest, tree about 25 m. high, sepals olivaceous yellow without, more or less red within, petals yellowish gray, 31 VIII 1940 *Asplund* 13410 (S). Tingo María, forest; tree 15 m., flowers dark red, 8 VIII 1940, *Asplund* 12911 (S). Maynas, Yurimaguas, "yurac-cacao" i.e., "Cacao album Peruvianum," March, 1831, *Poeppig* 2352 p.p. (GH, P, WU).

TRINIDAD (cultivated): On grounds of the I.C.T.A., from seeds from Mitú Vaupés region, Colombia; one branch damaged by *Marasmius perniciosus*. *Cuatrecasas, Cope, & Bartley* 25785 T (U.S.)

18. Theobroma hylaeum Cuatr., sp. nov. FIGURES 25, 39; MAP 11

Arbor circa 10 m. alta, apicaliter crescens, ramis primariis ternatis, ramulis brunneis juvenilibus minute ferrugineo-tomentosis denique glabratis, cortice rugoso-fissurato; stipulae lineari-subulatae acutae vel subacutae ferrugineo-tomentosae, circa 6 mm. longae, 1 mm. latae.

Folia mediocriter coriacea, petiolo crassiusculo subtereti minute ferrugineo-tomentoso, 6–10 mm. longo; lamina elliptico-oblonga vel obovato-oblonga, basi symmetrica attenuata obtusa vel subobtusa, apice leviter attenuata interdum rotundata subite acuteque acuminata, margine integra vel apicem versus leviter undulata, 12–20 cm. longa, 4–9 cm. lata, apiculo 6–15 mm. longo, supra in sicco viridi-brunnescens glabra, costa et nervis principalibus filiformi-impressis reliquis vix conspicuis, subtus cinereo-ochracea vel nervatione ferruginea, areolis venulisque cinereo-tomentosis pilis stellatis minutis albidis intricatis dense tectis et pilis stellatis crassioribus ferrugineis sparsis vel in nervis copiosis, costa crassa elevata, nervis secundariis 7 vel 8 utroque latere eminentibus arcuato-ascendentibus, prope marginem tenuioribus anastomosantibus, nervis tertiaris transversis prominentibus, nervulis venulisque tenuioribus sed prominulis reticulatis.

Inflorescentiae breves axillares cymis 1–3 floribus instructae, ramulis brevissimis tomentosis, pedunculis tenuibus erectis vel subflexuosis ad 12 mm. longis ferrugineo-tomentosis apice 3-bracetolatis et cum pedicello articulatis; bracteolae anguste lineares subacutae, 3–6 mm. longae, 1–2 mm. latae, extus tomentosae; pedicelli erecti tomentosi pedunculis leviter crassiores, 5–6 mm. longi.

Sepala crassiuscula ovato-oblonga acuta, basi ad 2 mm. coalita, patulo-reflexa, extus ochraceo-tomentosa, intus margine minutissime albido-tomentella excepta glabra, aurantiaca, basi ad insertionem pilis crassiusculis oblongis glandulosis annulum formantibus, 8–9 mm. longa, 4–5 mm. lata; petala cucullo aurantiaco obovoideo, basi angustato, apice rotundato, saccato-cucullato, 3 mm. longo, 2 mm. lato, extus glabro ruguloso, intus minute hispidulo, 7-nervato, pediculo 2.5 mm. longo, parce puberulo, lamina obovato-subrhomboidea crassa brunneo-rubra, faciebus sparsis minutissimis pilis margine pilis flexuosis tenuibus praedita, 4–5 mm. longa, circa 4 mm. lata; androecium tubo circa 1.5 mm. longo; staminodia petaloidea aestivatione reflexa in anthesin curvato-patula, brunneo-rubra obovato-oblonga apice rotundata vel leviter retusa, 5–5.5 mm. longa, 2.2 mm. lata, minute pilosula; filamenta fertilia 1 mm. longa; antherae 3. brevissime pedicellatae; ovarium obovatum 1.2 mm. longum, 1 mm, latum, crasse tomentosum; styli circa 1 mm. longi coaliti.

Fructus coriaceus circa 7 x 4 cm., viridi-brunnescens, adpresse tomentosus laevis ellipsoideus, utrinque rotundatus, epicarpio rigido lignoso in sicco 1 mm. crasso; pedunculus fructifer 1.5–1.8 cm. longus, 0.8 cm. crassus.

Type in the U.S. National Herbarium, No. 2028683, collected in the heavy rain forest around Villa Arteaga, northern region of An-

tioquia, Colombia, at 200 meters altitude, August 14, 1948, by J. Araque and F. A. Barkley no. 18C745.

COMMON NAMES.—Chocolate de monte, cacao silvestre.

DISTRIBUTION.—Presently known only from the Chocó region of northern Antioquia, Colombia, and probably also in Panama.

COLOMBIA: ANTIOQUIA: Villa Arteaga, heavy wet forests at 200 m. alt.; tree 10 m., flowers orange, corona cream orange, stigma black brown, 14 VIII 1948, *Araque & Barkley* 18C745 (holotype, US 2,028,683; isotype, US 2,028,684, COL). Ibidem; seedlings showing symmetrical branching in 3's, growth continuing from above the jorquette, 24 VII 1953, *Bartley & Holliday* T 166 (K, TRIN, US).

PANAMÁ: COLÓN: Along Río Fató, in forests or thickets 10–100 m. alt., VII 1911, *Pittier* 4194 (BM, GH, US) (probably; specimen sterile; identification needs confirmation by fertile specimens).

Theobroma hylaeum is closely related to *T. nemorale* from which it differs essentially by the narrow-linear bracts and stipules, by the subrhomboid lamina, and by the narrower obovate-oblong, rounded and notched staminodia; furthermore, the peduncles and the pedicels are short, the pedicels shorter than the peduncles, and the fruit is harder, smaller and not constricted above the base. From *T. subincanum* it differs by the shape of the petal-laminae and staminodes, by the tomentose ovary, by the smaller fruit and leaves, and by the venation, in which the minor veins are less conspicuous.

19. Theobroma nemorale Cuatr. FIGURES 3, 41, 42; MAP 11

Theobroma nemorale Cuatr., Rev. Acad. Colomb. Cienc. 8:487, *fig. 4.* 1952; Baker, Cope, & al. (1954) 13, *fig. 20;* León (1960) 323, *fig.* in 321.

TYPE.—Pacific coast, Colombia, *Cuatrecasas* 21291 (fruiting specimen), *Patiño* 24 (flowering specimen, paratype).

Small or medium-sized tree up to 15 m. high; growth pseudoapical; trunk up to 20 cm. in diameter; primary branches ternate; leafy branches ochraceous or ochraceous-ferruginous, or brownish, minutely and appressed tomentose, the older glabrate, dark grayish, rather smooth or granulate-lenticellate, nitidous, the hornotinous greenish ferruginous, tomentose; stipules subcoriaceous, oblong, obtuse, striolate, tomentose, about 8–11 mm. long, 2–3 mm. broad.

Leaves coriaceous, moderately rigid; petiole 9–12 mm. long, thick, subterete, densely and appressed ferruginous-tomentose; blades elliptic-oblong or obovate-elliptic-oblong, slightly attenuate and asymmetrical, or equilateral, rounded at base, rounded or obtuse and abruptly acuminate at apex, entire or upwardly sinuate or coarsely dentate, 10–32 cm. long, 3–12 cm. broad, the acute acumen 1.5–2.5 cm. long, above green, pale brown when dry, rather shining, glabrous, the costa depressed, thin, the other nerves rather inconspicuous, cinereous or greenish cinereous beneath, or pale tawny when dry, the costa very prominent, the secondary nerves about 8 on each side very

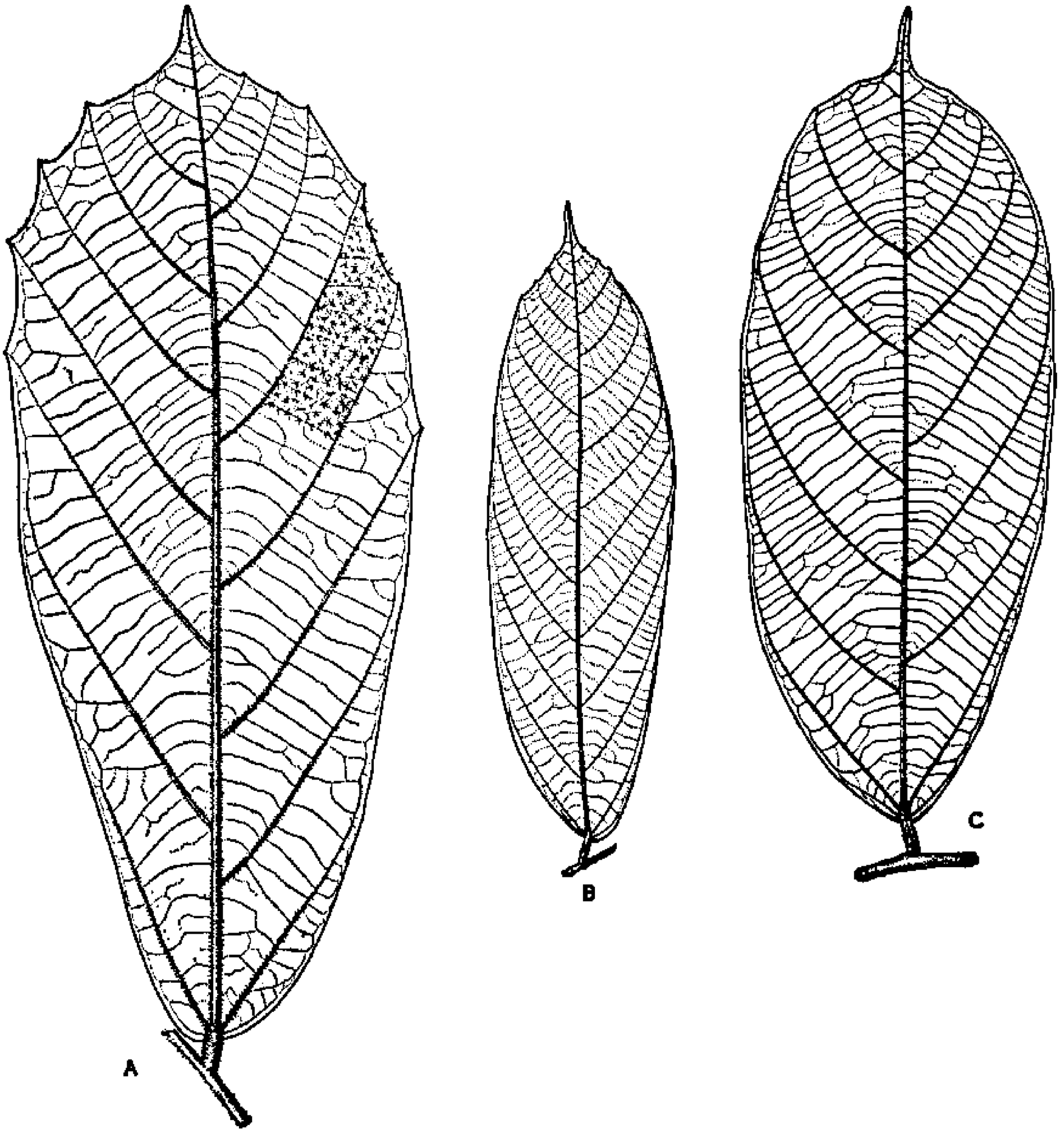


FIGURE 42.—Leaves of *Theobroma*, ×½: A, *sinuosum* (Pavon, s.n.); B, *mammosum* (Leon 1363); C, *nemorale* (Cuatr. 21291).

prominent, subparallel, ascending, curving and anastomosing near the margin, the transverse tertiary nerves prominent, parallel, the nerves of the fourth rank prominulous, broadly reticulate, the minor reticulate veins concealed, the whole nervation tomentose, greenish ochraceous or subferruginous, by rather thick, tawny, densely distributed stellate hairs, the surface within the veins covered by a dense and appressed cinereous tomentum of white, fine, minute stellate hairs.

