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C. E. WOOD, JR.
EDITOR

FRANCES M. JARRETT
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STUDIES IN ARTOCARPUS AND ALLIED GENERA,[1] I. GENERAL CONSIDERATIONS

FRANCES M. JARRETT

MEMBERS OF THE GENUS *Artocarpus* are the most commonly encountered representatives of the Moraceae in the lowland forest of the Old World tropics (Africa excepted) apart from the ubiquitous *Ficus*. The genus also includes two important food-plants, the Breadfruit (*A. incisus*) and the Jack (*A. heterophyllus*), which now have a circumtropical distribution as cultivated plants, owing to the efforts of man, which include, of course, the well-known voyage of Captain Bligh ending in the mutiny on the *Bounty*. The fruits of a number of other species are edible, some being planted for the sake of these, and many species provide valuable timber, although they do so in general as scattered members of the forest flora, for the only example of gregarious behaviour is that of *Artocarpus incisus* (probably little, if at all, modified from the original form) acting as a dominant member of the forests of the river-swamps of New Guinea.

The genus *Artocarpus* is singled out by its compound fruit or syncarpium, which attains a large size in some species, notably in the two cauliflorous species, the Jack and the Chempedak (*A. integer*, frequently cultivated in Malaysia). The structure of this fruit has been the subject of special attention in this study with the object of determining the differences between it and the syncarpous fruits of two other small genera of the same area and alliance, *Parartocarpus*, which has frequently been confused with *Artocarpus*, and *Hullettia*, which has proved, somewhat unexpectedly, to show a relationship with *Parartocarpus*, having previously been placed in a different subfamily of Moraceae. A third small genus, *Prainea*, which is more closely related to *Artocarpus* than either of these, although the female inflorescence is not a syncarpium, is also included. It provided another immediate problem, since details of the leaf anatomy had led an earlier author (Renner, 1907 [2]) to unite *Prainea* with *Artocarpus*, necessitating a re-evaluation of his work and its extension to cover all the species here

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[1] This series of papers is based on a thesis presented to the University of Cambridge, England, in July 1956 for the degree of Ph.D.

[2] The dates refer to the bibliography at the end of the paper.

recognized, from which it has been concluded that his action was not justified.

The four genera to be included in this study are thus *Artocarpus* J. R. & G. Forster, which is here recognized as consisting of about fifty species, *Prainea* King (four species), *Parartocarpus* Baillon (three species) and *Hullettia* King (two species). They are lactiferous trees or, less commonly, shrubs restricted in general to the lowland tropical evergreen forest of the Asiatic-Malaysian region although some species may extend to slightly higher altitudes or into areas of deciduous forest. A few of the latter are restricted to regions with a distinct dry season and are themselves either deciduous or evergreen, but the rest are merely tolerant of a short dry season, often adopting the deciduous habit when they grow in such a climate.

With an African genus, *Treculia* Decaisne ex Trécul, which has perhaps six species, they form a group within the Old World Moraceae characterized by condensed, capitate, unisexual inflorescences which is sufficiently distinct to justify independent study, although it cannot be entirely certain that it represents a natural assemblage of genera. These genera have been assigned to the subfamily Artocarpoideae tribe Artocarpeae and, as will be shown later, constitute the Old World members of this tribe. Although the three subfamilies of the Moraceae — Moroideae, Artocarpoideae and Conocephaloideae — which are distinguished by the position of the ovule and of the stamens in bud, may be valid groups if some exceptions are allowed for, it is not felt that the present classification of the Moraceae offers a sufficiently satisfactory basis for a detailed discussion of the position within the family of the genera being studied, and there will be given only a brief review of Bentham and Hooker's classification of the Artocarpeae. Full revisions of *Prainea*, *Artocarpus*, *Parartocarpus* and *Hullettia* will be given, in this order, in subsequent papers, while in this introductory paper the more general problems of the generic distinctions will be considered.

The genus *Artocarpus* was described by J. R. & G. Forster in 1776 and has been monographed as a whole once before in 1847 by Trécul, who established two subgenera, *Jaca* and *Pseudojaca*, which are here maintained (the former as subg. *Artocarpus*), on the basis of "alternate" (i.e., spiral) *vs.* distichous arrangement of the leaves and amplexicaul *vs.* non-amplexicaul stipules, as well as on a character of the male flowers which later proved untenable. *Parartocarpus* was described by Baillon in 1875, but was not very clearly distinguished by him from *Artocarpus*, and when King monographed the species of *Artocarpus* in India and the Malay Peninsula in 1889, he included unawares two species of *Parartocarpus*, the discordant characters of which led him to reject Trécul's subgenera. King had also described *Prainea* and *Hullettia* in 1888 but, mistaking the position of the ovule, he assigned them to the Conocephaloideae. In 1902 Beccari published an account entitled "Nuove specie di *Artocarpeae* Malesi e Papuane" in which he pointed out the affinity between *Prainea* and *Artocarpus* and briefly commented on the differences between the latter and

Parartocarpus. The final paper of major importance in the classification of the genera is Renner's study of the leaf anatomy of the Moraceae: Artocarpoideae and Conocephaloideae, published in 1907. Renner re-established Trécul's subgenera but treated them, together with *Prainea*, as three sections under *Artocarpus*, a proceeding which might be justifiable on the basis of leaf anatomy alone, but not if the inflorescence structure is also taken into account.

Various observations had thus been made on the differences between *Artocarpus*, *Prainea* and *Parartocarpus*, but the status and distinguishing characters of the genera had not been fully elucidated, nor had the true affinities of *Hullettia* previously been noted. Although the inflorescence structure of these genera is complex and its morphological derivation is not immediately apparent, no study of the development had been made, apart from a few superficial observations published by Baillon in 1863.

In this introductory paper the results of studies carried out in the course of this revision on the morphology and development of the inflorescences are described and their significance is discussed. Other characters that have been found to be of importance at the generic level, namely, seed structure and germination, shoot morphology and leaf anatomy are then considered. Reference is made as necessary to the work of earlier authors, but fuller historical accounts will be found under each genus. Before entering on the more detailed discussions a summary follows of the characters of these four genera, with their resemblances and differences as established in this survey, and a brief review of their position within the Moraceae.

The genera included in this study have condensed, unisexual, usually many-flowered, axillary inflorescences. (In *Parartocarpus* occasional abnormal inflorescences are bisexual.) The flowers are sessile upon or sunken into a pulvinate, globose, or cylindric, fleshy receptacle bearing interfloral (*Prainea* and *Artocarpus*) or involucral (*Parartocarpus* and *Hullettia*) bracts, the (upper) surface of the receptacle being completely covered. They have no rudiments of the organs of the opposite sex. The stamens or ovaries are enclosed in tubular or 2–4-lobed or -partite perianths (*Prainea* and *Artocarpus*) which may fuse partially or completely to form a syncarpium (*Artocarpus*), or they are sunken in cavities in the receptacle (*Parartocarpus* and *Hullettia*). If the latter, the anthers or styles are exserted either between indurated processes covering the surface and (?) representing perianths (*Parartocarpus*), or through simple perforations in the naked receptacle (*Hullettia*). The male flower has one (*Prainea* and *Artocarpus*), two (*Hullettia*) or up to three (*Parartocarpus*) stamens, which are erect in bud, and the female flower has a unilocular ovary with a pendulous ovule and a simple or bifid style. The seeds and embryos are large with little or no endosperm and no period of dormancy. The embryo has either equal or unequal, appressed cotyledons, and is straight (*Prainea*, *Artocarpus* and *Hullettia*) or curved, the cotyledons being folded just above the base and incumbent (*Parartocarpus*). Germination (otherwise unknown) is hypogeal in *Artocarpus* and epigeal in *Parartocarpus*. The leaves are penninerved (except in *Artocarpus altissimus*) with microscopic epidermal gland-hairs providing characters of taxonomic value and (in *Prainea* and *Artocarpus* subg. *Artocarpus*) resin-containing cells in the mesophyll. They are spirally (*Artocarpus* subg. *Artocarpus*, *Parartocarpus* and *Hullettia*) or alternately and distichously (*Prainea* and *Artocarpus* subg. *Pseudojaca*) arranged with paired or (in *Parartocarpus*) single stipules enclosing the terminal bud (amplexicaul in *Artocarpus* subg. *Artocarpus*, acicular in *Hullettia*).

From this brief account the more important distinguishing characters of the genera may be derived. In *Prainea* and *Artocarpus* the stamens and ovaries are enclosed by perianths, usually mixed with interfloral bracts, and a clearly differentiated involucre is lacking. The embryo is straight, or nearly so, and in *Artocarpus* germination is hypogeal, with no elongation of the hypocotyl. The primary difference between the genera is that in *Prainea* the perianths in the female inflorescence remain free, but in *Artocarpus* they are fused with each other to form a syncarpium, though the fusion usually occurs only in the superficial layer, leaving the perianths free at the level of the ovary. The subgenera of *Artocarpus* can be distinguished from each other and from *Prainea* by the characters of the shoot. In *Artocarpus* subg. *Artocarpus* the leaves are spirally arranged on the shoot with large amplexicaul stipules leaving annulate scars, while in subg. *Pseudojaca* and *Prainea* they are alternate and distichous with small lateral stipules; but the epidermal gland-hairs of *Prainea* and *Artocarpus* subg. *Artocarpus* have multicellular heads and the mesophyll contains resin-cells, while in *Artocarpus* subg. *Pseudojaca* the heads of the gland-hairs are usually unicellular and the mesophyll lacks resin-cells.

In *Parartocarpus* and *Hullettia* the stamens and ovaries are enclosed in cavities of the receptacle, the walls of which have been shown in the former to be intercalary in origin, and there is a well developed involucre of bracts which are basal in *Parartocarpus* and vary to an equatorial position in *Hullettia*. In *Parartocarpus* the embryo is curved, having the appressed cotyledons folded just above the base and incumbent, and germination is epigeal, the hypocotyl elongating markedly and carrying the cotyledons well above the ground, where they separate and become green. In this genus the surface of the inflorescence is armoured from indurated processes some of which are fused basally around the openings to the cavities in the receptacle. This suggests that they represent perianth segments, but their similarity to the interfloral bracts of the allied but less reduced African genus *Treculia* indicates that they may be derived from the latter. In *Hullettia* the fleshy receptacle is naked and both perianths and interfloral bracts appear to be completely absent. The shoot has spirally arranged leaves in both genera, but in *Parartocarpus* each leaf has a single triangular, intrapetiolar, non-amplexicaul stipule (distinguishing the genus from species of *Artocarpus* subg. *Artocarpus* in which the syncarpium is superficially similar), whereas in *Hullettia* the stipules are paired, lateral and acicular.

Within the subfamily Artocarpoideae of the Moraceae, which is characterized by the erect position of the stamens in bud and the pendulous ovule (compared with incurved stamens in the Moroideae and the erect ovule of the Conocephaloideae), these four genera, together with *Treculia*, represent the Old World members of the tribe Euartocarpeae of Bentham and Hooker (now to be written as Artocarpeae).[3] These authors also included *Cudrania*, which should have been assigned to the Moroideae and will not be considered further, and *Balanostreblus*, which has been shown (Jarrett, 1958) to be based on a species of the South American genus *Sorocea* introduced into the Botanic Garden, Calcutta.

The classification of the Moraceae is still fundamentally that of Bentham and Hooker (1880) and it may be in some need of revision, since the New World genera of the Artocarpeae do not appear to be closely related to those of the Old World. However, the latter form a fairly well-defined group, characterized by capitate, many-flowered inflorescences in which the flowers completely cover the surface of the receptacle (i.e., without the naked strips found in some American genera), and in which there were probably originally both interfloral bracts and a basal involucre. *Treculia*, which is the least reduced genus, is the only one to have both interfloral and involucral bracts well developed, as well as perianths enclosing stamens and ovaries. There is also a rudiment of the ovary in the male flower. It is allied with *Parartocarpus* by the presence of an involucre and the orientation of the embryo. Nevertheless, it must be realized that there is nothing except general similarity to justify the classification of *Prainea* and *Artocarpus* with *Treculia, Parartocarpus* and *Hullettia*; the superficial resemblance of the syncarp in *Artocarpus* and *Parartocarpus* is due to parallel evolution.

The study of this group was suggested to me by Mr. E. J. H. Corner, and was carried out under his guidance at the Botany School, Cambridge, England. I should like to record my grateful appreciation of Mr. Corner's continued and stimulating interest in the research and I am further indebted to him for the use of his notes made in Malaya on field characters and details of seed structure and germination. In addition, numerous specimens of inflorescences preserved in alcohol, which had been collected by him, were loaned for study from the Botanic Gardens, Singapore. These, together with preserved material sent from Kebun Raya, Bogor, Indonesia, and by Mr. T. B. Worthington, Peradeniya, Ceylon, and Mr. G. R. Proctor, Science Museum, the Institute of Jamaica, Kingston, Jamaica, were of great value in studying the structure of the inflorescences. Mr. Chew Wee Lek, now at the Botany School, Cambridge, also generously made available to me inflorescences and young seedlings of *Treculia africana* Decaisne ex Trécul preserved in alcohol which he had collected in Singapore. Seeds of various species of *Artocarpus* were kindly sent for germination by the director of the Botanic Gardens, Singapore.

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[3] Actually *subtribe* Euartocarpeae of *tribe* Artocarpeae of Bentham and Hooker, but the ranks and suffixes of these subdivisions have been altered to accord with the modern practice of treating their "Urticaceae" as consisting of the Ulmaceae, Moraceae, Cannabinaceae and Urticaceae (s.s.).

The material which has been examined in the course of this revision is that in the following herbaria:

Arnold Arboretum, Harvard University, Cambridge, Mass. (A)
British Museum (Natural History), London, England. (BM)
Herbarium Bogoriense, Bogor, Java, Indonesia. (BO)
Botanical Museum and Herbarium, Copenhagen, Denmark. (C)
Indian Botanic Garden, Calcutta, India. (CAL)
Botany School, University of Cambridge, England. (CGE)
Forest Research Institute and Colleges, Dehra Dun, India. (DD)
Herbarium Universitatis Florentinae, Firenze, Italy. (FI)
Gray Herbarium, Harvard University, Cambridge, Mass. (GH)
The Herbarium, Royal Botanic Gardens, Kew, England. (K)
Rijksherbarium, Leiden, Netherlands. (L)
New York Botanical Garden, New York. (NY)
Muséum National d'Histoire Naturelle, Laboratoire de Phanérogamie, Paris. (P)
Philippine National Herbarium, Manila, Philippines. (PNH)
Sarawak Museum, Kuching, Sarawak. (SAR)
Herbarium of the Botanic Gardens, Singapore. (SING)
Botanical Museum and Herbarium, Utrecht, Netherlands. (U)
U. S. National Museum (Department of Botany), Smithsonian Institution, Washington, D. C. (US)

Thanks are due to the directors and staffs of these institutions for the loan of material and also for hospitality at the British Museum (Natural History), The Herbarium, Kew, the Rijksherbarium, Leiden, the Muséum d'Histoire Naturelle, Paris, and the Botanical Museum and Herbarium, Utrecht.

The work on which this revision is based was carried out during the tenure of a Maintenance Grant from the Department of Scientific and Industrial Research, the Frank Smart Studentship for Research in Botany in the University of Cambridge, and a Caroline Turle Scholarship of Newnham College, Cambridge. A grant was also made by Newnham College toward the expenses of a visit to Leiden and Paris during March and April, 1955. Grateful acknowledgment is made for this support.

MORPHOLOGY AND DEVELOPMENT OF THE INFLORESCENCES

The morphology of the inflorescences in the genera under review has been studied by dissection and sectioning at anthesis and maturity and by examining different stages in the development where suitable material has been available. Material preserved in alcohol has been used as far as possible and has been supplemented by dried inflorescences, expanded by boiling in water, which can be quite suitable for study if they have been dried quickly (being sliced if they are at all large) and protected from insect attack. The development has not been studied previously except for brief observations on cultivated species of *Artocarpus* published by Baillon (1863) and Subba Rao (1940), which will be commented on below.

The arrangement of the inflorescence in the Urticaceae and Moraceae has been established as basically cymose by Bernbeck (1932) who showed that the dorsiventral inflorescences found in this alliance originate in the suppression of apical growth in a mono- or dichasium, the appearance of the primordia of the flowers and their subtending bracts being delayed, so that they arise on a variously shaped cushion of tissue representing the compressed inflorescence axis, or receptacle. He was able to do this both by making comparative studies in one genus (e.g., *Urtica*) showing progressive reduction in the inflorescence, and by analysing the arrangement and order of origin of the primordia in genera exhibiting a dorsiventral inflorescence only. The moraceous genera which Bernbeck studied were *Dorstenia* and *Ficus*: in the former the dichasial arrangement of the earliest primordia on the flattened receptacle was clearly distinguishable, although later this became obscured by the simultaneous origin of many primordia, but in the latter, though the first bracts were arranged cymosely, the flower primordia all appeared almost simultaneously.

It has been observed in the present study that the inflorescence of *Artocarpus incisus* shows a similar degree of reduction, the flower primordia in both male and female heads arising almost simultaneously and in no discernible order. The same phenomenon had earlier been noted for *A. heterophyllus* (as *A. integrifolia*) by Subba Rao (1940) in a paper on the cytology and embryology of this species. In both these species interfloral bracts are lacking, but in others where they are present (e.g., *A. hispidus* and *A. gomezianus* ssp. *zeylanicus*) they arise and mature a little earlier than the flower primordia, though they bear no definite relation to the latter. In the less reduced inflorescence of *Treculia africana*, however, the sympodial arrangement of the first few interfloral bracts is evident. These bracts, like those of most species of *Artocarpus*, terminate in a peltate scale and at the apex of the inflorescence there is always one conspicuously large scale, with a few somewhat smaller ones arranged meridionally and the rest of the surface covered by scales of irregularly decreasing size.

The inflorescences of *Prainea* and *Artocarpus*, on the one hand, and of *Parartocarpus* and *Hullettia*, on the other, have, as has already been indicated, a fundamentally different structure and hence they will be considered independently in the following account. The structure of the inflorescences is illustrated in *figs. 1–4*,[4] the species having been chosen both because they were typical and because, in *Artocarpus hispidus* and *Parartocarpus forbesii*, inflorescences preserved in alcohol were available.

In both male and female inflorescences of *Prainea* the perianths are tubular and free from each other, and are mixed with peltate to spathulate, long-stalked interfloral bracts. The male perianth is perforate or bilobed above and the apex of the female perianth is thick-walled and clavate, with a contracted mouth which is either perforate or very shortly 2–4-lobed. The female inflorescence of *P. papuana* is illustrated in *fig. 1, a–e* and the male inflorescence in *fig. 3, a–c*. As the female inflorescence ripens only

[4] For convenience of reference the figures will be numbered consecutively throughout this series of papers.

those perianths in which seeds are formed enlarge markedly. These become fleshy and appear as conical to globose projections from the general surface of the inflorescence, which is formed by the apices of the unexpanded flowers and the heads of the bracts, giving the typical appearance shown in *fig. 1, c*. Beccari (1902), in recognizing the affinities of *Prainea* with *Artocarpus*, stated that the only difference between the genera lay in the structure of the female inflorescence, but this is only correct with respect to the reproductive organs.

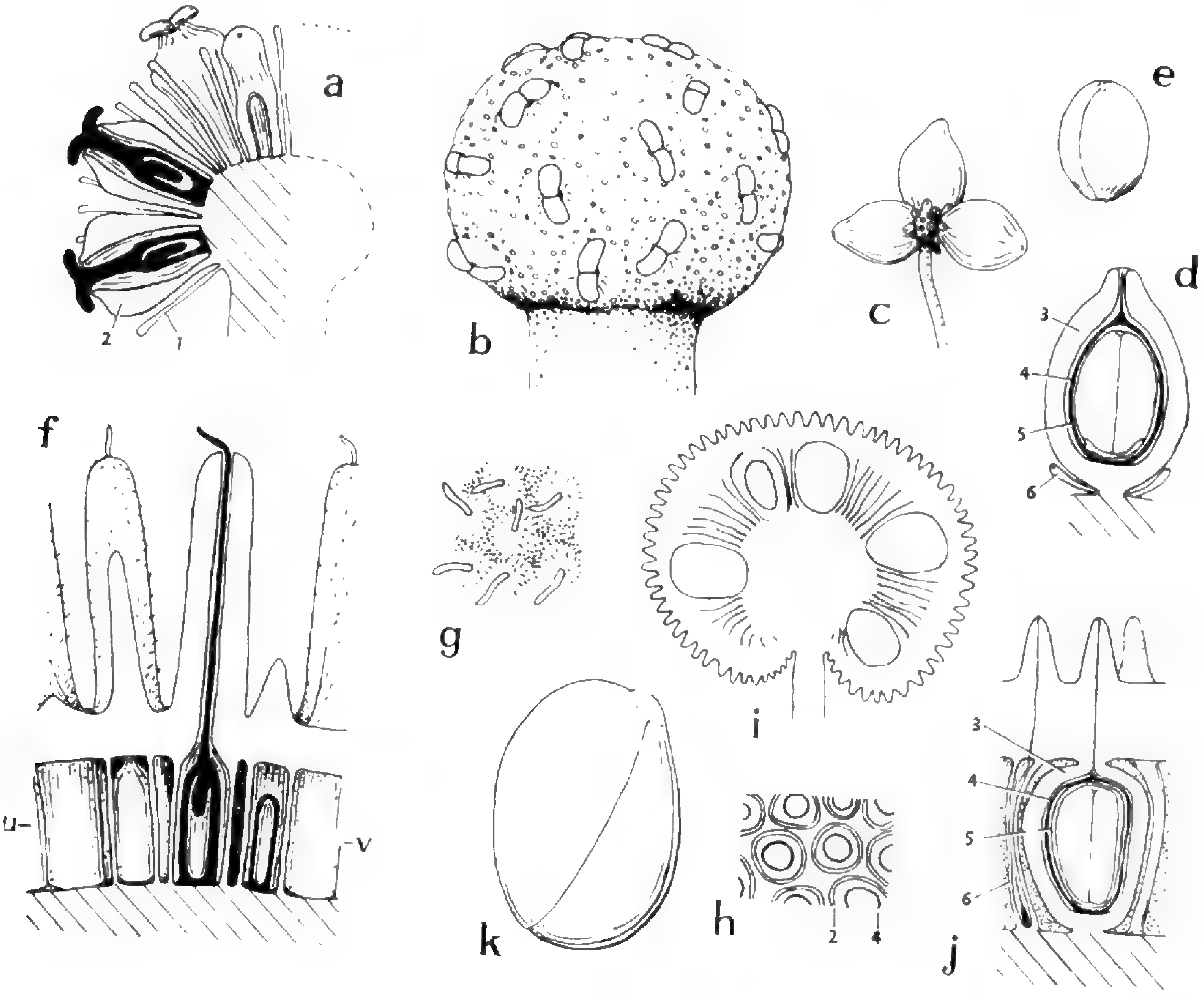

FIG. 1. The female inflorescence in *Prainea* and *Artocarpus*. a–e, *Prainea papuana*: a, b, longitudinal section and entire head at anthesis (× 5); c, mature head (× ½); d, fruiting perianth in longitudinal section (× 1); e, embryo (× 1). f–j, *Artocarpus hispidus*: f–h, longitudinal section, surface view and tangential section in plane u–v at anthesis (× 10); i, longitudinal section at maturity (× ½); j, part of the same (× 1). k, *A. incisus*, embryo (× 1).

Conventions used in *figs. 1–3*: ovaries and stamens are shown in black and receptacular tissue is crosshatched when cut in section. Abbreviations: 1, interfloral bract; 2, perianth; 3, fruiting perianth; 4, ovary; 5, testa; 6, unexpanded perianth; 7, involucral bract.