Inflorescences axillary or on exfoliated branchlets very small, reduced to 1–3 (–5) flowers, the cyme-axis extremely short, the peduncles 5–10 mm. long, erect, ferruginous-tomentose, 3-bracteolate at apex, the pedicels thicker, ochraceous-ferruginous tomentose, 2–5 mm. long, the bracts ovate, obtuse, 2.5–3 mm. long, 1.5–2 mm. wide; bracteoles 3, broadly cochlear, embracing the bud, orbicular or ovate-rounded,

ochraceous-greenish tomentose, 7–11 mm. long and broad, soon caducous.

Sepals thick, ovate-oblong, subacute or subobtuse, 9–10 mm. long, 4–5 mm. broad, united in the lower third or fourth, first curved-patulous, later reflexed, inside purplish or rose, shining, glabrous except for the minutely white-tomentose margin, and for the minute oblong-capitate, glandular hairs at the base, thick-tomentose outside, ochraceous, the stellate hairs with long, thin rays.

Petal-hoods thick-membranaceous, ochraceous or orange, obovate with rounded-cucullate apex, 7-nerved, glabrous and rugose outside, minutely hispidulous-pubescent, inside with 7 prominent veins, 3–3.5 mm. long, 2–3 mm. broad; petal-lamina pedicellate, carnose, rigid, red or crimson becoming brownish red, oblong-obovate-spatulate, rounded or subtruncate-emarginate at apex, with very minute, sparse hairs on the surface and copious longer, slender, weak, spreading hairs on the margins, 5–7 mm. long, 3–5 mm. broad; pedicel narrowly linear, folded, puberulous, at the broader base barbate, 3 mm. long; androecium tube 1.5–2 mm. long; staminodes laminar, rather thick, obovate-oblong, rounded or subspatulate at apex, purplish red or crimson, covered with sparse, thin, minute hairs, 6–7.5 mm. long, 3.5–4.5 mm. broad, reflexed in bud, spreading in anthesis; filaments moderately thick, 1–1.2 mm. long, pilose towards the base, 3-furcate (the branchlets 0.4 mm. long), 3-antheriferous, the anther lobes ellipsoid 0.5–0.6 mm. long, connivent; ovary 1.3–1.5 mm. long, oblong-ovoid, subtruncate, 5-ridged, thickly ochraceous, hirsute-tomentose; styles linear, glabrous, 1.5 mm. long, coherent.

Fruit ellipsoid, smooth, rounded at apex, slightly constricted above the base, 8–10 cm. long, 4.5–6 cm. broad; pericarp coriaceous, rigid, 1–1.5 mm. thick, when mature fragile, its surface densely appressed stellate-tomentose, greenish or bluish, at maturity yellowish, brown or tawny; seeds compressed ovoid or subellipsoid, 17–19 mm. long, 9–12 mm. broad, the surrounding pulp white, yellowish when ripe; cotyledons white; fruiting peduncle robust, 1.5–2 cm. long, about 0.8 mm. thick; germination hypogeous.

COMMON NAMES.—"Bacao de monte," "chocolate de monte," "bacao," "bacaíto," "cacao de monte," "cacaíto de monte."

USES.—It is said to produce a fairly good chocolate; not known to be used by the natives.

DISTRIBUTION.—Restricted to the Colombian Pacific coast and the Chocó area between the parallels 3° and 5°3′ N. latitude. It is recorded from the Calima, San Juan, and Cajambre Rivers.

This very interesting species is closely related to *T. subincanum* and *T. hylaeum*, but it differs specially by its three broad, orbicular bracteoles subtending the flowers, which before anthesis embrace

and cover the short-pedicellate bud. This feature is unique in the genus *Theobroma*.

The leaves of *T. nemorale*, as well as those of *T. hylaeum*, are very similar to those of *T. angustifolium*, but they are broader, more oblong-elliptic, with a tendency to an obovate shape, and the ochraceous or ferruginous hairs beneath are smaller, with shorter, somewhat thicker rays than in *T. angustifolium*.

COLOMBIA: Chocó: Río San Juan, Palestina; part of branch brought in by an Indian, one immature fruit 7 x 4.5 cm., 4 VIII 1953, *Holliday* T/149 (TRIN, US). Ibidem, young tree 3 m., sterile, 2 VII 1953, *Holliday* T/147 (TRIN, US). Ibidem, sucker 1½ m. from leafless fallen trunk, 2 VII 1953, *Holliday* T 148 (TRIN). Ibidem, Quebrada de las Sierpes; tree 10 m. tall, leaves green yellowish above, ashy beneath, 24 IX 1961, *Cuatrecasas & Willard* 26051 (COL, US). Istmina, tree about 7 m., sterile, flowers apparently borne only on branches, 2 VIII 1953, *Holliday & Bartley* T/173 (TRIN, US).

El Valle: Pacific Coast, Río Calima, La Trojita, 5–50 m. alt.; small tree; leaves coriaceous yellowish green, fruit ovoid-ellipsoid, 8 x 4.5 cm., light brown, "bacao de monte," 28 II 1944, *Cuatrecasas* 16544 (F, VALLE). Río Calima, Quebrada de la Brea, 20–40 m. alt.; tree 8 m., leaves subcoriaceous, medium green above, green cinereous beneath, nerves green ochraceous, fruits 10 x 6 cm., ellipsoid, rounded at apex, constricted at base, tawny, on the branchlets, "chocolate de monte," 24 V 1946, *Cuatrecasas* 21291 (holotype, F; isotypes, B, F, VALLE). Ibidem, La Brea, flowering specimens, *Patiño* 24 (paratype, F; type of flowers; isoparatypes, F, US). Estación Agroforestal del Calima, 30–50 m. alt.; erect tree with abundant handing pods, 8 I 1953, *Patiño* 117 (US, Herb. Cuatr.). Ibidem; small tree 8–10 m., "cacao," "cacaíto de monte," "bacaito," 8 I 1953, *Patiño* 116 (US, Herb. Cuatr.). Ibidem; tree with primary ternate branches from near the ground; leaves light green; twigs tomentose ochraceous or ferruginous, sepals thick, rose or purplish rose inside, ochraceous outside, petal-laminae and staminodes thick, rigid, purplish red or dark brown red, hoods ochraceous with 7 red veins, "bacao," 23 IX 61, *Cuatrecasas & Willard* 26007 (COL, US). Caño La Brea; young tree 1.5 m., sterile, 29 VI 1953, *Holliday* T/141 (TRIN, US). Estación Agroforestal; tree 8–10 m., in land cleared from forest, jorquette symmetrical, crimson and yellow flowers borne singly or in pairs on small branches, pods 8.5–10 x 5–5.5 cm., fruit peduncle 2 cm. long, 0.75 cm. thick, 29 VI 1953, *Holliday* T/146 (TRIN, US). Pacific coast, Rio Cajambre, Silva, Loma de la Vigia, 5–80 m. alt.; small tree, leaves green above, gray beneath, "bacao de monte," II–V 1944, *Cuatrecasas* 17503 (F, VALLE). Ibidem, Quebrada del Corosal 0–5 m. alt.; tree 15 m. tall, trunk 20 cm. diameter, leaves coriaceous, green above, ashy beneath, fruits ellipsoid rounded at apex, contracted above the base, smooth, brownish, 10 x 5.5 cm., "chocolate de monte," 17 V 1944, *Cuatrecasas* 17738 (F, VALLE).

TRINIDAD (cult.): Imperial College of Tropical Agriculture, River State Diego Martínez, Field 19; 7–8 years old tree, 31 VIII 1961, *Cuatrecasas, Cope, & Bartley* 25782 T (US).

20. Theobroma sinuosum Pavón ex Huber Figures 41, 42; Map 9; Plate 12

Theobroma sinuosum Pavón ex Huber, Bull. Herb. Boiss., II, 6:274. 1906.
Theobroma Tessmannii Mildbr. Notizbl. Bot. Gard. Berlin 11:139. 1931.
Theobroma sinuata Ruíz & Pavón, Fl. Peruv. et Chil. Fol. E, *Plate 417*, ined.

TYPES.—Chicoplaya, Peru, *Ruíz & Pavón* (lectotype, G). Marañón River, Peru, *Tessmann* 4928 (type of *T. tessmannii*).

Large tree with erect trunk; leafy terminal branchlets brownish ochraceous when dry, densely hirsute-tomentose, covered by minute, whitish, stellate hairs with intricate, slender rays (0.1–0.2 mm. long) and by larger stellate, ferruginous hairs with straight, acute, long rays (1 mm. long); stipules lanceolate, about 1 cm. long, deciduous.

Leaves subcoriaceous, firm; petiole short, thick, densely tomentose-hirsute, about 1 cm. long; blades obovate-oblong, slightly attenuate, rounded and slightly asymmetrical and emarginate at base, subrounded and abruptly triangular-cuspidate at apex, sinuate-dentate in upper third, otherwise entire, about 30 cm. long, 13 cm. broad, pale green brownish above, when adult glabrous with abundant reddish, punctiform scars, the midrib and secondary nerves filiform impressed, the other nerves less visible, softly tomentose beneath, subochraceous, covered by a dense, cinereous layer of minute, white, fine, stellate hairs and, especially on nerves, by larger ochraceous, stellate hairs, with 4–6, erect, acute, rays 1–1.5 mm. long; the midrib thick, prominent, densely tomentose-hirsute, the secondary nerves about 9 on each side, ascending, prominent, vanishing near the margin, hirsute, the tertiary, transverse nerves prominent, parallel, 5–10 mm. distant from each other, the minor veins reticulate and prominulous.

Sepals ovate-lanceolate united at base, reflexed; petal-hoods obovate, concave; petal-lamina obcordate-"trigonous"; staminodes lanceolate-obovate; stamens five, 3-antheriferous; ovary hirsute; fruit subrounded-pyriform, the epicarp smooth, hard, woody, ferruginous tomentose.

The preserved original specimens from the Ruíz and Pavón herbarium surely collected by Tafalla have only leaves; they have been used by me for the above description. The short description of flowering characters has been taken from the manuscript of the unpublished Flora of Peru and Chile of Ruíz and Pavón. This description was written by Ruíz or Pavón based on data sent by Tafalla. Some of the data were misinterpreted by the authors who describe the anthers "quinque in singulo filamento," and this is not the case. Tafalla wrote in his "notas" that each filament was divided in six "lacinias" bearing one anther each, and that the number of stamens was five in *T. alba*, *sinuata*, and *cordata*, whereas it was ten in *T. digitata*. Pavón described the inflorescences as being cauline; we have no basis either to affirm or deny that assertion. The petal-lamina is described as "trigona"; probably it was slightly 3-dentate, and this feature was extremely exaggerated by Pulgar in his drawing.