In the inflorescences of *Artocarpus* the flowers are also usually mixed with interfloral bracts, but these are frequently shed from the syncarp at or before anthesis and in some species they are altogether lacking. The perianths in the male inflorescence are likewise free from each other, varying from tubular to 2–4-partite, but in the female inflorescence the perianths, which are tubular with a contracted and perforate apex, are fused with each other to form the characteristic syncarp from an early stage in development. This fusion is, however, only partial in most species and is of an unusual nature. Each perianth consists of a proximal region which is thin-walled and encloses the ovary, and a distal region with thickened walls and a narrow lumen through which the style passes to the exterior. Proximally the perianths remain free from each other, but distally they are connate, forming a continuous layer evidently capable of withstanding a considerable degree of tension as the syncarp matures. The perianths may

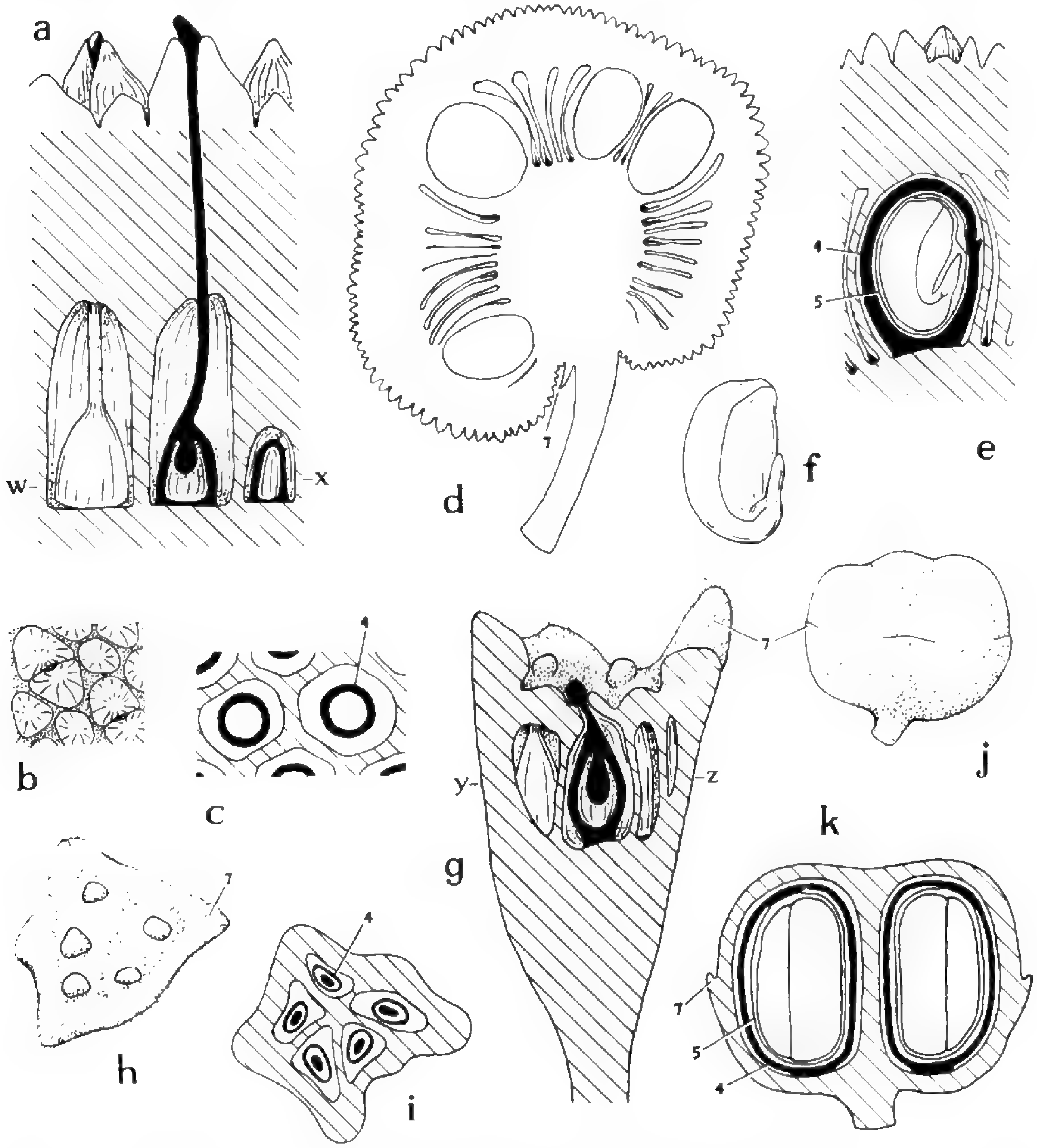

FIG. 2. The female inflorescence in *Parartocarpus* and *Hullettia*. a–f, *Parartocarpus forbesii*: a–c, longitudinal section, surface view and tangential section in plane w–x at anthesis (× 5); d, longitudinal section at maturity (× ½); e, part of the same (× 1); f, embryo (× 1). g–k, *Hullettia dumosa*: g–i, longitudinal section, surface view and tangential section in plane y–z at anthesis (× 5); j, mature head (× ½); k, the same in longitudinal section (× 1, approx.).

be completely fused distally to form a smooth covering layer to the syncarp with perforations through which the styles are exserted at anthesis, or their apices may remain free and project as cylindric, conical or obtuse processes on the surface. In *Artocarpus* (subg. *Artocarpus*) ***hispidus***, which is illustrated in *fig. 1, f–j*, the distal parts of the perianths are not completely fused to each other and the syncarp is echinate from their rigid, free apices. The longitudinal section of the female inflorescence at anthesis in *fig. 1, f* shows one perianth cut sagittally, while those on either side are cut in a tangential plane, and in those on the extreme right and left the proximal region and the free apices are seen in face view, the plane of the section having passed between neighbouring perianths. In contrast to *Prainea* the entire syncarp usually enlarges more or less uniformly although relatively few of the flowers set seed. In the proximal layer, however, where the perianths are free, only those containing seeds enlarge, and the others appear as narrow ribbons in the mature syncarp, as shown in *fig. 1, j*. In this and several other species of subgenus *Artocarpus*, including the Jack (*A.* ***heterophyllus***), the proximal region of the fruiting perianths becomes fleshy and provides the edible portion of the syncarp, in addition to the seeds, which are often roasted, though in the seedless form of the Breadfruit (*A.* ***incisus***) the entire head is eaten.

The syncarp has been examined in nearly all the species of *Artocarpus* subg. *Artocarpus* recognized in this study and the perianths have been found to be consistently free from each other at the level of the ovaries. The same structure is found in many species of subg. *Pseudojaca*, but in others the fusion between perianths is complete, although each perianth may still be distinguishable on the surface as an areole or papilla. In this subgenus the entire syncarp is fleshy and is eaten in a number of species.

It has been possible to examine very young inflorescences of *Artocarpus rigidus*, a species closely allied to *A.* ***hispidus***, and the longitudinal section illustrated in *fig. 4, a* shows that the perianths are at first entirely free from each other. The later fusion must be due to the pressure exerted on each other by the thick-walled distal portions of the very closely set primordia. The thinner-walled proximal portions, having less resistance to pressure, would remain free.

The partial fusion of the perianths was described and illustrated for *Artocarpus heterophyllus* (under the name *Sitodium cauliflorum*) by Gaertner in 1788 and again in 1939 by Corner, writing on this species and on *Artocarpus integer*, but other authors have assumed that the ovaries were embedded in a solid mass of tissue. Nearly all have regarded this tissue as representing the perianths, but Baillon, stated (1863) that the tissue surrounding the ovaries must be axial in origin, on the grounds that the belated fusion of neighbouring parts is very rare, as is indeed the case. He was able to study material of *Artocarpus incisus* preserved in alcohol, but, nevertheless, observing the very young pistils each in the centre of a ring-like emergence, he described them as becoming gradually more deeply sunken in pits of the receptacle and failed to notice the more complex adult structure.

In *Prainea* the male and female inflorescences are more or less globose and are not always easily distinguishable before anthesis, but in *Artocarpus* there is a considerable range of variation especially in the male head, and the two sexes usually differ markedly in size and shape. In neither genus is there a clearly differentiated involucre, although there may be few sessile bracts similar to the interfloral bracts at the base of the head. In *Artocarpus* there may be a slight enlargement of the top of the peduncle and in *A. heterophyllus* this forms a distinct annulus.

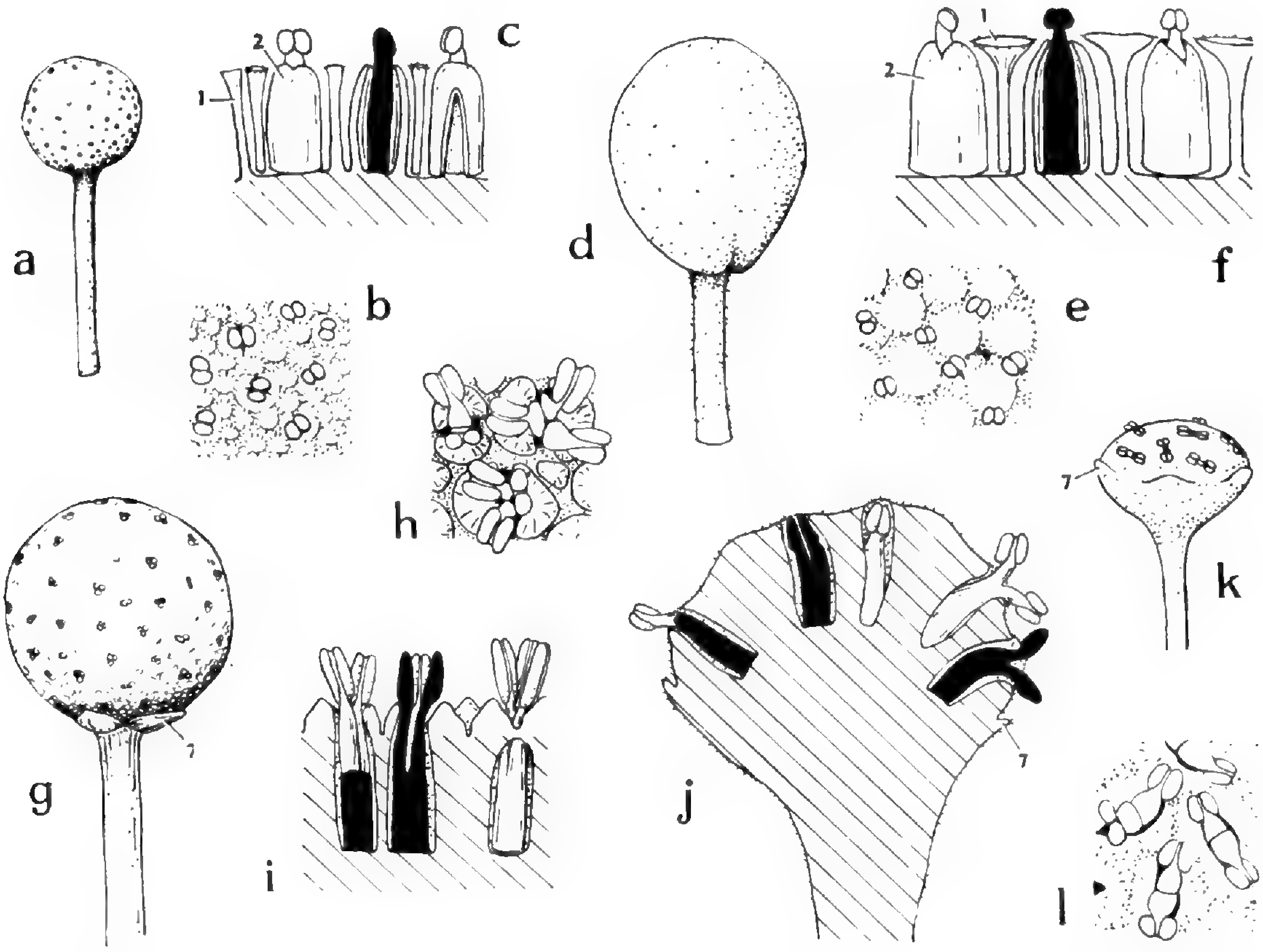

FIG. 3. The male inflorescence. a–c, *Prainea papuana*: a, entire head (× 1); b, c, surface view and longitudinal section (× 5). d–f, *Artocarpus hispidus*: d, entire head (× 1); e, f, surface view and longitudinal section (× 20). g–i, *Parartocarpus forbesii*: g, entire head (× 1); h, i, surface view and longitudinal section (× 5). j–l, *Hullettia griffithiana*: k, entire head (× 2); l, j, surface view and longitudinal section (× 5).

In *Parartocarpus* the inflorescences of the two sexes are similar to each other in structure, with both stamens and ovaries contained in cavities in the apparently continuous tissue of the capitula. Careful examination has revealed no sign of fusion having taken place between neighbouring perianths in the walls separating the cavities and developmental studies show that they are intercalary in origin. Details of the structure in *Parartocarpus forbesii* are shown for the female inflorescence in *fig. 2, a–f* and for the male inflorescence in *fig. 3, g–i*; comparison of the tangential section of the female inflorescence at the level of the ovaries (*fig. 2, c*) with that of *Artocarpus hispidus* (*fig. 1, h*) will show the difference between the syncarps of the genera. The surface of the receptacle in *Parartocarpus* is closely covered by indurated processes, which are acutely conical or spinous in *P. forbesii*. Some are arranged in groups of two to four around the openings of the cavities containing the stamens or ovaries, and are fused basally to each other around the opening. The rest, which are identical in appearance, are free from each other and cover the intervening surface, bearing no relation to a cavity. The processes surrounding the openings are fused to each other only at the base at anthesis, but, since they grow from below, the fusion becomes more marked during the ripening of the syncarp. In spite of its different origin, this syncarp is superficially very similar to that of some species of *Artocarpus* in which the perianth apices are indurated.

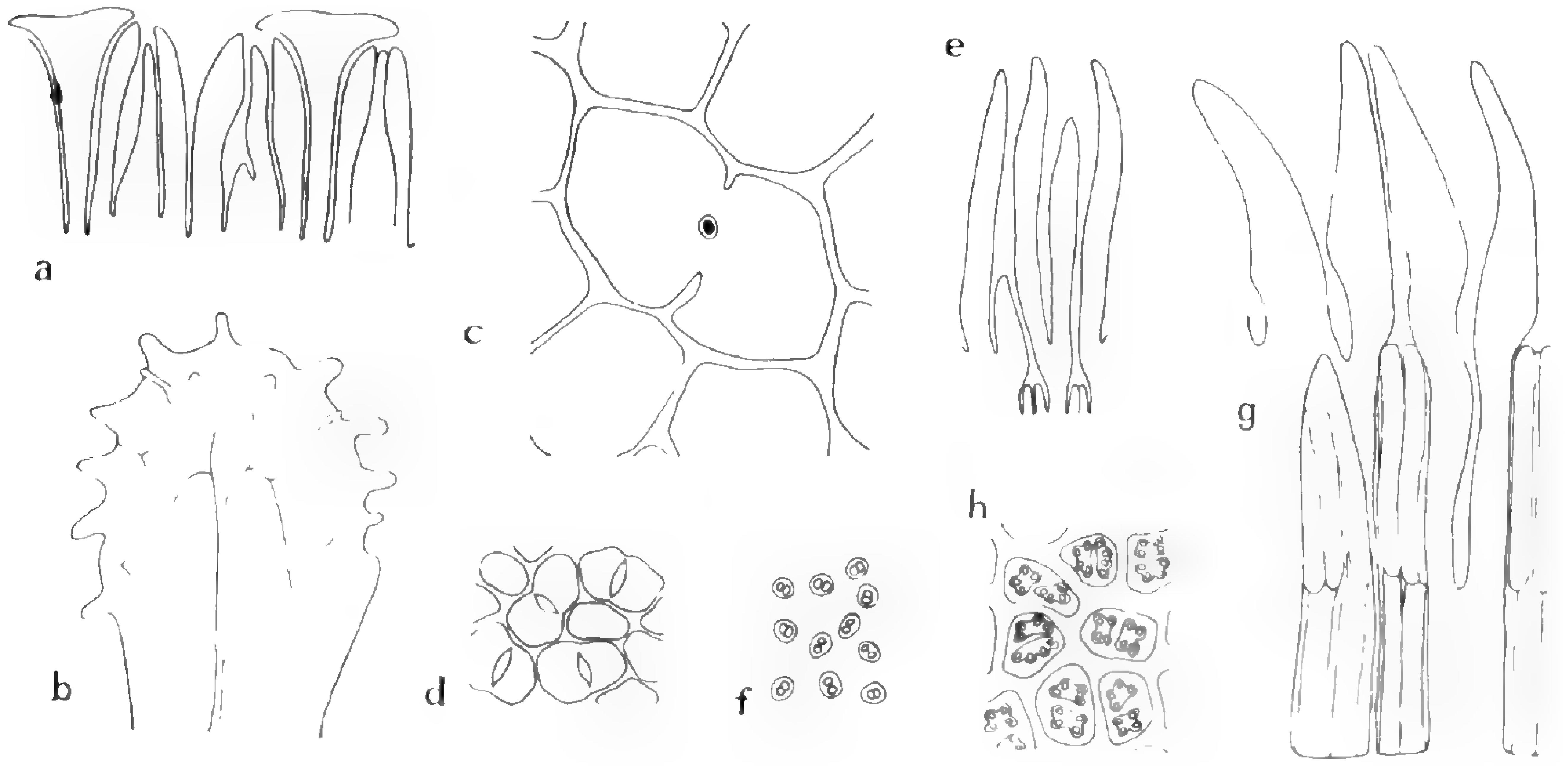

FIG. 4. Details of inflorescence structure. a, b, Longitudinal sections of young female inflorescences in *A. rigidus* (× 12.5) and *A. styracifolius* (× 2.5). c, d, Transverse sections through bases of perianths in female inflorescence of *Parartocarpus venenosus* at anthesis and in male inflorescence of *P. forbesii* before anthesis (× 5). e–h, Development of male head in *Parartocarpus bracteatus*: e, f, longitudinal and tangential sections from head 7 mm. in diameter (× 10); g, h, the same from head 25 mm. in diameter (× 5).

The development of the inflorescences is illustrated by the sections, both longitudinal and tangential at the level of the stamens, through male heads of *Parartocarpus bracteatus* in *fig. 4, e–h*. In this species the processes are spinous and the considerable enlargement of the cavities relative to the processes during their growth is evident on comparison of the figures. In the younger inflorescence (diameter of the head 7 mm.) the stamens are merely finger-like projections, while in the older one (diameter 25 mm.) they are nearly at anthesis. It has not been possible to examine any younger stage but it is probably justifiable to assume that the stamens arise between the processes on the surface of the receptacle and are only later enclosed within cavities. The intercalary origin of the walls is confirmed by the vertical lines of cells that are seen in longitudinal section. The processes are indurated from an early stage in development and can therefore grow only at the base, while they must also enlarge laterally to cover the increasing surface area of the receptacle. It has not been possible to determine whether the processes surrounding each cavity are originally free, or whether they arise from a ring of tissue surrounding the androecium or gynoecium.

Varying opinions have been expressed as to the identity of the processes. In view of the similarity of the "fertile" and "sterile" processes it may be assumed that they are all equivalent; thus they presumably represent either perianths or interfloral bracts. Baillon, who was working with limited material of the male inflorescence, inaccurately stated in the original description of *Parartocarpus beccarianus* (1875) (= *P. venenosus* (Zoll. & Mor.) Becc.) that the stamens were intermingled with stalked bracts (the processes on the surface representing their heads), and hence supposed that the difference between this and the male inflorescence of *Artocarpus* lay in the absence of perianths. Boerlage (1897), who described the same species independently under the name *Gymnartocarpus venenosa* (based on *Artocarpus venenosa* Zollinger & Moritzi) likewise distinguished it from *Artocarpus* by the absence of perianths, but he described the stamens and ovaries correctly as sunken in cavities of the receptacle, regarding the processes alone as representing bracteoles. He failed to observe the fusion of the processes grouped around each cavity, which is not conspicuous in this species, since they are short and often truncate. The fusion is shown in the tangential section through the bases of the processes in *fig. 4, c.* Beccari, in discussing the inflorescence structure of *Artocarpus* and *Parartocarpus* in 1902, was the first to note the fusion of some of the processes in the latter. He considered that they represented the apical lobes of tubular perianths, which were completely fused to each other below, and that the free processes represented the solid apices of sterile perianths. While he realised that the processes thus differed from the tubular perforate perianth apices of *Artocarpus* he did not observe any difference in the internal structure.

Although the fusion of the processes around each cavity indicates that Beccari's interpretation is correct, apart from the fact that the tissue enclosing the stamens and ovaries is intercalary in origin and only the processes themselves can be regarded as representing the perianths (and even in these the base is also intercalary), the allied African genus *Treculia* must here be considered, since its less reduced condition may throw light on the structure of *Parartocarpus.*

In *Treculia africana*, well differentiated perianths, interfloral bracts and basal involucre are all present (illustrated in Engler, 1898, *t. 12–14*). The stalks of the abundant interfloral bracts are fused for about half their length, so that the flowers are enclosed in cavities between them. That this tissue represents the stalks of the bracts is shown by its continuity with the free distal portions of the stalks and the abrupt transition to receptacular tissue below the level of the flowers. In the male inflorescences the flowers consist of (2–)3–4(–5) stamens enclosed in a membranous tubular perianth. In the female inflorescence each ovary may be accompanied by up to four linear perianth segments, and numerous abortive male flowers are also present. In this species each bract is terminated by a peltate scale, but in other species of the same genus the shape of the heads of the bracts is various. In *Treculia zenkeri* Engler (l.c., *t. 15*) the bracts have some peltate and some capitate heads, while in the male head of *Treculia obovoidea* N.E.Br. (as examined in *Zenker 2526*) the bracts terminate in minute spinous processes surrounding the cavities containing the flowers and bluntly conical processes covering the intervening surface. Hutchinson (1917) considered that *Acanthotreculia winkleri* Engler (1908) probably represented the female inflorescence of the latter species and in this the free spinous processes surrounding each emerging style were described as conspicuous and strongly differentiated from the other short and obtuse processes. The processes in both *Treculia zenkeri* and *T. obovoidea* have a general similarity to those on the surface of the inflorescences of *Parartocarpus* and the possibility must be considered that in the latter the bracts have secondarily assumed the function of perianth segments, those surrounding the openings of the receptacular cavities becoming partially fused to give added protection; that perianths containing the stamens and ovaries have been lost; and that walls of intercalary origin enclosing the latter have replaced the stalks of the now sessile bracts.

The inflorescence structure of *Hullettia* is fundamentally similar to that of *Parartocarpus*, although interfloral bracts and perianths are apparently entirely lacking and the fleshy, pubescent receptacle is naked, having perforations in the surface leading to cavities containing either stamens or ovaries. The female inflorescence of *Hullettia dumosa* is illustrated in *fig. 2, g–k* and the male inflorescence of *H. griffithiana* in *fig. 3, j–l.* No material has been available for studies in development, and the homology of the structure with that of *Parartocarpus* is inferred from examination of the inflorescences at anthesis and maturity and from other characters which the genera have in common.

The most immediately obvious of these similarities is that in *Hullettia*, as in *Parartocarpus* and *Treculia*, there is a clearly differentiated involucre. In *Parartocarpus* this consists of three to eight basal bracts which are triangular to ovate and indurated or thickly coriaceous. In *Hullettia* there are three to six fleshy flattened triangular projections which at anthesis are marginal on the obturbinate or pulvinate receptacle and on the subglobose mature syncarp vary from a basal to an equatorial position. In both genera the bracts may be somewhat obscured, especially on the mature syncarp of *Hullettia*. In *Parartocarpus* the inflorescences are globose or nearly so, like those of *Prainea*, and the male and female inflorescences can only be identified before anthesis by dissection, but in *Hullettia* it is only the very young inflorescences that are indistinguishable externally.

Details of the flowers have not been included in this discussion of the generic characters of the inflorescences, but those of the ovary will be considered in the following section. In *Prainea* and *Artocarpus* there is little variation in the male flowers and in distinguishing the species the entire inflorescence is the unit of variation. However, the male perianth in *Artocarpus* subg. *Artocarpus* is nearly always tubular and bilobed above, whereas in subg. *Pseudojaca* it is frequently 2–4-partite, and, in the former, slight differences in the size of the anthers are of some assistance in establishing the subdivisions. There are also small differences in the stamens of the various species of *Parartocarpus* and *Hullettia.*

In conclusion, some aspects of the variability of the inflorescence within *Artocarpus,* which is in marked contrast to its relative uniformity within the other genera, will be commented on. In the syncarp, as in the male inflorescence, there is some overlapping in the characters of the two subgenera, so that they are most readily defined by the characters of the shoot. However, in subgenus *Pseudojaca* the syncarp is always more or less globose, with a surface varying from smooth to tuberculate, but never (except in *A. styracifolius,* discussed below) bearing distinctly elongate processes. In subgenus *Artocarpus,* on the other hand, the syncarp is always covered (at least at anthesis) by distinct processes, except in *A. sepicanus* and *A. kemando,* and in these, as in a majority of the other species, the syncarp is ellipsoid to cylindric.