Theobroma sinuosum, because of the little information available, was disregarded by most of the authors who listed cacao species; Chevalier

who saw specimens of it considered it as a synonym of *T. ferrugineum*, which was not well defined by him in his revision. My study of the sterile specimens of the type convinces me that *T. sinuosum* is a very different species, unique in possessing an indument comparable to that of the young plants of *T. chocoense* and *T. simiarum*. On the other hand, after careful study of the description and photograph of *T. tessmannii* Mildbr. which I had formerly associated with *T. subincanum*, I arrived at the conclusion that the Tessmann specimen is definitely distinct from *T. subincanum* and that it coincides with *T. sinuosum*. Unfortunately the Tessmann specimens are not existing any more, but the Mildbraed's detailed description of the indument permits us to differentiate his species from the closest allied species growing in the same area, namely *T. subincanum*. Some doubts may remain about the identity of *T. sinuosum* and *T. tessmannii*. The Tessmann plant definitely had axillary inflorescences, whereas the Pavón plant was described as being cauliflorous, but the species could well have both cauline and axillary inflorescences. The geographical range and the identical kind of indument are the reasons that I consider the species synonymous.

I wish to supplement the description given above with the data taken from Mildbraed's description: Leaves subcordate at base, 25–35 cm. long, 8–12 cm. broad, with about 10 secondary nerves; sepals lanceolate, acute, about 10 x 4 mm., connate at base for 2 mm.; petal-hood whitish, lamina red, subquadrate-rounded and apiculate, 3 x 3 or 2 x 3 mm.; staminodes dark red, subspatulate-elliptic, 6 mm. long, 3 mm. broad; stamens 3-antheriferous; pedicels 2 cm. long.

COMMON NAMES.—Cacao de monte, Pako Kakao (*Tessmann*).

USES: The pulp of the fruits is eaten by the natives.

DISTRIBUTION.—Upper river valleys of the Huallaga and Marañón in Peru.

PERU: Chicoplaya, "*Pavón*," collected by Tafalla (lectotype, G; BM). Rio Marañón from Iquitos to the mouth of Santiago, near Pongo de Manseriche, ca. 77°30′ W., *Tessmann* 4928 (type of *T. tessmannii*, photo F. M. 17942).

21. Theobroma canumanense Pires et Fróes, sp. nov. FIGURE 43; MAP 9

Arbor 18 m. alta pauciramosa ramulis dense ferrugineo-tomentosis, pilis crassiusculis mediocribus stellatis 8–14 radiis acutis 0.3–0.7 mm. longis instructis.

Folia rigide coriacea, petiolo crasso dense ferrugineo-tomentoso 8-10 mm. longo. Lamina oblongo-obovata vel obovato-elliptica basi paulo angustata rotundataque leviter asymmetrica apice subrotundata subite breviterque acuminata margine integra vel sursum leviter grosseque dentata, 8–20 cm. longa, 3–8.5 cm. lata, supra in sicco tabacina subnitida leviter rugosa juventute pilosa deinde glaberrima, costa nervisque secundariis filiformibus impressis ceteris paulo con-

spicuis, subtus ferrugineo-tomentosa, costa valde elevata, nervis secundariis 5 vel 6 utroque latere elevatissimis duobus basilaribus ascendentibus ceteris patulo-ascendentibus arcuatisque ad marginem decurrentibus anastomosantibus, nervis tertiariis transversis bene elevatis 3–6 mm. inter se distantibus, nervulis quaternariis elevatis transversis, minoribus prominenter minuteque reticulatis, pilis dimorphis: a) pilis stellatis albidis minutissimis dense intricatis areolas tectis, b) pilis ferrugineis crassiusculis mediocribus stellatis radiis patulis supra nervationem copiosissimis.

Flores in cymis axillaribus vel extra-axillaribus paucifloris congeste glomerati; pedunculi ad 6 mm. longi tomentosi apice 3-bracteolati, bracteolis 1–1.5 mm. longis triangularibus tomentosis; pedicelli tomentosi 1 mm. longi. Alabastra globosa crasse ferrugineo-tomentosa circa 5 mm. diam. Calyx sepalis crassiusculis carnosis in anthesin subpatulis paulo reflexis, circa 7 mm. longis, 4 mm. latis, basi 1.5 mm. longitudinaliter coalitis, intus glabris basi excepto, pilis densis crassis glandulosis ad marginem insertione praeditis extus dense stellato-tomentosis margine dense minutissime pilosulis.

Cucullus petali obovoideo-ellipsoideus circa 3–3.5 mm. longus, 2–2.2 mm. latus, carnosulus extus glaber intus 7 costis elevatis strigulosis instructus. Lamina petaloidea rubra crassa semirotundata apice emarginata, circa 2 mm. longa, 3 mm. lata, sursum utrinque minutissime pilis margine ciliata, basi subite in pediculum circa 2 mm. longum longe ciliatum contracta.

Androecium rubrum; tubus circa 1.5–1.6 mm. altus glaber. Staminodia crassa curvata subspathulata sursum dilatata apice leviter emarginata, circa 6 mm. longa, 2.4–2.8 mm. lata, margine longe flexuoso-ciliata cetera glabra. Stamina filamentis glabris crassis, 1.2–1.4 mm. longis triantheriferis, lobis antherae ellipsoideis circa 0.4 mm. longis. Ovarium 1.2–1.5 mm. longum obovatum pentagonum in angulis et subapicem hirsutulum. Styli circa 2 mm. longi glabri versus apicem plus minusve liberi. Fructus ignotus.

Type in the U.S. National Herbarium, No. 2404642, collected in low, firm land, Rio Canumão, tributary of Madeira River, municipality of Borba, State of Amazonas, Brazil, October 5, 1957, by *R. L. Fróes* (No. 33783). Isotype in the herbarium of Instituto Agronomico do Norte, Belém do Pará.

Theobroma canumanense is closely related to *T. sinuosum;* its leaves and indumentum conform well with those of the type of this species showing only some differences due to the fact that the *T. sinuosum* specimens came from a young plant. The vegetative characters of the Fróes plant also coincide with the description of *T. tessmannii* given by Mildbraed, but I found a few differences which indicate that the Fróes specimens belong to a different species.

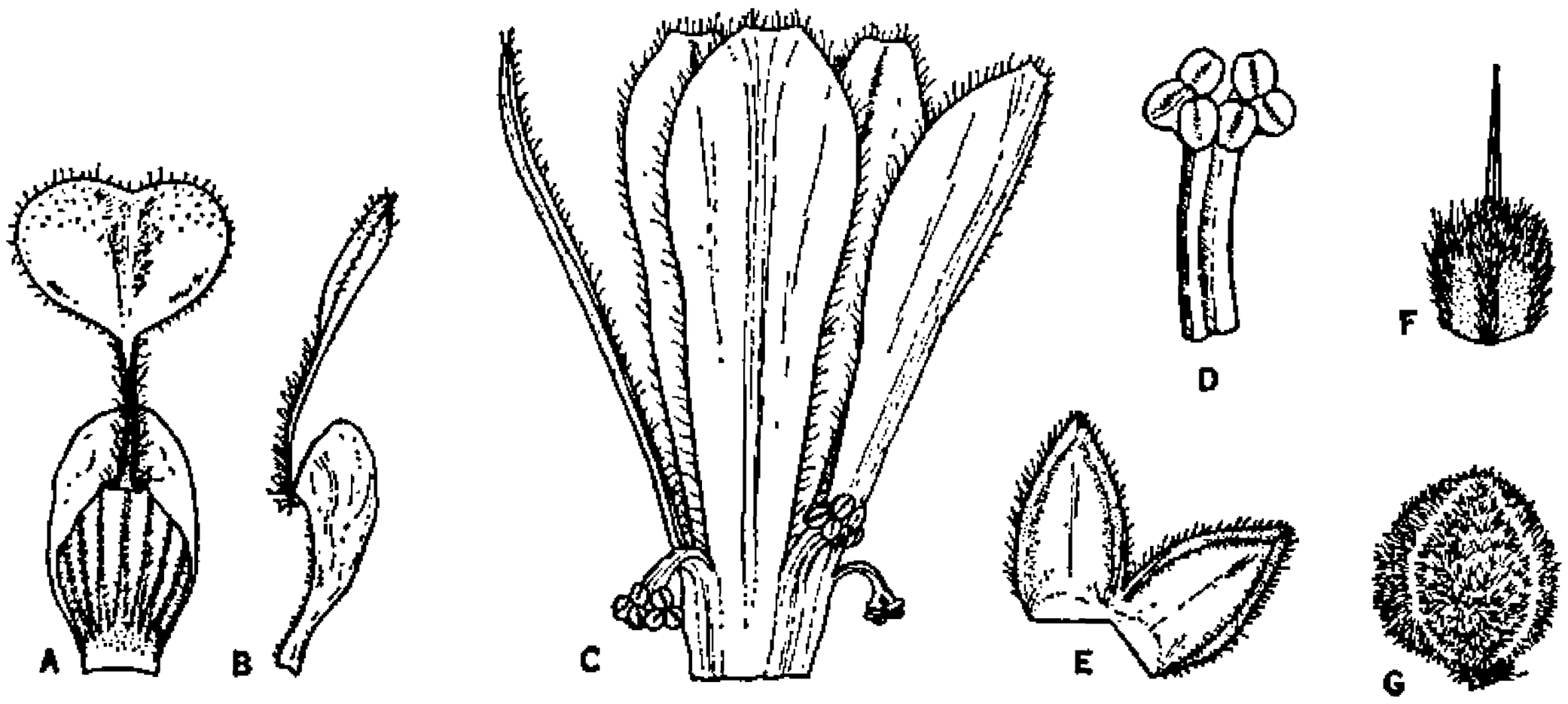


FIGURE 43.—*Theobroma canumanense* (Fróes 33783): A, petal, inside view; B, petal, lateral view, × 5; C, androecium, × 5; D, stamen, × 10; E, sepals, inside view, × 2; F, pistil, × 5; G, bud, × 2.

T. canumanense has smaller flowers, the sepals being only 7 mm. long; they are 10 mm. in *T. tessmannii* which also has a longer androecium (8.5 mm. high); the petals and staminodes are glabrous in the Tessmann plant according to the Mildbraed description and drawings, while they are long-ciliate in *T. canumanense*. The inflorescences are more compact in this species than in *T. tessmannii*. The photograph of the latter shows the adult leaves to be subcordate and broader at base and provided with one or two additional pairs of basal veins (not conspicuous in *T. canumanense*); the secondary nerves are more numerous (8–11 pairs) in Tessmann's plants. *T. canumanense* also differs from all related species by its extremely short pedicels (up to 1 mm. long).

COMMON NAMES.—Names and uses not recorded.

DISTRIBUTION.—Limited to the region of Rio Canumão, a tributary of the Rio Madeira in Brazil.

BRAZIL: AMAZONAS: Região do Rio Madeira, Rio Canumão, municipio de Borba, 5 XI 1957, *R. L. Fróes* 33783 (US, holotype; IAN, isotype).

Section 6. Andropetalum

Theobroma sect. *Andropetalum* Cuatr., sect. nov. FIGURE 4

Lamina petalorum anguste spathulata longe attenuato-stipitata; cucullum 7-nervatum; staminodia crassa latissima petaloidea arcuato-reflexa petala obtegentia; stamina 3-antherifera; fructus ellipsoideo-oblongus laevis tomentosus supra basim constrictus ad apicem angustato-mammillatus epicarpio duro lignoso; semina germinatione hypogaea; folia subtus adpresse stellato-tomentosa; inflorescentiae axillares brevissimae; caulis incrementum pseudoapicale; rami

primarii ternati; calyx cymbiformis 3-lobatus, sepalis usque ad tertiam partem vel ad medium connatis.