The variety in the shape of the processes on the syncarp in *Artocarpus* subg. *Artocarpus* is considerable and will be illustrated in a plate accompanying the key to the subgenus. In a few species solid sterile perianths are present with elongate apices projecting markedly beyond those of the fertile perianths; in *A. multifidus, A. elasticus, A. sericicarpus* and *A. tamaran* the dimorphism is complete, but in *A. teysmannii* intermediates occur, all except the longest apices being perforate. This feature has either been unnoticed or its significance has been unrecognized by earlier authors. Elongate sterile perianths also occur in the male inflorescences of the first and last of these species. That these elongate processes represent sterile perianths and not enlarged interfloral bracts is shown by the finding of the latter in the same inflorescences, and by the close similarity of the perforate and solid processes in the syncarp.

In subgenus *Pseudojaca,* on the other hand, the flexuous, solid, terete processes that cover the surface of the syncarp of *A. styracifolius,* and between which the styles emerge through perforations in the surface, appear to be enlarged interfloral bracts. They have a single longitudinal vascular bundle, and in the young syncarp they look very similar to the clavate interfloral bracts found in the male inflorescence. A longitudinal section at this stage is shown in *Fig. 4, b.*

STRUCTURE OF THE SEED AND ITS GERMINATION

These genera are characterized by large seeds which have little or no endosperm and no period of dormancy or ability to withstand desiccation. Differences in the shape and orientation of the embryo and in the mode of germination confirm alliances indicated by the structure of the inflorescences. The ovule is pendulous at anthesis, being attached at or a little below the apex of the ovary, and the style is terminal or nearly so, but in the mature ovary the position of the style and the attachment of the seed vary from apical to sub-basal, owing to differential growth in the walls of the ovary.

In *Prainea papuana*, the only species of the genus of which material was available for detailed study, the style is strictly terminal throughout, but, while at anthesis the ovule is attached laterally slightly below the apex of the ovary, at maturity it is sub-basal. The mature ovary is membranous and the testa is totally absorbed except for a thickened basal saucer-shaped region, at one side of which is the hilum. The embryo, which is illustrated in *fig. 1, e*, is symmetrical, with two equal cotyledons having their long axes parallel to the median plane of the ovary but their appressed faces at an angle of about 45° to it. The radicle and plumule are small and apical.

In *Artocarpus* there is great variation in the ovary and embryo and also in the consistency and relative thickness of the fruiting perianth, ovary and testa. In subgenus *Artocarpus* the terminal or lateral position of the style in the mature ovary delimits two natural groups of species. The seed is attached just below the base of the style and, since the radicle is usually directed approximately at the hilum, in the first group the embryo is longitudinally aligned and the radicle is apical, whereas in the second the long axis of the embryo is more or less oblique and the radicle is ventral. In the first group the appressed faces of the cotyledons are at an angle of 30–90° to the median plane of the ovary and the radicle and plumule are apical and minute so that the appearance of the embryo and its orientation relative to the ovary are similar to *Prainea*, although the hilum is apical instead of sub-basal. In these species the inner wall of the ovary forms a horny endocarp, while the exocarp decays leaving the "seed" free within the proximal region of the perianth which may be thickened and fleshy. In species in which the style is lateral or sub-basal in the mature ovary and the long axis of the embryo is hence more or less oblique, the appressed faces of the cotyledons may be in the median plane of the ovary (in which case the embryo is usually symmetrical), or they may also be oblique or at right angles to the median plane (in which case one cotyledon lies above the other in the seed and is frequently reduced in size). Such an embryo is illustrated in *fig. 1, k*. The variation in this second group will be discussed in more detail in considering the subdivision of subgenus *Artocarpus*. In this group the cotyledonary petioles and the radicle lying between them are relatively well developed and, if the latter is large enough, it is curved downward. The chalaza is always basal, with a conspicuous ventral raphe, so that in the first group the embryo is anatropous, whereas in the second it is campylotropous.

In *Artocarpus* subg. *Pseudojaca* the style is terminal or nearly so and the embryo is longitudinally aligned, with the appressed faces of the equal cotyledons in the median plane of the ovary or at varying angles to it. In some species of this subgenus, also, the seed is enclosed by an indurated endocarp which lies free in the cavity of the perianth at maturity.

The primary difference between the embryo in these genera and in *Parartocarpus* is that in the latter it is folded. The ovary has a terminal style at anthesis, but at maturity it is lateral and the hilum lies just above it. The ovary wall differentiates into a bony endocarp and an exocarp which finally decays. The testa is attached to an indurated hilar plug and is thin-walled, with a relatively small apical vascular cap. The embryo fills it almost completely but, unlike *Artocarpus*, there are distinct remains of the endosperm in the region of the hilum. The markedly unequal cotyledons are appressed to each other and are incumbent, being folded transversely a little above the base so that the large, straight radicle lies along the median line of the inner and smaller cotyledon. The plane of the appressed faces of the cotyledons is longitudinal and at right angles to the median plane of the ovary. The tips of the cotyledons are enclosed in the vascular cap of the testa, which makes a distinct indentation in them, and the radicle lies on the side of the seed facing the style, its tip being directed upward to the hilum and enclosed in a pocket of endosperm. The embryo of *P. forbesii* is shown in *fig. 2, f*. The same type of embryo occurs in *Treculia* (*africana*) and has been illustrated by Trécul (1847) and Engler (1898) (but in *Acanthotreculia* Engler (1908) the embryo is shown with very unequal, straight cotyledons and a small, apical radicle).

The embryo of *Hullettia*, on the other hand, is straight, with equal or slightly unequal cotyledons arranged longitudinally; the small radicle, however, is basal. The ovary is pergamaceous and the testa has a shallow, thickened, apical cap (not shown in *fig. 2, k*) attached centrally, immediately below the subterminal style, and making an indentation in the tips of the cotyledons, but is otherwise thinly membranous. Thus, whereas in *Prainea* and *Artocarpus* the chalazal region is basal, in *Parartocarpus* and *Hullettia* it is apical (relative to the ovary), and since the tips of the cotyledons are in contact with this region, except in some species of *Artocarpus*, the orientation of the embryo with respect to the ovary is also reversed.

It has been possible to study germination in the following species of *Artocarpus*: (subg. *Artocarpus*) *A. rigidus*, *A. integer*, and *A. heterophyllus*, and (subg. *Pseudojaca*) *A. borneensis*. In addition I have been able to use Mr. Corner's notes on germination in *Artocarpus* (subg. *Artocarpus*) *anisophyllus*, *A. lanceifolius* and *A. elasticus* and *Parartocarpus bracteatus* and *P. forbesii*, and to examine herbarium specimens of seedlings of *Artocarpus incisus* and *A. nobilis*.

Germination in *Artocarpus* and *Parartocarpus* differs chiefly in whether or not there is elongation of the hypocotyl. In *Artocarpus* there is no elongation, and germination is hence hypogeal. The cotyledons usually remain enclosed within the testa and the plumule is enabled to emerge from between them by the elongation of their petioles (illustrated for *A. hirsutus* and *A. chaplasha* in Troup, 1921, *figs. 323, 325*). In *A. heterophyllus* (l.c., *fig. 324*, and Gaertner, 1788) and *A. integer*, however, the cotyledons separate to allow the emergence of the plumule. A further variation occurs in subgenus *Artocarpus* in the nature and arrangement of the first leaves borne by the seedling. The first pair subsequent to the seed leaves may be opposite and fully developed and be followed by spirally arranged leaves (*A. anisophyllus*, *A. lanceifolius*, *A. rigidus*, *A. chaplasha*, *A. hirsutus* and *A. nobilis*) or the leaves may be spirally arranged from the first, the youngest being scale leaves (*A. incisus*, *A. heterophyllus*, *A. integer* and *A. elasticus*). The two types correspond, but only approximately, to the species groups distinguished above by the terminal and lateral position, respectively, of the style, and will likewise be discussed in more detail under subgenus *Artocarpus*. In *Artocarpus* subg. *Pseudojaca* the seedling bears scale leaves before the fully developed leaves, as in the second group above, but in *Artocarpus borneensis* (ssp. *griffithii*) these are strictly alternate and distichous from the first. It is not clear from Troup's illustration (l.c., *fig. 326*) of *A. lakoocha* whether the leaves are spirally or distichously arranged. Photographs of seedlings of *A. rigidus* and *A. borneensis* are reproduced in *fig. 5*.

In *Parartocarpus* germination is epigeal and the hypocotyl elongates markedly, carrying the folded cotyledons well above the ground. As they straighten and open out, becoming green and photosynthetic, the endocarp and testa are split off. The plumule grows out from between them and the first pair of leaves is opposite, with paired stipules, but the later leaves are spirally arranged, each with a single stipule. The seedlings of *Treculia africana* show an exactly similar mode of germinaton.

MORPHOLOGY OF THE SHOOT

The morphological characters of the shoot which are of importance in distinguishing the genera under review are principally those provided by the arrangement of the leaves and by the stipules, which enclose the terminal bud and are either intrapetiolar or lateral to the base of the petiole, being paired except in *Parartocarpus*. They are illustrated in *fig. 6*. It is in these characters that the most easily discernible distinctions are to be found between the two subgenera of *Artocarpus*. In subg. *Artocarpus* the leaves are spirally arranged and the stipules are intrapetiolar and amplexicaul, leaving annulate scars, whereas in subg. *Pseudojaca* the leaves are strictly alternate and distichous and the stipules are non-amplexicaul, leaving lateral or partially intrapetiolar scars. The latter arrangement is also found in *Prainea* but the leaves of this genus can usually be recognized by the abruptly and narrowly acuminate apex and the conspicuous and regular inarching of the lateral veins (in addition to details of the anatomy). In *Parartocarpus* the leaves are spirally arranged and in the axil of each is a single non-amplexicaul stipule which forms a scar extending slightly to either side of the petiolar scar. J. J. Smith (1922) was the first author to realize that these stipules were single and not paired. In the seedling, as already mentioned, they may be paired or have a bifid apex, indicating that each has originated from two stipules fused along their intrapetiolar margins. The leaf arrangement, together with the non-amplexicaul stipular scars, distinguishes the genus from both the preceding ones. The leaves of *Hullettia* are also spirally arranged but the stipules

FIG. 5. Seedlings of *Artocarpus*; left, *Artocarpus* (subg. *Artocarpus*) *rigidus*; right, *Artocarpus* (subg. *Pseudojaca*) *borneensis*; insets, details of stipules.

are distinctive, being linear, acute and frequently persistent. They are lateral to the leaf-axils and the scars are small and round.

Differences in the arrangement of the foliage are associated with the two types of phyllotaxy. In the groups with spirally arranged leaves the ultimate shoots and usually also the main branches are ascending. In *Parartocarpus* and *Hullettia* the leaves are markedly clustered at the tips of the shoots and there is greater elongation of the internodes at the base of each lateral branch, so that one leaf cluster is separated from the next.