TYPE SPECIES.—*Theobroma mammosum* Cuatr. & León.

This section comprises a single species. It is characterized by the broad, obovate-spatulate staminodes (as broad as long), which are reflexed even during anthesis, completely covering the petals, and by the reduction of the petal-laminae, which are narrower and smaller than in the closely related section *Glossopetalum*.

22. Theobroma mammosum Cuatr. & León

FIGURES 6, 36, 41, 42, 44; MAP 9

Theobroma mammosum Cuatr. & León, in León, Inst. Interamer. Cienc. Agr. Bol. Técn. 2:1–6, *figs.* 1949; León (1960) in 320, 317, *fig.*

TYPE.—Siquerres, Limón, Costa Rica, *León* 291.

Small tree, 6–7 m. high; trunk about 25 cm. in diameter with rather smooth, brown bark 1 mm. thick and white, hard wood; growth pseudoapical; branches ternate, from near the base, spreading or more or less descending; terminal branchlets grayish or somewhat ochraceous, appressed and minutely stellate-tomentose, later glabrous, gray, rugose; stipules subulate, acute, 4–5 (–10) mm. long, 0.6 mm. wide, deciduous.

Leaves subcoriaceous; petiole rather thick, subterete, straight or somewhat flexuous, ochraceous or ferruginous, stellate-tomentose, 5–12 mm. long; blade elliptic-oblong or oblanceolate, slightly attenuate to the apex and suddenly acuminate, slightly narrowed toward the asymmetrical base, rounded in one side, subrounded or subcuneate at the other side, the margin entire or sinuate-dentate near the apex, 10–25 cm. long, 3.5–10.5 cm. broad, including the acumen, this acute, 8–20 mm. long, glabrous above, dark green, when dry pale brownish, the costa filiform, depressed, the other nerves hardly noticeable, cinereous beneath, except for the main nerves densely and appressed stellate-tomentose, covered by thin and minute, white stellate hairs, the costa very prominent, the prominent secondary nerves 9–12 on each side, regularly parallel, subascending, curved and vanishing near the margin, the transverse tertiary nerves filiform, prominent, the lesser veins reticulate, thin, prominulous, but covered by the tomentum, the midrib, secondary, and tertiary nerves with scattered or copious, larger, thicker, spreading, stellate hairs.

Inflorescences very small, axillary, cymose with few (usually 2) flowers (1–3), the axis extremely short, tuberculate, giving rise usually to a single ferruginous-tomentose branch 8–12 mm. long, this 2- or 3-furcate at apex into 2 or 3 peduncles; peduncles very short, about 1 mm. long, 3-bracteolate at apex, each articulate to a pedicel; bracteoles linear, 2–4 mm. long, tomentose; pedicels rather thick, tomentose,

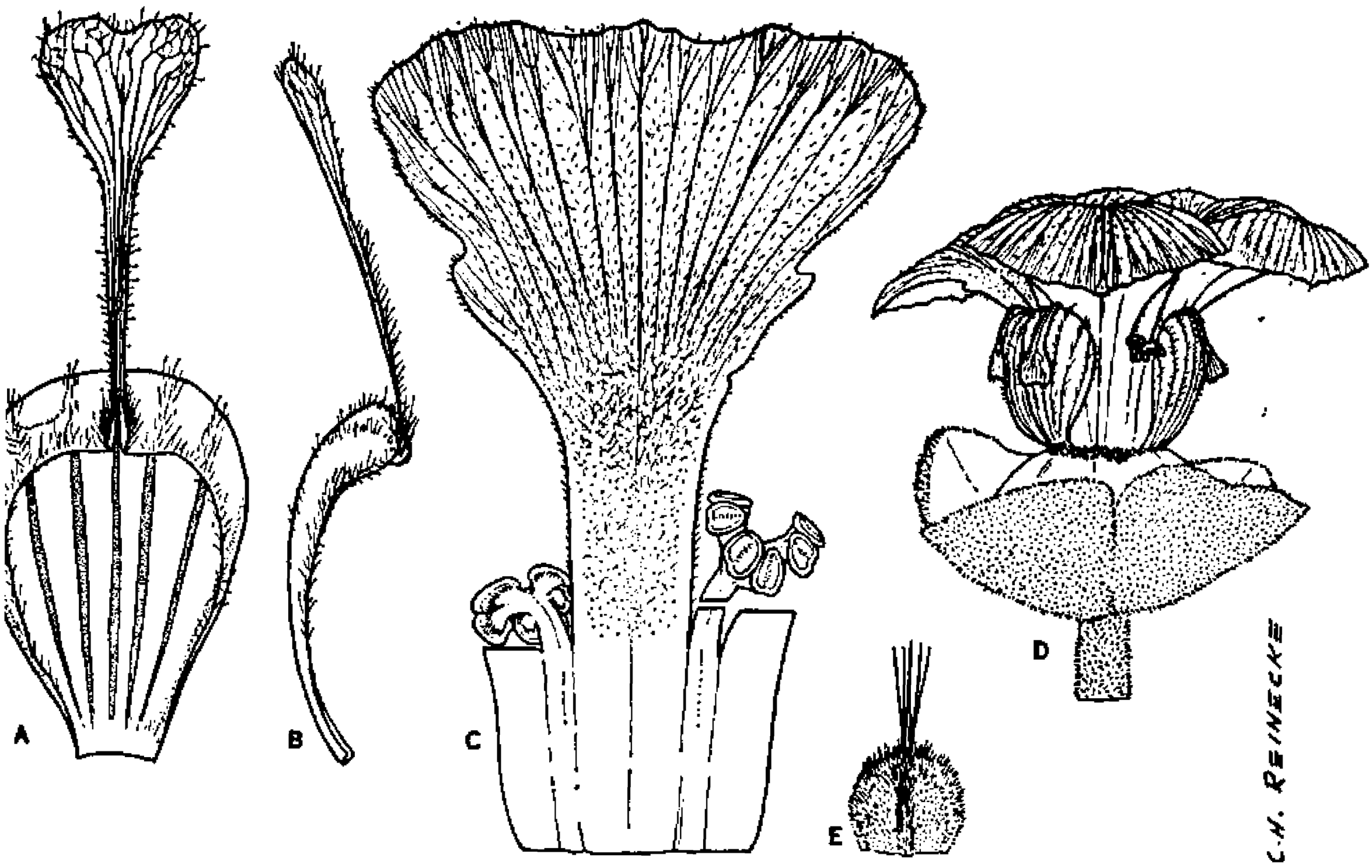


FIGURE 44.—*Theobroma mammosum* (León 1363): A, petal, inside view, × 5; B, petal, laterally, × 5; C, part of androecium, × 5; D, flower in anthesis, × 2.5; E, gynoecium, × 5.

8–12 mm. long; buds globose, densely ferruginous tomentose, about 1 cm. in diameter.

Sepals 11–12 mm. long, 5–6 mm. broad, thick, triangular-ovate, united completely by pairs or by 2 and 3, and all five in the lower third, forming a cupular, umbilicate, 2 or 3 short-lobate calyx, yellowish green inside, red tinged, glabrous except for the glandular, thick, erect, fasciculate, congested trichomes at the inner base, these 0.4–0.7 mm. long, densely, thickly, stellate-tomentose outside, greenish ochraceous or ferruginous.

Petal-hoods about 7–8 mm. long, 5–7 mm. broad, elliptic-obovate, broadly rounded-cucullate at apex, dark red, rather carnose with 7 thick nerves, between the nerves veined with yellowish or rose by transmitted light, minutely papillose inside, rugulose outside with sparse, long, acute, straight or slightly flexuous hairs throughout, these more copious at margin; petal-lamina erect in full anthesis, narrow, thick, dark red or purplish red, truncate-spatulate or slightly emarginate, usually plicate, with long, ferruginous, slightly flexuous hairs, these scattered outside, abundant at margin and inside, 3 mm. long, 2.5–3 mm. broad, gradually narrowed toward the base into a plicate pedicel about 4 mm. long, 0.5 mm. wide.

Androecium purplish red or dark red, the tube carnose, about 4 mm. high, 3–4 mm. broad, glabrous; staminodes large, petaloid, reflexed, the lower part thick, carnose, toward the apex gradually thinner, membranaceous, transparent-veined, obovate-spatulate, subtruncate and slightly sinuate at apex, laterally usually 1-dentate, the lower half suddenly narrower, about 11–12 mm. long, 10–12 mm. broad at top and 2.5 mm. wide at base, glabrous or with sparse hairs near the top outside, with copious, ferruginous, simple or stellate, rather long hairs inside; filaments thick, glabrous, about 1 mm. long, shortly 3-furcate, 3-antheriferous, the lower branchlet extremely short, the other two lateral about 1 mm. long; anther lobes ellipsoid, suborbicular, about 1 mm. long after anthesis; ovary subglobose, slightly 5-angulate, whitish, densely tomentose-hirsute, about 1.8 mm. high and thick; styles 2 mm. long, glabrous, erect, acute, connivent, only united at base.

Fruit at maturity 16–22 cm. long, 6–8.5 cm. broad, cylindric-oblong, terete or seldom slightly pentagonous, broad and umbilicate at base, strongly contracted and slightly pentagonal above the base, suddenly narrowed near the apex forming a mammiform, umbilicate end 2–3 cm. long and 2–2.5 cm. broad. Pericarp coriaceous, hard, smooth or slightly verrucose downward, pale green, covered by dense, short, ferruginous tomentum, the woody epicarp 1.5–2 mm. thick with a tomentose epiderm outside, the mesoendocarp carnose, white, about 7 mm. thick; pulp enveloping each seed fleshy, fibrous, white; seeds ovoid-amygdaloid, brownish, 22–27 mm. long, 14–17 mm. broad, 10–13 mm. thick; cotyledons white; germination hypogeous.

COMMON NAME.—Cacao silvestre.

DISTRIBUTION.—Eastern coastal mountains of Costa Rica, where it is extremely rare in primary forest. It has been found wild only twice, at altitudes from 300 to 800 meters. Cultivated in few agricultural experimental stations.

COSTA RICA: LIMÓN: La Lola, 100 m. alt., 12 V 1948, *Escamilla*, s.n. (MO). Síquirres, Finca La Lola, 300 m. alt., I 1949, *León* 291 (holotype, TURRI). La Lola, cerca de Madre de Dios, 100 m. alt., cultivated, 30 I 1949, *León* 1363 (paratype, F, TURRI). Ibidem, Experimental Station I.I.C.A., cultivated; tree 6 m., stem 20–25 cm. diam., leaves chartaceous, firm, green above, pale beneath, branches ternate, growth pseudoapical, flowers dark red and brown red, fruit ellipsoid, contracted at apex, 6 XI 1961, *Cuatrecasas & Paredes* 26535 (US).

HEREDIA: Puerto Viejo, Sarapiquí, 700–800 m. alt., IV 1959, *Holdridge* 146 (TURRI).

CARTAGO: Turrialba, grounds of I.I.C.A., cultivated, 600 m. alt., 4 XI 1961, *Cuatrecasas & León* 26516 (US).

TRINIDAD: River State Diego Martinez, I.C.T.A., Field 19, cultivated from seed received from Belém do Pará; tree 8 m. high, stem rugose-tuberculate, brown, abundant dry fruits hanging from branchlets, 1 IX 1961, *Cuatrecasas & Cope* 25791 (US).

Hybrids

Theobroma angustifolium Moc. & Sessé ♂ × **mammosum** Cuatr. & León ♀.

Trinidad, I.C.T.A., *Cuatrecasas & Cope* 25800. Well-developed tree, with intermediate characters.