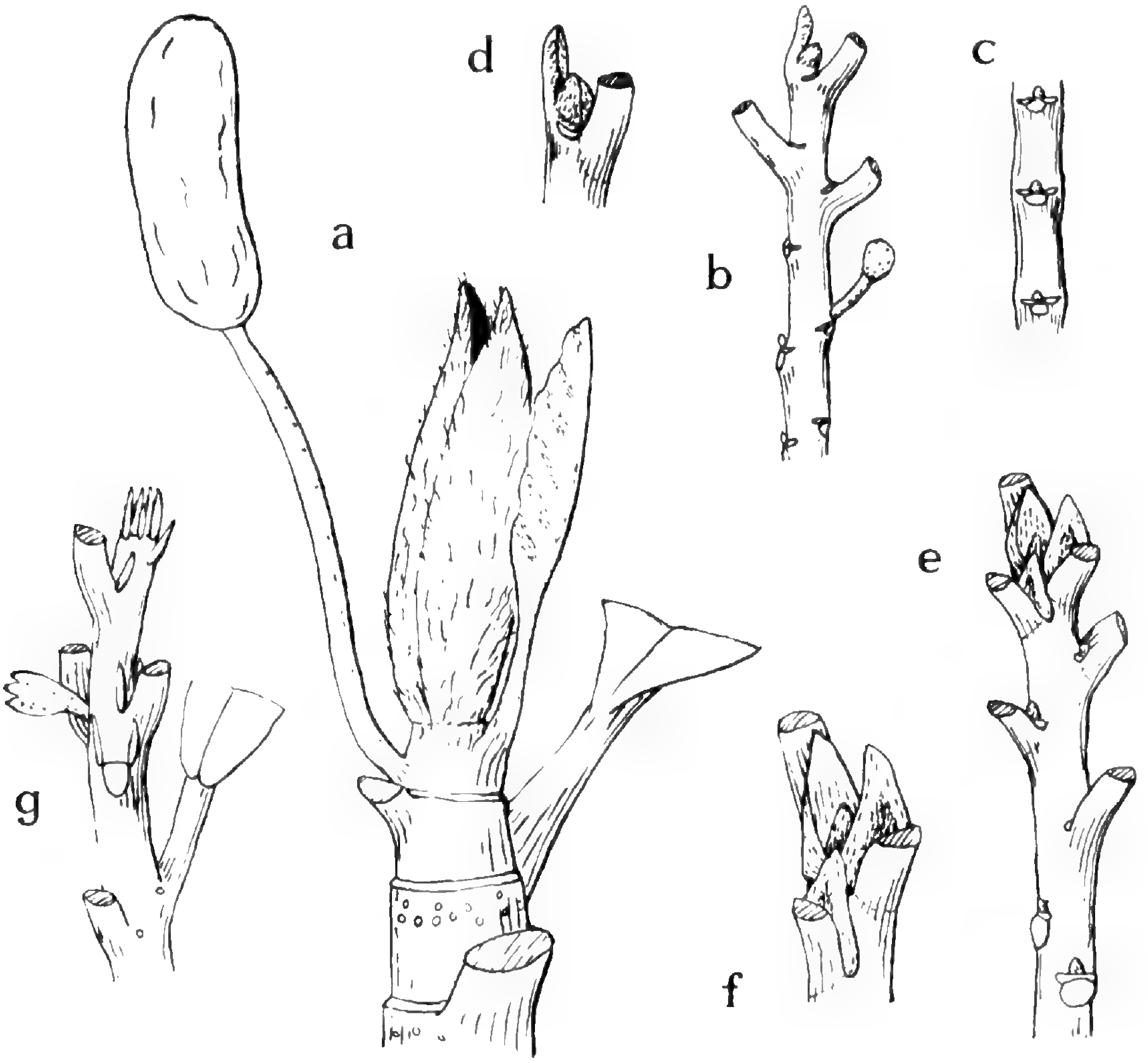

FIG. 6. Details of stipules; a, *Artocarpus sericicarpus* (× 1); b, c, *A. gomezianus* ssp. *zeylanicus* (× 1); d, terminal bud of the same (× 2); e, *Parartocarpus bracteatus* (× 1), f, terminal bud of the same (× 2); g, *Hullettia dumosa* (× 1).

In the groups with alternate leaves, on the other hand, at least the ultimate shoots are more or less applanate. As already mentioned, study of the seedlings of species belonging to both subgenera of *Artocarpus* has shown that the difference in leaf arrangement may exist from the earliest stage.

Leaf form in *Artocarpus* is variable, ranging from simple to pinnatifid. In most species the adult leaf is simple, but in one group within subg.

Artocarpus it is frequently pinnatifid, while in another species, *A. anisophyllus*, it is pinnate. In many other species of this subgenus the juvenile leaves are more or less pinnatifid and sometimes very large — to six feet in length in *A. elasticus* (Corner, 1940). *Artocarpus tamaran* is remarkable in having a nearly pinnate juvenile leaf, distinguished from that of *A. anisophyllus* by a continuous wing of lamina along the rachis. In some species of subg. *Pseudojaca* the juvenile leaves are irregularly pinnatifid or the lamina may be reduced to a sinuous wing along the midrib, but in the rest, as in the other genera, the leaf is always entire and the juvenile leaf is merely elongate. Juvenile leaf-forms are shown in *fig. 7*. As noted by Corner (1940) the pinnate leaves of *Artocarpus anisophyllus* are unusual in falling as a whole instead of disarticulating at the base of each pinna.

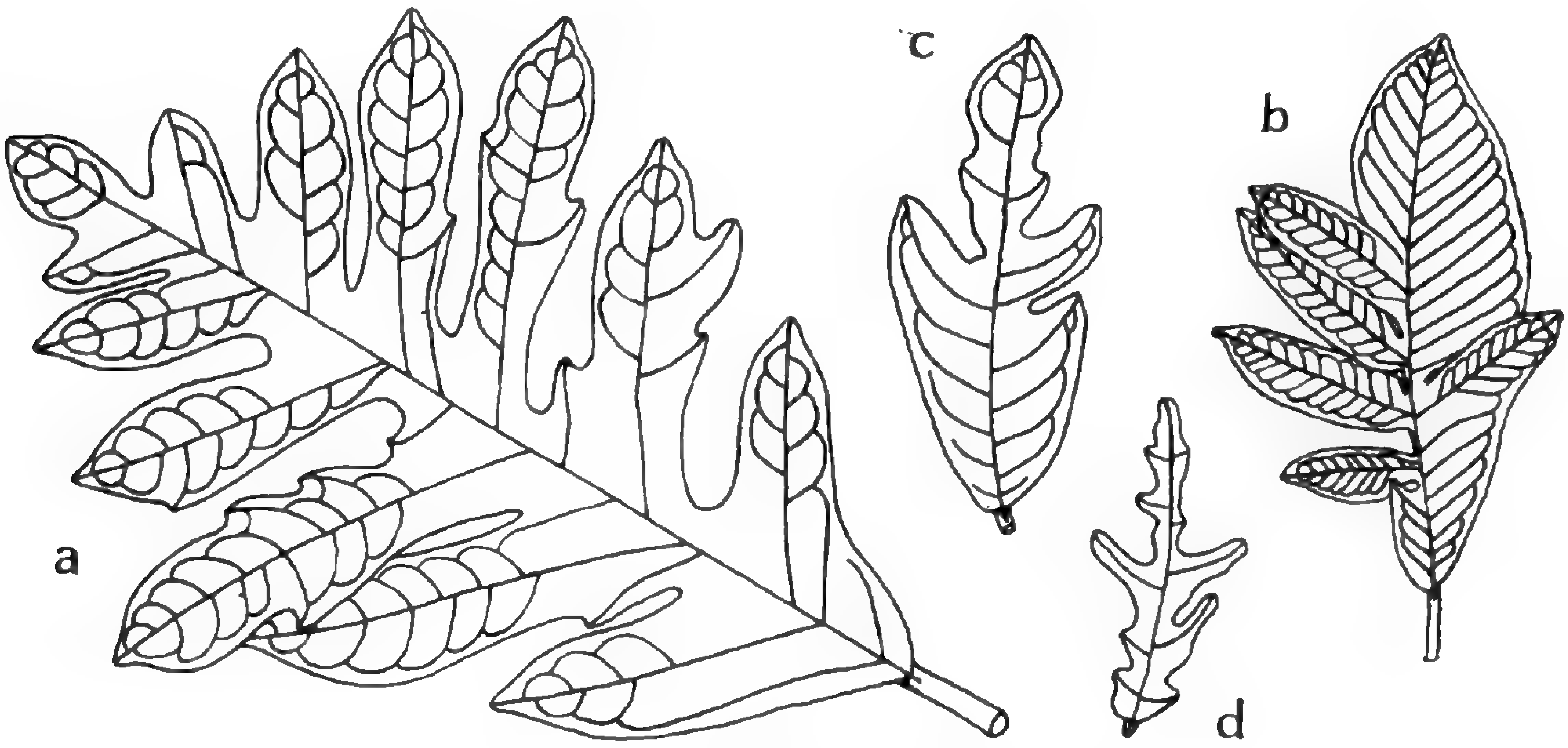

FIG. 7. Juvenile leaves in *Artocarpus*; a, *A. odoratissimus*; b, *A. tamaran*; c, d, *A. dadah* (× 1/7).

In the field *Artocarpus* and *Parartocarpus* are easily distinguished by characters of the bark. In *Artocarpus* the bark on the roots is red and that on the trunk peels off in flakes. In *Parartocarpus* the bark of the roots is yellow, while the trunk is covered by numerous large and prominent lenticels (conspicuous in the photograph in Browne, 1955).

LEAF ANATOMY

A detailed account of the leaf anatomy of the Artocarpoideae and Conocephaloideae was published by Renner in 1907. From this it may be concluded that the most important anatomical characters distinguishing the genera under consideration are those of the microscopic glandular epidermal hairs and of the spongy mesophyll. Renner considered that the fact that leaf anatomy of *Prainea* was in some ways intermediate to that of the two subgenera of *Artocarpus* necessitated the unification of the two genera, but this view is here rejected as a misinterpretation of the vegetative characters.

Renner's observations have been repeated in the course of this revision and expanded to cover all the species here recognized. They have in general been confirmed, but in the following discussion a few points of disagreement are indicated. The leaves were examined by means of surface and transverse sections cut from fragments of herbarium specimens boiled up in water, or from material preserved in alcohol when available. The sections were mounted in a solution of polyvinyl alcohol and lactic acid (Metcalfe and Richardson, 1950).

In addition to normal epidermal hairs the Artocarpoideae have gland-hairs on or sunken into the surface of the leaf, with a unicellular stalk and a variously shaped head. Renner stated that he was unable to find any anatomical characters distinguishing the tribes of the Artocarpoideae, but this may have been due in part to the fact that some genera were misplaced or studied from misidentified specimens. However, the Old World genera of Artocarpeae do show a wide range of variation in the gland-hairs, especially within the genus *Artocarpus.*

In *Prainea* and *Artocarpus* subg. *Artocarpus* the heads of the gland-hairs are 4–16-celled with a thick-walled stalk. In the former they are always and in the latter they are frequently sunken in pits in the epidermis. In *Prainea* the heads are depressed-globose and divided by vertical and horizontal walls into four to eight cells. In *Artocarpus* subg. *Artocarpus* the heads are either globose or depressed-globose with one or two tiers (rarely four) of four to six cells, or they are flattened and peltate with eight or rarely sixteen cells. An account of the gland-hairs is included in each specific description for this subgenus. In several species there is a hypodermis of cells which are either isodiametric or elongate in surface view. Both the gland-hairs and the hypodermis provide characters of taxonomic value and will be discussed further in considering the classification of the species of the subgenus.

In most species of *Artocarpus* subg. *Pseudojaca,* on the other hand, the gland-hairs have a unicellular globose head and a thin-walled stalk. Renner found the head to be 2–4-celled in *Artocarpus lakoocha* and in this study it also has been found to be 1–6-celled in *A. tonkinensis.* The gland-hairs of *Parartocarpus* likewise have a thin-walled stalk and a unicellular head, but the latter is markedly elongate and thus cylindric. In *Hullettia,* which was omitted by Renner as being of doubtful affinities, the gland-hairs have a thick-walled stalk and a globose unicellular head. According to Renner the gland-hairs of *Treculia* have an elongate head often divided by a longitudinal wall. In none of these are the gland-hairs sunken, except for a few species of *Artocarpus* subg. *Pseudojaca* in which they are only slightly so, and in none is there a hypodermis.

In the characters of the spongy mesophyll the two subgenera of *Artocarpus* again differ widely, while *Prainea* occupies a somewhat intermediate position. All the genera being studied have a bifacial leaf with one or two rows of palisade cells, and a well developed spongy mesophyll. This is more or less compact in *Artocarpus* subg. *Pseudojaca, Parartocarpus* and *Hullettia,* but in *Artocarpus* subg. *Artocarpus* it is extremely loose, consisting of a mesh of long-armed ("hyphenartig") cells and including some conspicuous ellipsoid or globose cells with resinous contents. The resin cells are absent in *A. heterophyllus* and *A. integer*, but not, as stated by Renner, in *A. odoratissimus* (as *A. mutabilis* Becc.). In *Prainea* the spongy mesophyll is rather loose with relatively large cells nearly all having slightly resinous contents.

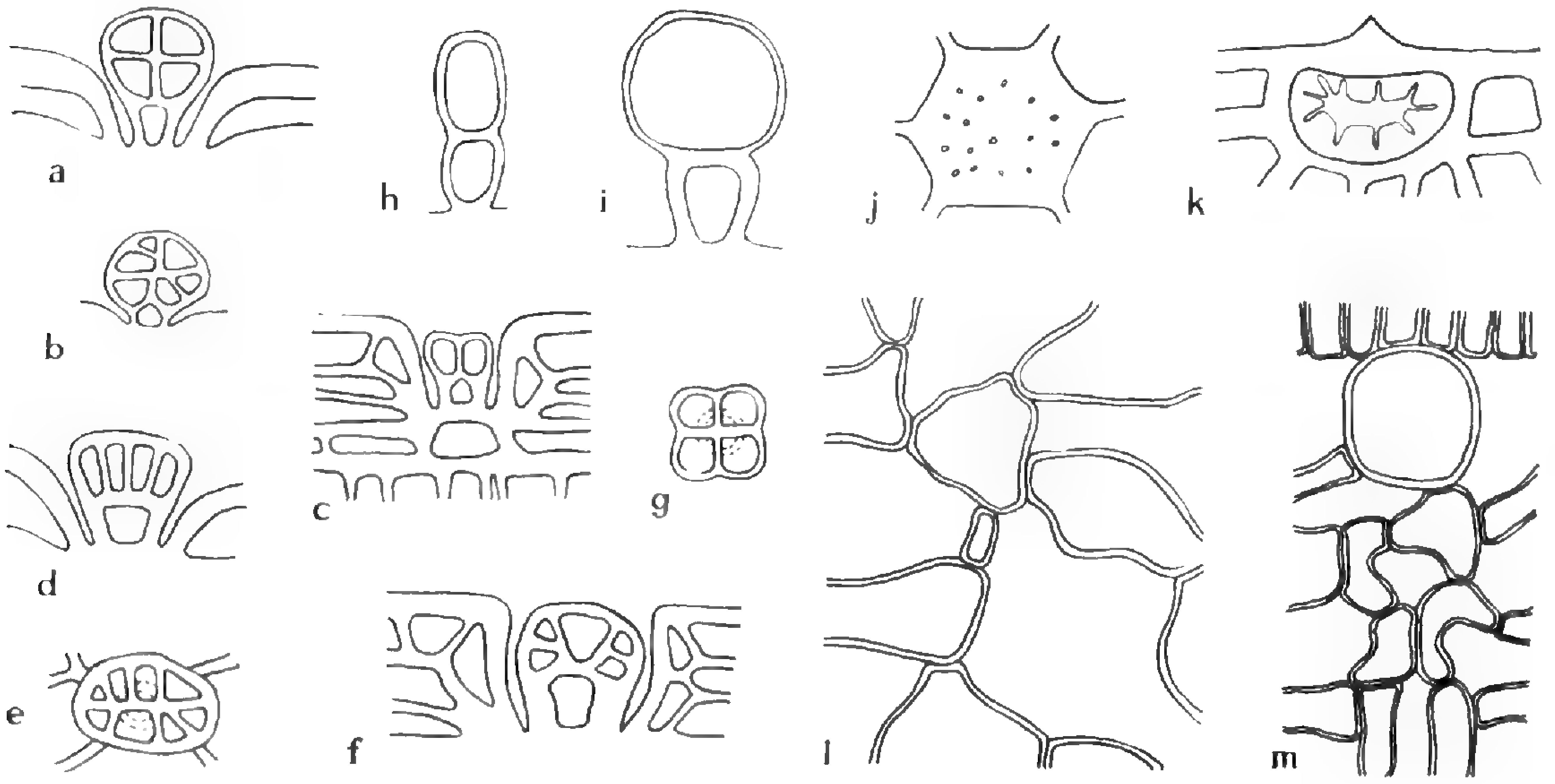

FIG. 8. Details of leaf anatomy. a–i, Epidermal glands: a–c, *Prainea limpato*, *Artocarpus odoratissimus* and *A. lanceifolius* in longitudinal section (the last also showing hypodermis); d, e, *A. treculianus* in longitudinal section and surface view; f, *A. integer* in longitudinal section; g, *A. sericicarpus* in surface view; h, i, *Parartocarpus venenosus* and *Hullettia dumosa* in longitudinal section. j, k, Enlarged epidermal cells in *Hullettia dumosa* in surface view and longitudinal section. l, m, Spongy mesophyll in *Prainea frutescens* and *Artocarpus rigidus* in longitudinal section (the latter showing resin cell in contact with palisade tissue) (× 200, approx.).

On the grounds that, firstly, *Prainea* showed more similarity in anatomical structure to *Artocarpus* subg. *Artocarpus* than the latter did to subg. *Pseudojaca*, and that, secondly, according to Beccari (1902) the only difference between the genera lay in the free or fused female perianths, Renner treated all three groups as sections under *Artocarpus*. However, the mesophyll of *Prainea* could well be regarded as a type from which the two subgenera of *Artocarpus* have diverged, while subg. *Artocarpus* and subg. *Pseudojaca* may show an advance and a reduction respectively in the development of the gland-hairs. In leaf and stipular arrangement *Prainea* resembles *Artocarpus* subg. *Pseudojaca*. The interrelations between the three groups thus appear reticulate, indicating that parallel evolution has occurred. This is least likely to have occurred in the unique sycarpium of *Artocarpus* and most probable in the development of distichous leaves and non-amplexicaul stipules. It is therefore concluded that *Prainea* and *Artocarpus* should be retained as distinct genera and that the anatomical characters of the latter have probably arisen by divergence from a common ancestor with *Prainea*. The anatomical characters, in conjunction with the difference in leaf and stipular arrangement, provide the best evidence that the subgenera of *Artocarpus* represent natural groups.

In their indumentum (apart from the gland-hairs) all the genera are variable, except for *Prainea*, in which the leaves are glabrous. The hairs frequently have enlarged bases and papillate walls, though, as was noted by Renner, there may be a few hairs with hooked tips and these are always smooth walled. In *Prainea* there are likewise enlarged cells in the epidermis which may be produced into a very short point. In *Artocarpus* the hairs are usually restricted to the veins, but in some species of subg. *Pseudojaca* nearly all the cells of the areolae grow out to form thin-walled, often crisped hairs, so that the lower surface appears greyish-glaucous from the minute tomentum. In *Hullettia* there are numerous enlarged cells with strongly thickened and narrowly pitted walls in the lower epidermis, which bear hairs of varying length and cause the lower surface to appear minutely punctate under a lens.

GENERAL CONCLUSIONS

The conclusions reached in the foregoing discussion are summarized below in the order in which the characters were taken up.

The inflorescences of *Prainea* and *Artocarpus* are covered by well developed perianths enclosing the stamens and ovaries and mixed with interfloral bracts, but they lack a clearly differentiated involucre. In the female inflorescence of *Artocarpus* the perianths are fused to form a syncarpium. Dissection shows that the proximal portions of the perianths, enclosing the ovaries, usually remain free, while the distal portions fuse, either completely or leaving the apices free, to form an external wall. The perianths have been found to be completely free in the very young inflorescence. In some species (in subg. *Pseudojaca*) the fusion between the perianths is complete, but it is assumed that the structure of the syncarp is homologous.

In *Parartocarpus* the stamens and ovaries are sunken in cavities which are described as receptacular, and have been shown to be separated by walls that are largely if not entirely of intercalary origin. The surface of the receptacle is covered by indurated, spinous, conical or truncate processes that may represent either perianth segments fused basally around the opening of each cavity and solid sterile perianths between these, or secondarily modified interfloral bracts, taking into account the less reduced structure of the related African genus *Treculia*. In *Treculia* perianths are present (tubular in the male, and of linear segments in the female) and are sunken with the stamens of ovaries between the fused stalks of interfloral bracts, the heads of which somewhat resemble the processes in *Parartocarpus*. In both these genera there is a well developed basal involucre. The ovule has been found to be pendulous rather than basal in *Hullettia* and the genus is therefore removed from the Conocephaloideae to the Artocarpoideae. The stamens and ovaries are apparently enclosed in cavities as in *Parartocarpus* and there is an involucre of fleshy bracts. It is assumed that the structure of the receptacle is homologous, and that the surface is naked, perianths and interfloral bracts being absent.

The orientation of the embryo and the mode of germination confirm the above alliances. In *Prainea* and *Artocarpus* the embryo is straight (or nearly so) and germination in the latter is hypogeal. In *Parartocarpus* and *Treculia* the embryo is curved, with folded incumbent cotyledons, and germination is epigeal. The embryo of *Hullettia* resembles that of *Parartocarpus* in its orientation but is straight.

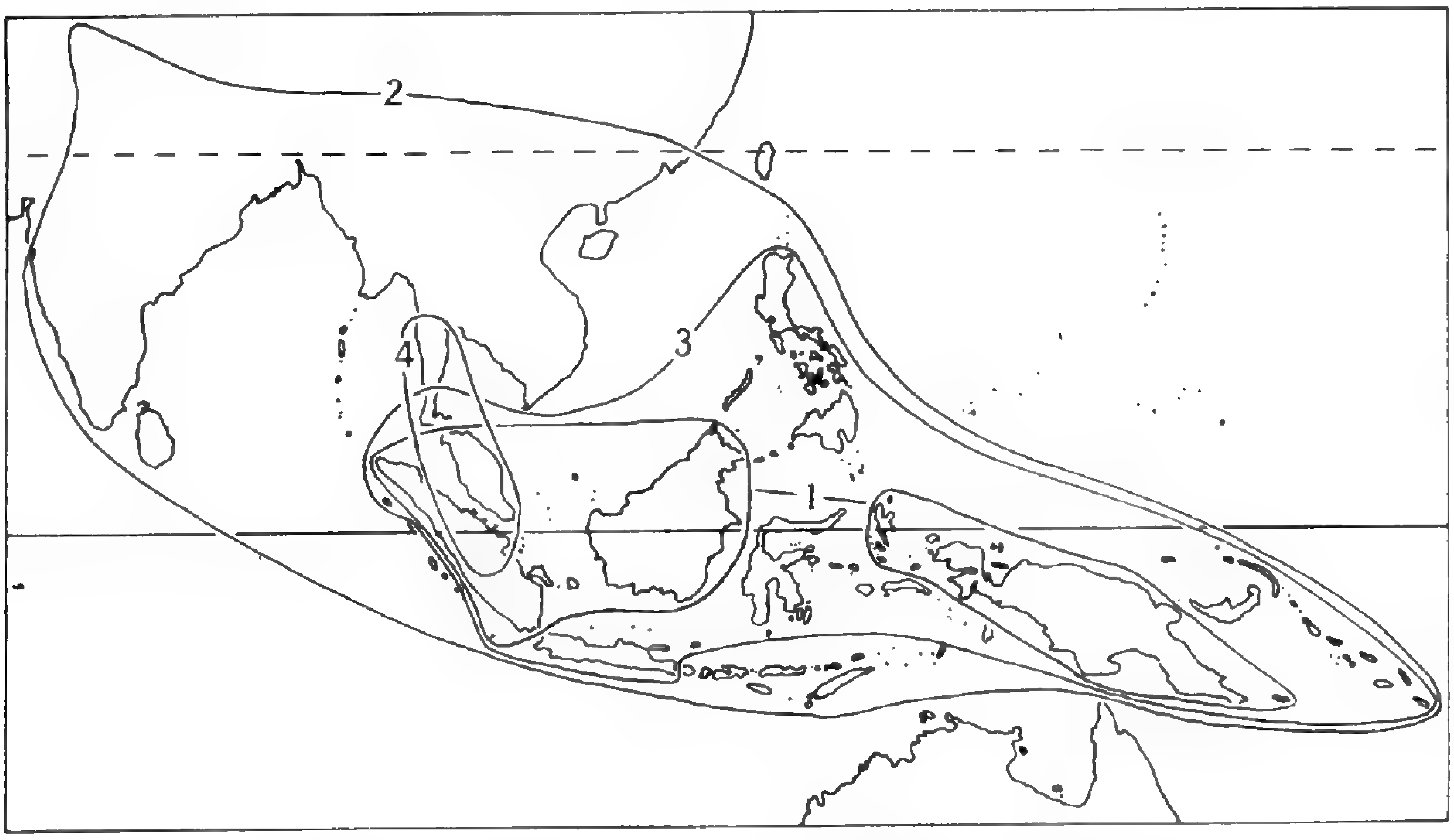

FIG. 9. Distribution of the genera. 1, *Prainea*; 2, *Artocarpus*; 3, *Parartocarpus*; 4, *Hullettia*.

The arrangement of the leaves and stipules serves to distinguish *Parartocarpus* and *Hullettia* from each other, and also from *Prainea* and *Artocarpus*. In the last genus this character readily defines two natural subgenera, *Artocarpus* and *Pseudojaca*, further differentiated by details of the glandular epidermal hairs and the spongy mesophyll which also separate them from *Prainea*. Renner's observations (1907) on leaf anatomy have been expanded and confirmed but his reduction of *Prainea* to the status of a section under *Artocarpus* is not upheld. In vegetative characters the interrelations between the three groups are reticulate, but these indicate the occurrence of parallel evolution and the differences in the female inflorescences override them.