Theobroma grandiflorum (Spreng.) Schum. × **obovatum** Klotzsch.

Belém do Pará, Brazil, Museu Goeldi, arvore 480, 22 XII 1958, *Cavalcante* 937 (MG, US).

Theobroma grandiflorum (Spreng.) Schum. ♀ × **subincanum** Mart. ♂.

Hybrid fertile obtained by Addison and Miranda (1951) 13. Intermediate features of parents.

Theobroma grandiflorum (Spreng.) Schum. ♀ × **obovatum** Kl. ♂.

Brazil. Fertile hybrid obtained by Addison (1951) 10, *pl. 1, fig. 3, pl. 2, fig. C.* F. cultivated at Belém do Pará, 6 XI 52, *Pires* 4343 (IAN). Ibidem, *Pires* 4344 (IAN).

Theobroma mammosum Cuatr. & León ♂ × **simiarum** Donn. Smith.♀

Costa Rica, Turrialba IICA, robust young trees obtained by Soria.

Theobroma mammosum Cuatr. & León ♀ × **simiarum** Donn. Smith ♂.

Costa Rica, Turrialba, IICA, robust young trees obtained by Soria.

Theobroma obovatum Klotzsch ♂ × **subincanum** Mart. ♀.

Fertile hybrid obtained by Addison and Miranda (1951) 14, *pl. 13, fig. 13, pl. 4, fig. C.* Also found spontaneous by Cope & Holliday in Colombia: Río Caquetá, Remolino, tree 11-12m., with some characters of *T. obovatum* and others of *T. subincanum*, 2 V 1953; it has almost smooth pods but bears flocose, woolly pubescence on the young shoots and leaves, *Holliday & Cope* T 122 (COL, TRIN, US). Caquetá, Río Caguán, tree 8 m., 27 IV 1953, *Cope & Holliday* T 117 (COL, TRIN). Brazil, Amazonas, Fonte Bõa; tree 15 m. alt. "cupurana," *Fróes* 20648 (IAN, US). Trinidad, ICTA, experimental camps, *Cuatrecasas & Cope* 25797 (US).

Theobroma speciosum Willd. ex Spreng. ♂ × **sylvestre** Mart. ♀.

Belém do Pará, Brazil, 6 XI 1952, *Pires* 4345 (IAN, COL). Experimental hybrid by Addison. It has intermediate characters as described and illustrated by Addison & Miranda (1951) 14, *pl. 5 fig. 3, pl. 6, fig. C.*

Theobroma speciosum Willd. ex Spreng. ♀ × **sylvestre** Mart. ♂.

Belém do Pará, Brazil. Experimental hybrid obtained by Addison, similar to the former. Addison & Miranda (1951) 15.

At the Instituto Interamericano, Costa Rica, Dr. Soria (1961) tried to hybridize *T. cacao* with *T. angustifolium, mammosum, simiarum,* and *bicolor.* The cross *T. angustifolium* ♂ × *cacao* ♀ gave small

plants which did not grow more than about 10 cm. in two years. *Theobroma cacao* ♀ × *mammosum* ♂ gave fruits, but the seeds were very weak; the same happened with *T. cacao* ♀ × *simiarum* ♂. The cross *T. bicolor* ♂ × *cacao* ♀ was negative. See also Addison and Miranda in the Historical Sketch above.

Rejected Names and Excluded Species

Theobroma Kalagua de Wildeman, Bull. Herb. Boiss. 7:957, *pl. 11.* 1899.

TYPE.—Panama, *Patin*, s.n. (lectotype, BR, leaf) (F. M. Photo 40742).

This species was described by de Wildeman as very remarkable, because of the extraordinary combination of flowers similar to those of *T. angustifolium* and *T. simiarum*, fruits resembling *T. simiarum*, and quite different leaves which although resembling those of *T. angustifolium* in shape differed by the lack of pubescence. But Patin gave assurance to Wildeman that these different parts came from a single tree. De Wildeman wrote: "qui appartiendraient sans le moindre doute à la même plante. Une confusion aurait cependant pu être possible parce que le *Th. simiarum* existe également en Colombie, où M. Ch. Patin, qui s'adonne a la recherche des plantes utiles, l'a découvert à Choco, province de Cauca" (Wild. p. 958). In the U.S. National Herbarium, attached to a herbarium sheet (1,382,338), is a letter sent to J. Donnell Smith by Ch. Patin, dated Brussels 19 Oct. 1900. Here Patin states "As concerns *T. Kalagua* . . . there was a doubt about the leaves used to determine the specy [sic]: the young plants which we have just got here from seeds have proved that it occurred really a mistake in the description made of the leaves brought to me by my collector." This contradicts the earlier assurances given by Patin about all his specimens having been collected from a single tree and shows that he was not the collector himself. Later on Patin writes, "I think that the *T. Kalagua* is just your *T. Simiarum*." Patin never explained where his specimens were collected. Probably they came from the region of Panamá. Regarding the specimens sent with the above cited letter, the seedling leaves and small fragments of fruits might well be those of *T. simiarum*.

To clear up this question, in 1953 I asked Dr. Robyns, director of the Jardin Botanique de l'Etat, Brussels, to send me the material of *T. kalagua* preserved at that herbarium. Very kindly, Dr. Robyns sent me the only existing herbarium sheet of the type material of *T. kalagua*, which is represented only by one leaf, undoubtedly the same used to illustrate the plate in the publication. To a further request to Dr. Robyns the answer was given that no other material

of this species existed except for some fruits which "selon toute vraisemblance appartiennent au matériel *Patin* s.n. recolté en 1899, se trouvaient dans nos collections de fruits."

Examination of the Patin specimens proves that the leaf mounted on this sheet at BR (photo F. M. No. 40742) is the original Patin leaf used for de Wildeman's illustration and that this leaf belongs to *Theobroma cacao*. This leaf is the only unquestionable part of the type apparently existing, and I select it as the lectotype. The three fruits received on loan from Brussels labeled *T. kalagua* were: 1) A half shell, to be discarded as belonging to *Theobroma bicolor*. 2) An entire pod with a modern label from "J. Bot. Br." reading "*Th. Kalagua* Wild. Colombie, sans date Coll. Patin." This fruit is smooth, ellipsoid, oblong, slightly attenuate and rounded at apex and broadly rounded, umbilicate at base, 18–20 cm. long, and 8.8 cm. broad; the surface is tomentose, the woody epicarp about 1.5 mm. thick, the dried, spongy mesoendocarp 2–4 mm. thick; a fragment of this shell is lacking, and this could be the fragment of fruit sent by Patin to Donnell Smith and preserved at the U.S. National Herbarium (1,382,338). This fruit is not that used for the illustration, because the original was sectioned; furthermore, this pod looks somewhat more oblong than the one figured in the plate. It may well belong to *T. simiarum*, as may also the seedling leaf sent to Donnell Smith. 3) The third fruit received from Brussels bears two labels; one reads "*Theobroma kalagua*, Colombie, Chocó, Prov. de Cauca, leg. Ch. Patin 1899," and the number 823; the other label reads "*Theobroma simiarum* D. Sm. Colombie, leg. Ch. Patin"; it consists of half a shell whose section is ovate-ellipsoid, 19 cm. long and 14.2 cm. broad and about 2 cm. thick; the woody epicarp is 1.5–2 mm. thick; the thick mesoendocarp is compact. It is different from all species of *Theobroma* known to date; it might be an undescribed species, but it could also belong to another genus.

In conclusion, we may infer that Patin gathered several specimens of different *Theobroma* species collected by different persons and coming from several places (Panama, Chocó . . .). The flowers described by de Wildeman could well be flowers of *T. angustifolium* or *T. simiarum;* the possibility of their growing in Panama, perhaps planted, cannot be discarded. They also could have been flowers from trees of *T. stipulatum*, *T. chocoense*, or from some undescribed species. An important character of the flower, its color, was not mentioned by Patin. The fruit shown in the plate is thicker than that of *T. simiarum;* it recalls very much that of *T. grandiflorum*, a species more or less widespread in gardens, and it is also similar to that of *T. chocoense* and *T. stipulatum*. It may also belong to an undescribed species. To ascertain to what species such a fruit belongs,

it would be necessary to see at least two associated organs from the same tree, that is to say fruit and leaves, fruit and flowers, or, also, flowers and leaves. The above comments on the available data prove the disorderly way of Patin's work and his unreliability. There is no reason to believe that the flowers and fruits of Patin's collections were brought from the same tree or from the same species. Patin never mentioned the locality of the specimens sent to de Wildeman or who collected them. Colombia is always cited but at that time Panama was part of Colombia. At present the only identifiable Patin specimen from his syntypes is the leaf (BR) and that is *T. cacao*. Consequently, *T. kalagua* becomes a synonym of *T. cacao*.

Theobroma guianense (Aubl.) Gmel., Syst. Veg. ed 13, 2:1151. 1796.
Cacao guianensis Aubl. Pl. Guian. 2: 683, pl. 275. 1775.

SYNTYPES.—Aublet illustrations (l.c.) and specimens at British Museum (Natural History).

Under *Cacao guianensis*, Aublet gave a detailed and illustrated description made up of a mixture of three different species. There is complete agreement between the description of each part and the corresponding illustration. The flowers were described from specimens of *Theobroma cacao* L.; the branches and leaves from *T. subincanum* Martius; the fruits cannot be identified with any other species included in Bernoulli's and Schumann's treatments. The illustration of this fruit (*Pl. 275, figs. 16 & 17*) agrees unmistakably with only one recent collection of *Theobroma* fruits, namely that from French Guiana by Benoist, which is the type of *T. velutinum* Benoist. Aublet's short diagnoses of the fruit, especially the French description "l'ovaire devient une capsule ovoide à cinq arrêtes arrondies saillantes" also agree perfectly with it. It seems that Aublet considered the most typical part of his "species" the fruit, since he headed the description of his *Cacao guianensis* with a short definition based only on the fruit: "CACAO (*Guianensis*) fructu ovato, quinquangulari, tomentoso, rufescente (Tabula 275)" (p. 683); furthermore, as Sandwith pointed out, the French name given by Aublet [Le Cacaoier anguleux. (Planche 275)] was taken from the same diagnosis. Thanks to Benoist we know now that this kind of fruit belongs to a species with a kind of leaves very different from those described by Aublet, the species described by Benoist as *T. velutinum*.

But the nomenclatural problems have to be solved on the basis of types according to the International Code. At the British Museum there are preserved Aublet specimens and among them type specimens of *Cacao guianensis* which are syntypes. In 1954, I could identify by close examination an herbarium sheet (with foliage, one flower,

and an immature fruit) as belonging to *T. subincanum* Mart.; this specimen agrees with the description and drawings given by Aublet for the leaves and branchlets; this evidence could easily incline us to use this specimen as lectotype for *C. guianensis*. But in the carpological collection of the British Museum there is a fragmentary fruit, also a syntype of Aublet's species, which belongs to *T. cacao*.

Until now, there has been only confusion about the identity of *Theobroma guianense*. Bernoulli (p. 7) wrote: "*Cacao guianensis* bleibt somit eine vollstaendig ungewisse Art. Sie scheint auch von keinem weitern Autor gesehen worden zu sein, sondern immer nach Aublet citiert zu werden." Schumann placed it as synonym of *Theobroma cacao*, surely on account of its flowers. Chevalier considered the species synonymous with *T. speciosum* Willd., erroneously interpreting Aublet's descriptions and drawings of the leaves and a photograph of the Aublet herbarium specimen (syntype) at the British Museum; these, as I have pointed out above, belong to *T. subincanum* Mart. He also identified the Benoist collections of *T. velutinum* erroneously as *T. speciosum*.

Consequently, *Cacao guianensis* Aubl. is not a true species, but a mixture of three species. Therefore the Aublet "species" and name has to be rejected as "nomen confusum" (articles 63(3), 65, and 66 of the Code of Nomenclature). The name *Theobroma guianense* has never been consistently used in monographs and general books for any known species.

"Theobroma fossilium" Berry, Proc. U.S. Nat. Mus. **75**(24):8, *pl. 1, figs. 13, 14*. 1929.

In regard to this unfortunate name, the following opinion of R. W. Brown, former paleobotanist of the U.S. Geological Survey, is final: "This specimen, considered by Berry to be the first fossil record of *Theobroma*, is a section of the forepart of a reptilian jaw. Berry mistook the bony structure for the pulp, and the teeth for the seeds of a chocolate-bean pod. Although described among Tertiary plants, the specimen, as stated by Berry, came from near Leiva, Department of Boyacá, Colombia, where Cretaceous strata crop out." (Journ. Washington Acad. Sci. **36**:353. 1946).

Theobroma alba Bernoulli, Uebers. Art. Theobroma 14. 1869; Jumelle (1899) 35; De Wildeman (1902) 98. 1902.

TYPE.—Essequebo et Cuyaunic, British Guiana, *C. F. Appun* 1, 1860 (holotype, Herbarium Hookerianum, K).

The type of this species consists of leaves of a young, sterile plant of the genus *Licania*. I have identified it by comparison from the abundant material existing in the Royal Botanic Gardens, Kew, with

L. venosa Rusby, a widespread species of the Guianas. The following new combination is necessary:

Licania alba (Bernoulli) Cuatr., comb. nov. *Theobroma alba* Bernoulli, Uebers. Art. Theobroma 14. 1869. *Licania venosa* Rusby, Descr. New Sp. So. Am. *Pl. 26.* 1920.

Theobroma albiflorum (Goudot) De Wildeman, Pl. Trop. Gr. Cult. 90. 1902=*Herrania albiflora* Goudot, Ann. Sci. Nat. III, **2**:230, *pl. 5.* 1844.

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Theobroma augusta L. Syst. Nat. **3**:233. 1776; Willd. Sp. Pl. **3**:1424. 1803=*Abroma augusta* (L.) L. f. Suppl. 341. 1781.

Theobroma balaënsis (Preuss) De Wildeman, Pl. Trop. Gr. Cult. 89. 1902=*Herrania balaensis* Preuss, Exped. Centr. und Süd-Amerika 253, *pl. 7.* 1901.

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Theobroma celtifolia Salisburg, Prodr. 387. 1796=*Guazuma ulmifolia* Lam. Encycl. Méth. **3**:52. 1789.

Theobroma guazuma L. Sp. Pl. 782. 1753=*Guazuma tomentosa* H. B. K. Nov. Gen. Sp. **5**:320. 1823. Freytag (1951) 214.

Theobroma hastata Chevalier, Rev. Bot. Appl. **26**:273. 1946, *nomen nudum; lapsus calami* for *T. sagittata* Pavón ex Chevalier.

Theobroma laciniifolium (Goudot ex Triana et Planchon) De Wildeman, Pl. Trop. Gr. Cult. 90. 1902=*Herrania laciniifolia* Goudot ex Triana et Planchon, Prodr. Fl. N. Granat. 209. 1862.

Theobroma mariae (Martius) Schumann in Mart. Fl. Bras. **12**^{3}:71, *pl. 15.* 1886=*Herrania mariae* (Mart.) Decaisne ex Goudot Ann. Sci. Nat. III, **2**:233. 1844.

Theobroma montana Goudot ex Bernoulli, Uebers. Art. Theobroma 15. 1869, *nomen nudum.* No description.

Theobroma nitidum (Poepp. et Endl.) Schumann in Mart. Fl. Bras. **12**^{3}:72. 1886. (*Abroma nitida* Poepp. et Endl., Nov. Gen. Sp. Pl. **3**:73. 1845)=*Herrania nitida* (Poepp. et Endl.) Schultes, Caldasia **2**:16, 17, *pl.* 1943.

Theobroma purpureum Pittier, Repert. Sp. Nov. Fedde **13**:319. 1914=*Herrania purpurea*(Pittier) Schultes, Caldasia **2**:333. 1944.

Theobroma pulcherrimum (Goudot) De Wildeman, Pl. Trop. Gr. Cult. 89. 1902=*Herrania pulcherrima* Goudot, Ann. Sci. Nat. III, **2**:232, *pl. 5.* 1844.

Theobroma sagittata Pavón ex Chevalier, Rev. Bot. Appliq. **26**:274. 1946, *nomen nudum*=*Herrania nitida* (Poepp. et Endl.) Schultes, Caldasia **2**:16, 17, *pl.* 1943.

Theobroma tomentosa (H. B. K.) Gómez, An. Hist. Nat. **19**:217. 1890=*Guazuma tomentosa* H. B. K. Nov. Gen. Sp. **5**:320. 1823.

Theobroma undulata Pavón ex Chevalier. Rev. Bot. Appliq. **26**:268. 1946, *nomen nudum: lapsus calami* for *T. sinuosum* Pavón ex Huber.

Collections Cited

ACOSTA SOLÍS, M., & GILER, M.
12392 gileri
12423 gileri

ALLEN, P. H.
3105 grandiflorum
4593 bicolor
6259 angustifolium
6341 angustifolium

APPUN, C. F.
1 Alba

ARAQUE, J., & BARKLEY, F. A.
18C745 hylaeum

ARCHER, W. A.
7517 subincanum
7537 obovatum
7549 grandiflorum
7551 microcarpum
7619 speciosum
7721 speciosum
7734 grandiflorum
7820 subincanum

ASPLUND, E.
10271 bicolor
12911 subincanum
13410 subincanum

AUBLET, J. B. C. F.
s.n. cacao (fruit)
s.n. subincanum

BAFOG (BUREAU AGR. ET FORESTIER GUYANAIS)
136M velutinum
7386 velutinum

BAILEY L. H.
s.n. angustifolium

BAKER, C. F.
62 grandiflorum
421 grandiflorum
2102 angustifolium

BAKER, R. E. D.
16 grandiflorum
33 subincanum
34 bicolor
37 glaucum
38 subincanum
s.n. angustifolium

BAKER, R. E. D., BARTLEY, B. G., & HOLLIDAY, P. C.
31 subincanum
32a subincanum

BAKER, R. E. D., & COPE, F. W.
2 bicolor
3 subincanum
4 subincanum
5 grandiflorum
6 grandiflorum
7 subincanum
11 glaucum
11a bicolor
12 subincanum
13 subincanum
21 subincanum
25 subincanum
26 bicolor
27 obovatum
28 microcarpum
29 microcarpum
30 obovatum
31 subincanum
32 subincanum

BARTLEY, B. G., & HOLLIDAY, P. C.
T 46 grandiflorum
T 47 bicolor
T 65 subincanum
T 66 bicolor
T 68 subincanum
T 69 glaucum
T 70 glaucum
T 71 subincanum
T 72 subincanum
T 74 glaucum
T 75 subincanum
T 166 hylaeum

BENOIST, R.
516 velutinum

BERNOULLI, G.
94 bicolor
95 angustifolium

BERNOULLI, G., & CARIO, R.
3188 angustifolium
3145 bicolor

BLACK, G. A.
47–1496 obovatum
47–1502 grandiflorum
47–1889 speciosum

BLACK, G. A., CORDEIRO, E. & FRANCISCO, J.
52–14649 microcarpum
52–14655 speciosum

BLACK, G. A. & LEDOUX, P.
50–10644 sylvestre

BLACK, G. A. & SCHULTES, R. E.
46–61 grandiflorum
46–61 (USDA) subincanum
46–III grandiflorum

BOEHLMER, F. DE
12229 bicolor

BONPLAND, A.
s.n. bicolor

BRENES, A. M.
12333 bicolor

BRITISH HONDURAS FORESTS CONSERVATION
H2192/29 bicolor

BROADWAY, W. E.
8935 angustifolium

BURCHELL, W. J.
9375 grandiflorum
9467 grandiflorum

B. W. [BOSCHWEZEN]
1161 velvutinum

CALDERÓN, S.
627 bicolor
630 angustifolium
23610 bicolor

CAMARGO, F. C.
8 microcarpum
2395 speciosum

CAPUCHO, P.
397 speciosum

CARDEÑOSA, B., MURGUEITIO, P. R. & BARKLEY, F. A.
17C934 bicolor

CARDONA, F.
2379 subincanum

CAVALCANTE, P.
310 bicolor
339 obovatum
937 grandiflorum × obovatum
938 subincanum

COPE, F. W., & HOLLIDAY, P. C.
(see Holliday & Cope)

COOK, O. F.
4 bicolor

COOK, O. F., & DOYLE, C. B.
50 bicolor

COOK, O. F., & GRIGGS, R. F.
756 bicolor

COOPER, J. J.
10244 simiarum

COOPER, G. P., & SLATER, G. M.
242 angustifolium

COWAN, R. S.
38164 subincanum
38186 subincanum

CUATRECASAS, J.
6890 subincanum
7277 subincanum
7178A subincanum
14897 cirmolinae
15336 cirmolinae
15700 cirmolinae
16160 bernouillii subsp. capilliferum
16526A bicolor
16544 nemorale
16896 chocoense
17034 bernouillii subsp. capilliferum
17034A bernouillii subsp. capilliferum
17350 bernouillii subsp. capilliferum
17350A bernouillii subsp. capilliferum
17503 nemorale
17738 nemorale
21291 nemorale
21339 stipulatum

CUATRECASAS, J., & COPE, F. W.
25788 obovatum
25789 angustifolium
25790 angustifolium
25791 mammosum
25792 simiarum
25794 simiarum
25795 bicolor
25797 obovatum × subincanum
25800 angustifolium × mammosum
25801 grandiflorum

CUATRECASAS, J., COPE, F. W., & BARTLEY, B. G.
25780T grandiflorum
25781T grandiflorum
25782T nemorale
25783T obovatum
25784T bicolor
25785T subincanum
25786T bicolor
25787T bicolor

CUATRECASAS, J., & LEÓN, J.
26515 simiarum
26515A simiarum
26516 mammosum

CUATRECASAS, J., & PAREDES, A.
26534 bicolor
26535 mammosum
26536 simiarum
26537 angustifolium
26538 microcarpum

CUATRECASAS, J., & WILLARD, L.
26007 nemorale
26051 nemorale
26074 chocoense
26167 gileri

CUFODONTIS, G.
92 bicolor
599 simiarum

DAHLGREN, B. E., & SELLA, E.
10 microcarpum
438 grandiflorum
634 grandiflorum
733 grandiflorum
739 grandiflorum

DAVIDSON, G. W. R.
s.n. bicolor

DAWE, M. T.
83 bicolor

DODGE, C. W., & GOERGER, V. F.
9420 simiarum

DODGE, C. W., & NEVERMANN
7164 simiarum

DODGE, C. W., & THOMAS, W. S.
6399 angustifolium
6823 obovatum
7200 subincanum
7202 bicolor
7202B bicolor
7216 sylvestre
7397 bicolor
7638 bicolor
7679 subincanum
7704 obovatum
7822 sylvestre
7884 speciosum
7975 speciosum
10669 sylvestre
12187 sylvestre
14734 sylvestre
14925 subincanum
16458 grandiflorum
16464 subincanum
16466 microcarpum
21044 obovatum
21045 microcarpum

DUQUE JARAMILLO, J.
1205 bicolor
4403A bicolor

EGGERS, H. F. A.
14244 bicolor

ELLENBERG, H.
2551 obovatum
2565 speciosum

ESCAMILLA, G.
s.n. mammosum

FAGERLIND, F., & WIBOM, G.
2371 bicolor

FERNÁNDEZ P, A.
2275 subincanum

FOSBERG, F. R.
21310 bicolor

FRANCISCO, J.
1966 grandiflorum

FRÓES, R. L.
20463 sylvestre
20518 subincanum
20555 subincanum
20556 sylvestre

DUCKE, A.
100 sylvestre
103 sylvestre
265 obovatum
281 speciosum
283 microcarpum
598 grandiflorum
4878 sylvestre
6773 microcarpum
20625 bicolor
20645 glaucum
20646 obovatum
20648 obovatum × subincanum
20655 sylvestre
20750 microcarpum
20885 glaucum
20942 glaucum

21162 subincanum
21482 subincanum
21556 grandiflorum
23343 subincanum
23926 obovatum
23963 microcarpum
25554 sylvestre
26526 speciosum
28382 sylvestre
29732 speciosum
30180 speciosum
30432 speciosum
31414 speciosum
33783 canumanense
33788 sylvestre
34663 subincanum
34949 sylvestre

FRÓES, R. L., & FILHO, J. P.

29465 sylvestre

GARCÍA BARRIGA, H.

11178 bicolor
14203 subincanum
14224 subincanum
14253 subincanum
14380 glaucum
14416 bicolor
15139 subincanum

GARCÍA BARRIGA, H., SCHULTES, R. E., & BLOHM, H.

16064 subincanum

GARDNER, C. A.

870 bicolor

GENTLE, P. H.

3464 bicolor

GEOFFROY,

s.n. speciosum

GILER, M.

162 gileri
168 gileri

GILER, M., & PATIÑO, V. M.

164 gileri
165 gileri
166 gileri

GINZBERGER, A.

802 speciosum

GINZBERGER, A., &. HAGMANN, M.

801 subincanum

GINZBERGER, A., & ZERNER, H.

800 grandiflorum

GLAZIOU, A. F. M.

9633 speciosum
9633a subincanum
9643 grandiflorum

GOELDI, ANDREAS

4225 subincanum
4226 obovatum
4228 microcarpum

GONGGRYP, J. W.

4108 velutinum
4127 velutinum
4148 velutinum

GOUDOT

s.n. bicolor

GUERRERO, H.

26074 chocoense

HANBURY

9471 grandiflorum

HART, J. H.

158 bicolor
5381 augustifolium

HOFFMANNSEGG, W.

s.n. speciosum

HOLDRIDGE, L. R.

146 mammosum
5133 gileri
s.n. bicolor

HOLLIDAY, P. C.

T 43 subincanum
T 139 cirmolinae
T 140 cirmolinae
T 141 nemorale
T 142 bernouillii subsp. capilliferum
T 143 chocoense
T 144 chocoense
T 145 bernouillii subsp. capilliferum
T 146 nemorale
T 147 nemorale
T 148 nemorale
T 149 nemorale

HOLLIDAY, P. C., & BARTLEY, B. G.

T 163 gileri
T 165 stipulatum
T 167 gileri
T 172 bernouillii subsp. capilliferum
T 173 nemorale
T 175 stipulatum
T 176 chocoense var. bullatum
T 177 bernouillii subsp. capilliferum
T 178 bernouillii subsp. capilliferum

HOLLIDAY, P. C., & COPE, F. W.
T 77 bicolor
T 79 glaucum
T 79A glaucum
T 81 subincanum
T 90 obovatum
T 91 subincanum
T 94 glaucum
T 95 obovatum
T 96 glaucum
T 98 obovatum
T 101 subincanum
T 103 subincanum
T 114 obovatum
T 115 glaucum
T 116 subincanum
T 117 obovatum×subincanum
T 118 glaucum
T 119 obovatum
T 122 obovatum×subincanum
T 123 obovatum
T 124 subincanum
T 125 microcarpum

HUBER, H.
162 subincanum
1567 speciosum
1748 speciosum
4008 grandiflorum
4295 obovatum
7081 microcarpum

HUMBOLDT, A., & BONPLAND, A.
s.n. bicolor

IDROBO, J. M., & SCHULTES, R. E.
776 subincanum

INPA (INSTITUTO NACIONAL DE PESQUISAS DA AMAZONICA, MANAOS)
1966 grandiflorum
2125 sylvestre

JOBERT, DR.
903 speciosum

JOHNSON, H.
237 bicolor

KARSTEN, G.
s.n. glaucum

KILLIP, E. P., & SMITH, A. C.
30006 bicolor
30011 grandiflorum
30320 grandiflorum

KLUG, G.
87 subincanum
857 subincanum
1523 bicolor
2021 bicolor
2983 obovatum

KRUKOFF, B.
1080 speciosum
1117 speciosum
1274 grandiflorum
1644 microcarpum
1668 obovatum
5295 speciosum
5388 obovatum
5759 obovatum
6203 microcarpum
6263 obovatum
6592 microcarpum
7016 subinçanum
8226 subincanum
8275 obovatum
8280 microcarpum
9019 bicolor

KUHLMANN, J. G.
18110 subincanum

LABROY
s.n. grandiflorum

LANGE
12056 bicolor

LEHMANN, F. C.
7909 bicolor
9021 bicolor

LEÓN, J.
291 mammosum
937 angustifolium
1363 mammosum
3189 simiarum
4267 angustifolium
4832 gileri

LINDEMAN, J. C.
5725 simiarum

LITTLE, E. L., & LITTLE, R. R.
9544 subincanum
9598 bicolor

LLANO, E.
s.n. bicolor

LÓPEZ, J. R.
s.n. angustifolium

LUCAS, A.
1 bernouillii subsp. asclepiadiflorum

LUETZELBURG, PH. V.
22007 grandiflorum
22079 subincanum
23065 bicolor
23287 grandiflorum
23895 bicolor

MARTIUS, C. E. P.
862 bicolor
863 bicolor
864 bicolor
865 bicolor
871 sylvestre
872 subincanum
873 p.p. grandiflorum
873 p.p. subincanum
874 grandiflorum
875 grandiflorum
876 grandiflorum
884 microcarpum
885 microcarpum
886 microcarpum
887 sylvestre
888 sylvestre
889 sylvestre
890 sylvestre
891 sylvestre
893 subincanum
894 subincanum
895 subincanum
896 subincanum
897 subincanum
898 subincanum
899 subincanum
900 subincanum
Observ. 2832 sylvestre
Observ. 2890 microcarpum

MATUDA, E.
16690 bicolor
16733 bicolor
16840 bicolor

MEXÍA, Y.
7214 bicolor

MIRANDA BASTOS
68 subincanum

MOCIÑO, J. M., & SESSÉ, M.
3618 angustifolium
3620 bicolor
3621 bicolor
s.n. angustifolium
s.n. bicolor

MONTEIRO DA COSTA
121 grandiflorum

MULLER, J. V. S.
s.n. bicolor

PATIN, C.
s.n. cacao

PATIÑO, V. M.
22 subincanum
24 nemorale
115 chocoense
116 nemorale
117 nemorale
163 grandiflorum
169 chocoense var. bullatum?
171 chocoense var. bullatum
171A chocoense var. bullatum
171B chocoense var. bullatum
s.n. speciosum

PAVÓN, J.
617 bicolor
201 subincanum
s.n. bicolor
s.n. sinuosum

GENTLE, PERCY
3464 bicolor

PHILIPSON, W. R., IDROBO, J. M., & FERNÁNDEZ, A.
1552 glaucum

PIRES, J. M.
136 sylvestre
4340 bicolor
4343 grandiflorum × obovatum
4344 grandiflorum × obovatum
4345 speciosum × sylvestre
6575 simiarum

PIRES, J. M., & BLACK, G. A.
695 speciosum
740 speciosum
742 microcarpum
743 obovatum
744 grandiflorum
746 bicolor
1414 subincanum
s.n. obovatum

PIRES, J. M., FRÓES, R. L., & SILVA, N. T.
5886 speciosum

PIRES, J. M., NILO, T., & SILVA, A.
4339 obovatum

PITTIER, H.
4105 bernouillii
4194 hylaeum?
6883 bicolor
11112 angustifolium
14016 simiarum
16142 angustifolium
s.n. angustifolium

PITTIER, H., & DURAND, T.
3925 simiarum
8536 angustifolium

PITTIER, H., & TONDUZ, A.
4074 angustifolium
POEPPIG, E.
18 bicolor
1845 obovatum
2352 p.p. subincanum
2352 p.p. obovatum
2746 p.p. obovatum
2746 p.p. bicolor
s.n. bicolor
s.n. obovatum
POITEAU, A.
s.n. subincanum
PREUSS, P.
1381 angustifolium
RANGHEL, A.
195 subincanum
REKO, B. P.
6068 bicolor
RICHARD, L. C.
s.n. grandiflorum
RIEDEL, L.
1373 grandiflorum
s.n. grandiflorum
RIVERO
1836 subincanum
ROMERO CASTAÑEDA, R.
5405 bernouillii subsp. capilliferum
5500 stipulatum
s.n. bicolor
RUIZ, H., & PAVÓN, J.
s.n. bicolor
s.n. sinuosum
s.n. subincanum
RUSBY, H. H.
647 speciosum
654 speciosum
SAGOT, P.
1206 velutinum
SANDEMAN, C.
2233 grandiflorum
SCHOMBURGK, R.
870 p.p. bicolor
870 p.p. obovatum
s.n. grandiflorum
SCHULTES, R. E.
3471 bicolor
3922 bicolor
6536 subincanum
6921 obovatum
8065 grandiflorum
8178 grandiflorum
8385 subincanum
12104 subincanum
SCHULTES, R. E., BAKER, R. E. D., & CABRERA, I.
18552 subincanum
SCHULTES, R. E., & BLACK, G. A.
8146 grandiflorum
SCHULTES, R. E., & CABRERA, I.
14140 subincanum
15116 subincanum
17005 subincanum
17775 obovatum
17780 microcarpum
17781 grandiflorum
18695 gileri
SCHULTES, R. E., & CORDEIRO, E.
6507 speciosum
SCHULTES, R. E., & LÓPEZ, F.
9204 grandiflorum
SCHULTES, R. E., & SILVA, A.
8066 speciosum
SCHULTZE-RHONHOF
2312 glaucum
SESSÉ, MOCIÑO, CASTILLO, & MALDONADO
3618 angustifolium
3620 bicolor
3621 bicolor
SIBER
4 grandiflorum
s.n. speciosum
SILVA, J. F.
143 subincanum
155 obovatum
SILVA, A.
237 subincanum
317 subincanum
SIQUEIROS, R.
4008 grandiflorum
SMITH, J. DONN.
6457 simiarum
7313 simiarum
7731 simiarum
SNETHLAGE, E. H.
300 grandiflorum
10044b speciosum
SPRUCE, R.
97 subincanum
166 sylvestre
456 speciosum
1609 bicolor
1737 speciosum
1822 grandiflorum

s.n. bicolor
s.n. speciosum
s.n. sylvestre

STANDLEY, P. C.

22317 angustifolium
36822 simiarum
37374 bicolor
37377 simiarum
79068 angustifolium
79069 bicolor
82446 bicolor

STERN, W., & CHAMBERS, K.

140 angustifolium

STEYERMARK, J. A.

44941 bicolor
49317 bicolor

STOCKDALE, J. A.

s.n. bicolor

SUCHTELEN, N. J. v.

s.n. simiarum

TATE, G. H. H.

944 subincanum

TESSMANN, G.

3433 obovatum
4079 bicolor
4115 subincanum
4928 sinuosum
5398 speciosum
s.n. subincanum

TONDUZ, A.

4074 angustifolium
6852 simiarum
8373 simiarum
11304 bicolor
12822 simiarum
13110 bicolor
18222 simiarum

TRAILL, J. W. R.

59 subincanum
60 bicolor
61 obovatum
62 glaucum
s.n. bicolor

TRIANA, J. J.

5333(-3) bicolor
s.n. bicolor

TUERCKHEIM, H. v.

7824 bicolor

ULE, E. H. G.

5030 bicolor
5637 obovatum
9609 speciosum
14448 speciosum

WEBERBAUER, A.

6245 bicolor

WEDEL, H. v.

681 bernouillii subsp. asclepiadiflorum
1535 p.p. bernouillii subsp. asclepiadiflorum
1535 p.p. Lauraceae sp.

WICKHAM, H. A.

s.n. grandiflorum

WILLIAMS, R. O.

12121 angustifolium

WILLIAMS, LLEWELYN

161 obovatum
230 obovatum
1076 subincanum
1233 subincanum
2149 bicolor
2401 grandiflorum
3254 subincanum
3346 bicolor
5268 obovatum
9345 bicolor
15204 subincanum
15614 grandiflorum

Collections of Theobroma cacao L. Seen

Acosta Solís, M., 6332. 10724a.
Allen, Cyril, 880, 881.
Asplund, E., 13408, 14464, 14583, 14788.
Baker, C. F., 61, 63, 125.
Baker, R. E. D. & Cope, F. W., 15.
Banks, s.n.
Barkley, Araque, & Gomez, 410.
Bartlett, H. H., 13108.
Bartley, B. G., & Holliday, P. C., 51.
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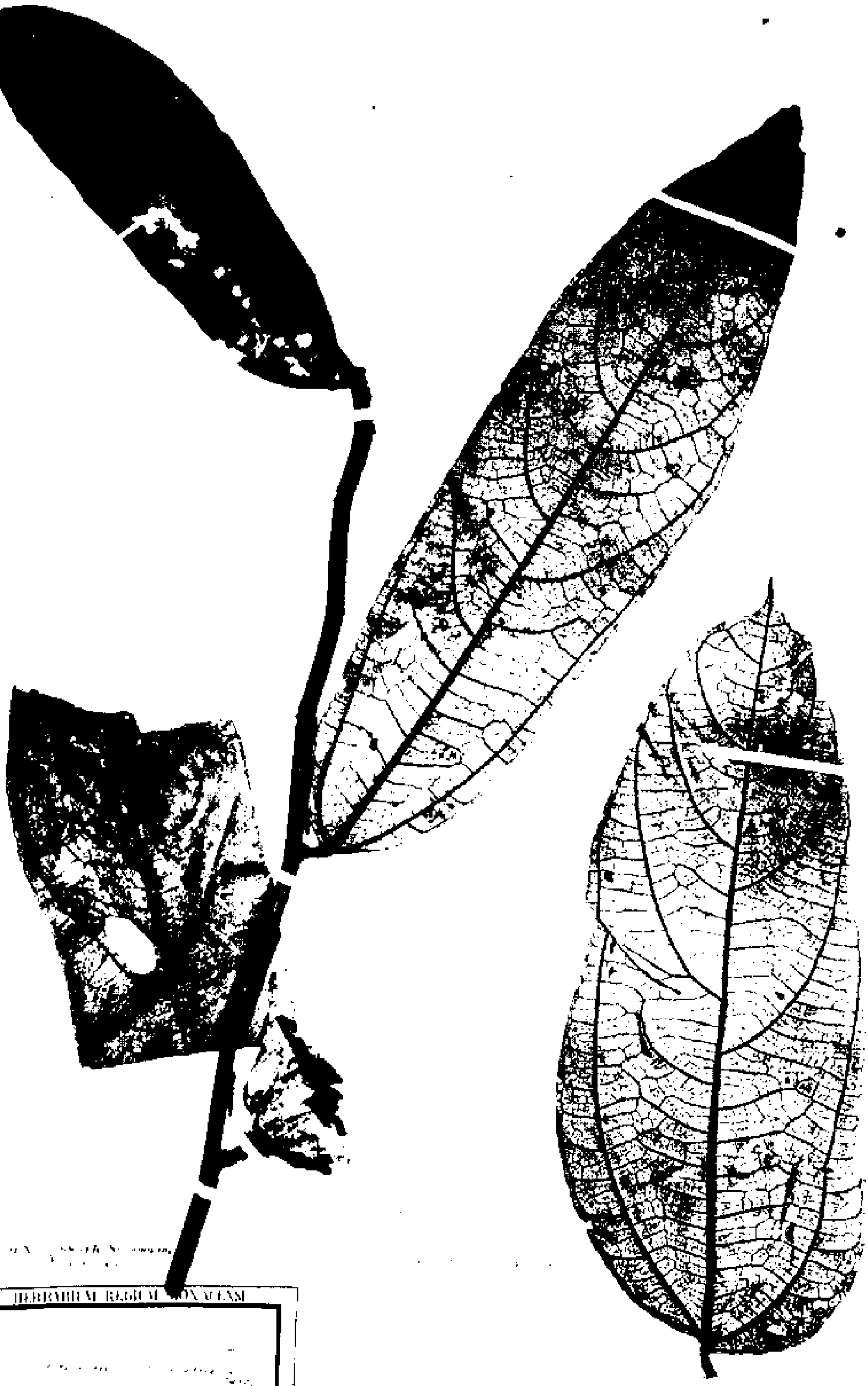


Theobroma sylvestre Mart., lectotype at Munich (photo FM 1964).

Theobroma speciosum Willd. ex Spreng., isotype formerly at Berlin-Dahlem; identical with the holotype in the Willdenow Herbarium (photo FM 9640).

Theobroma speciosum Willd. ex Spreng., isotype of *T. quinquenervia* Bern., *Spruce 1737* at Berlin-Dahlem (photo FM 9639)

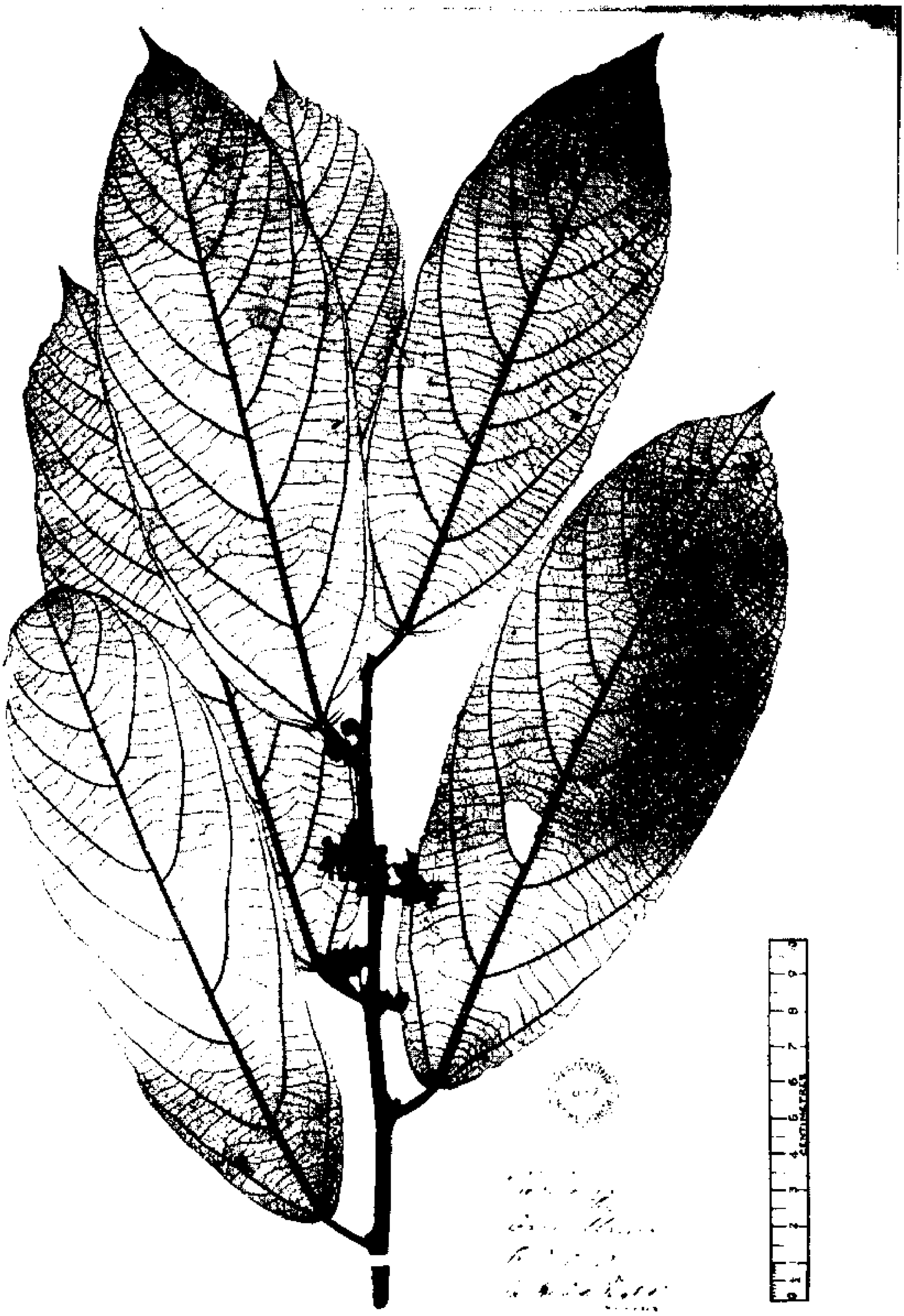
Theobroma fanchonii Karsten, holotype at Vienna (photo FM 322015).

Theobroma bernoullii subsp. *capilliferum* Cuatr., in the rain forest, Pacific coast, Colombia (photo Cuatrecasas C. 2202).

Theobroma cacao subsp. *sphaerocarpum* (Chev.) Cuatr. cultivar "amelonado" at San José del Guaviare, Colombia (photo Cuatrecasas C-1560).

Theobroma circolinae Cuatr.; caulinar inflorescences on trunk, with opening buds and yellow flowers, at the western Andes in El Valle, Colombia (photo Cuatrecasas C. 2132).

Theobroma grandiflorum (Spreng.) Schum., lectotype of *T. macrantha* Bern. and neotype of *T. grandiflorum* Schum., *Spruce 1822*, at Munich (photo CNHM 40705).



Theobroma subincanum Mart., holotype of *T. ferruginea* Bern. at Kew, collect. R. & P. (photo Royal Botanic Gardens, Kew).

Theobroma subincanum Mart., lectotype of *Cacao sylvestris* Aublet in the British Museum (photo BM 4029, Mo. Bot. Gard.).

Theobroma subincanum Mart., syntype (part) of *Cacao guianensis* Aublet, in the British Museum (photo BM 4028, Mo. Bot. Gard.).

Theobroma sinuosum Pavón ex Huber; type of *T. tessmannii* Mildbr. formerly at Berlin-Dahlem (photo FM 17942).

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