Prainea, Artocarpus, Parartocarpus and *Hullettia*, together with *Treculia*, form a group of genera united by their condensed capitate inflorescences and large embryos. *Prainea* and *Artocarpus* are closely related to each other, while *Treculia, Parartocarpus* and *Hullettia* form a less closely allied series, both groups showing increasing reduction of the inflorescences. Whether these genera together form a natural group within the Moraceae cannot be certain until an up-to-date revision of the entire family has been carried out, but, from a review of the other Old World genera, it seems probable. The syncarpia of *Artocarpus* and *Parartocarpus* are striking examples of parallel evolution. These two genera and *Hullettia* each represent a highly specialized evolutionary end-point, though reflecting a general tendency for the female inflorescence to become a syncarpium having the ovaries enclosed in either floral or axial tissue.

KEYS TO THE OLD WORLD GENERA OF THE ARTOCARPEAE

NATURAL KEY

1. Inflorescences without an involucre; embryo straight.
    2. Female perianths free, only fruiting perianths enlarging and projecting beyond surface of mature head; leaves alternate and distichous; stipules and scars lateral or partially intrapetiolar; gland-hairs with 4–8-celled head; mesophyll loose, cell-contents resinous. . . . 1. *Prainea.*
    2. Female perianths fused to form a syncarp; entire head enlarging at maturity. . . . . 2. *Artocarpus.*
        3. Leaves spirally arranged; stipules amplexicaul, scars annulate; gland-hairs with 4–16-celled head; mesophyll long-armed with globose or ellipsoid resin-cells. . . . . Subgenus *Artocarpus.*
        3. Leaves alternate and distichous; stipules and scars lateral or partially intrapetiolar; gland-hairs with 1(–6)-celled head; mesophyll compact, lacking resin-cells. . . . . Subgenus *Pseudojaca.*
1. Inflorescences with an involucre of triangular, ovate or orbicular bracts; embryo curved (except *Hullettia*).
    4. Involucre multiseriate; stamens enclosed in tubular perianths, these and ovaries sunken between partially fused interfloral bracts; stipules amplexicaul, scars annulate. . . . . (*Treculia*).
    4. Involucre uniseriate; stamens and ovaries sunken in cavities in receptacle; stipules non-amplexicaul, scars not annulate.
        5. Surface of receptacle armoured from indurated, spinous, conical or truncate processes; stipules fused, intrapetiolar, triangular. . . . . 3. *Parartocarpus.*
        5. Surface of receptacle not armoured, smooth; stipules paired and lateral, linear. . . . . 4. *Hullettia.*

ARTIFICIAL KEY BASED ON VEGETATIVE CHARACTERS

1. Stipules amplexicaul, leaving annulate scars.
    2. Leaves spirally arranged. 2. *Artocarpus* subg. *Artocarpus.*
    2. Leaves, at least on ultimate branches, alternate and distichous. (*Treculia*).
1. Stipules not amplexicaul, scars not annulate.
    3. Leaves spirally arranged.
        4. Stipules paired, linear, scars lateral, round; leaves minutely punctate beneath. . . . . 4. *Hullettia.*
        4. Stipules fused, intrapetiolar, scars elongate; leaves not as above. . . . . 3. *Parartocarpus.*
    3. Leaves alternate and distichous.
        5. Leaves abruptly and distinctly acuminate, glabrous; gland-hairs sunken, head 4–8-celled; mesophyll loose, cell contents resinous. 1. *Prainea.*

5. Leaves usually not abruptly acuminate, often pubescent; gland-hairs not sunken, head 1(–6)-celled; mesophyll compact, without resin. .... 2. *Artocarpus* subg. *Pseudojaca.*

NOTES ON THE TAXONOMIC TREATMENTS

Keys. These are intended to indicate, as far as is practicable, the natural affinities of the species and to enable the identification of most material bearing either male or female inflorescences and, where possible, of sterile specimens. Distinguishing characters for sterile material of species with overlapping areas of distribution have been given in the notes under the species.

Types. These have been listed, where known, at the end of the references for each accepted name and synonym. All these specimens have been examined unless otherwise stated. Detailed localities have been given here only when the type or a duplicate has not been seen, since they otherwise appear in the lists of specimens. Lectotypes have been selected for most species where the original description gave syntypes and for those species where the holotype has been destroyed, but isotypes exist. Neotypes have only been chosen, where necessary, for accepted names.

Specific descriptions. These have been prepared from herbarium material, with the addition of details from field notes. The inflorescences have been described from material preserved in alcohol when this has been available. Otherwise the male flowers have been described from material boiled up in water. Where measurements in published descriptions differ greatly from those found in the specimens seen they have been given, together with the source. Measurements of the female inflorescences are probably frequently too small, since fully ripe fruits are not often collected, and many of the species will certainly have larger sapling leaves than indicated here. Descriptions of new species have been prepared from the types and supplemented by details from other collections enclosed in brackets.

Details of the stipules have only been given for *Artocarpus* subg. *Artocarpus*, *Parartocarpus* and *Hullettia*, since in the other groups they do not show significant variation between the species. For the same reason, details of the glands on the leaves and of the presence or absence of a hypodermis have only been given for *Artocarpus* subg. *Artocarpus*. In describing the leaves the term "main veins" includes the midrib and the lateral veins, while the term "reticulum" includes the intercostals unless these have been mentioned separately. In counting the lateral veins all those at the base have been included as well as all those clearly distinguishable at the apex.

The inflorescences have been described as immature before anthesis and the female inflorescence has been described as submature between anthesis and maturity. In *Prainea* and *Artocarpus* the interfloral bracts (as opposed to the involucral bracts of *Parartocarpus* and *Hullettia*) are referred to as bracts in the descriptions. In describing the syncarp of *Artocarpus* and *Parartocarpus* the variously shaped projections of the surface, excluding peltate interfloral bracts, are referred to as processes or papillae. The morphological nature of these, which has already been discussed, differs both within *Artocarpus* and between *Artocarpus* and *Parartocarpus*. The terms "core" and "wall" refer respectively to the receptacle and the surface layer formed by the fused perianths.

Citation of specimens. These have been listed by areas, arranged from west to east in continental Asia (excluding Malaya) and according to the enumeration of geographical units by van Steenis (1950) in Malaysia, except that in the latter the order of the first four units has been changed to Malaya, Sumatra, Borneo, Java, in order to reflect the geographical continuity of Malaya with Asia and the close connection of Borneo with Malaya and Sumatra. In the Philippine Islands, Luzon and Mindanao have been further subdivided into provinces, and specimens from eastern New Guinea have also been listed according to recent political subdivisions.

The herbaria in which the collections have been seen are indicated by the abbreviations of the Index Herbariorum, Part I. ed. 3. 1956. These have been given above in conjunction with the acknowledgements. In addition, the following abbreviations may be noted which have been used preceding the collection numbers.

bb — Bossen buitengewesten; i.e., collections made by the Netherlands Indies Forest Service from areas outside Java.
BS — Bureau of Science, Manila, Philippines.
CF — Conservator of Forests series, Forest Institute, Kepong, Malaya.
FB — Forestry Bureau, Manila, Philippines.
NIFS — Netherlands Indies Forest Service; this has been prefixed to those collections made by the service which do not have bb numbers. (They are numbered in several series, distinguished by various abbreviations indicating where they were collected.)
PB — Piante Bornensi; collected by Beccari.
PP — Piante Papuane; collected by Beccari.
SB — Species Blancoanae; collected by Merrill to illustrate his book of that title.
SFN — Singapore field number.

Localities have been cited as given on the original label, apart from some minor corrections. Where important alterations have been necessary, these have been added in brackets. The Dutch *oe* has been transliterated throughout as *u*. The presence of male and female inflorescences has been indicated, but in *Prainea, Parartocarpus* and *Hullettia* the sex of immature inflorescences can often be determined only by dissection, and these have been recorded as "infl."

Vernacular names. Only those names have been cited which are of fairly common occurrence for a given species, or which are of particular interest. The following names are applied to any species of *Artocarpus* subg. *Pseudojaca*: *Chay* or *Cay chay* (Annamite), *Kwai muk* or *Hung kwai muk* (China), *Tampang* (Malay), and *Cubi* and *Anubing* (Philippines). The name *Tampang* is also applied to *Prainea limpato*. In *Artocarpus* subg. *Artocarpus*, *Terap* is the Malay name for *A. odoratissimus*, *A. scorte-*

chinii, *A. elasticus*, *A. sericicarpus* and *A. tamaran*. Many other species of this subgenus are distinguished by their own names, which are usually accurately applied.

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STUDIES IN ARTOCARPUS AND ALLIED GENERA. II. A REVISION OF PRAINEA

FRANCES M. JARRETT

Prainea King in Hook. f. Fl. Brit. Ind. **5**: 546. 1888; King, Ann. Bot. Gard. Calcutta **5**(*2*): 162. *t. 196.* 1896; Engler & Prantl, Nat. Pflanzenfam. Nachträge II–IV. 122. 1897; Boerl. Handl. Fl. Ned. Ind. **3**: 337, 372. 1900; Becc. For. Borneo 635. 1902, Webbia **5**: 563. 1923; Ridley, Fl. Malay Penin. **3**: 358. 1924; Van Steenis, Bull. Jard. Bot. Buitenzorg III. **12**: 259. 1932; Jarrett, Jour. Arnold Arb. **40**: 8, 11. *fig. 1, a–e, fig. 3, a–c.* 1959. TYPE SPECIES: *Prainea scandens* King.

Artocarpus section *Prainea* Renner, Bot. Jahrb. **39**: 366. 1907.

Trees (? or climbers). *Leaves* alternate and distichous, simple, entire, penninerved, glabrous; epidermal gland-hairs sunken, heads globose, 4–8-celled; spongy mesophyll loose, cell contents somewhat resinous; juvenile leaves elongate. *Stipules* paired, small (to 5 mm. long), lateral or intrapetiolar, scars non-amplexicaul.

Inflorescences unisexual, capitate, heads globose, or the male short-obovoid, pedunculate, solitary or paired in leaf-axils; flowers mixed with numerous narrowly peltate, clavate or spathulate interfloral bracts; perianths free, enclosing a single stamen or ovary; involucre absent. *At anthesis* perianths and bracts compactly covering surface; *male head* with numerous flowers; perianths tubular, bilobed or perforate above; stamens shortly exserted; *female head* with fewer flowers (c. 20–100); perianths tubular, clavate, fleshy above, the mouth contracted, very shortly 2–4-lobed or merely perforate; ovary unilocular, style apical, bifid, the branches exserted, ovule subapical. *Mature female head* with 1–20 flowers forming fruit, perianths greatly enlarged and projecting from surface, fleshy, subglobose to ellipsoid; remaining perianths elongating somewhat or not at all and surface hence loose or compact; mature ovary membranous, style apical, seed large, attached laterally near base, testa absorbed except the thickened saucer-shaped basal portion, endosperm none, embryo straight, longitudinal, cotyledons equal, appressed faces oblique to median plane of ovary, radicle and plumule minute, apical; interfloral bracts persistent.

DISTRIBUTION: Malaya, Sumatra, Borneo, Moluccas, New Guinea.

The genus *Prainea*, described by King in 1888, was based on a single species from Malaya, *P. scandens*, which he illustrated in 1896 in "A Century of New and Rare Indian Plants." King described the ovule as basal and hence placed the genus incorrectly in the Conocephaloideae. However, although the mature seed is attached sub-basally (in *P. papuana*, the only species of which adequate material has been available for study), if the ovary is examined at anthesis the position of the ovule is found to be lateral just below the apex of the loculus.

In 1902 Beccari, in the appendix to "Nelle Foreste di Borneo" entitled "Nuove Specie di *Artocarpeae* Malesi e Papuane," briefly discussed the inflorescences of *Prainea*, stating that he had found the ovule to be pendulous [at anthesis] in spirit material of his *P. cuspidata* (= *P. limpato*) and that the genus was allied to *Artocarpus*, differing only in the structure of the female inflorescence. He also questioned King's description of *Prainea scandens* as a climber. He described as new the three other species of *Prainea* here recognized and a fourth which was an identification of Rumphius' *Metrosideros spuria* (= *Artocarpus fretissii* Teysmann & Binnendijk).

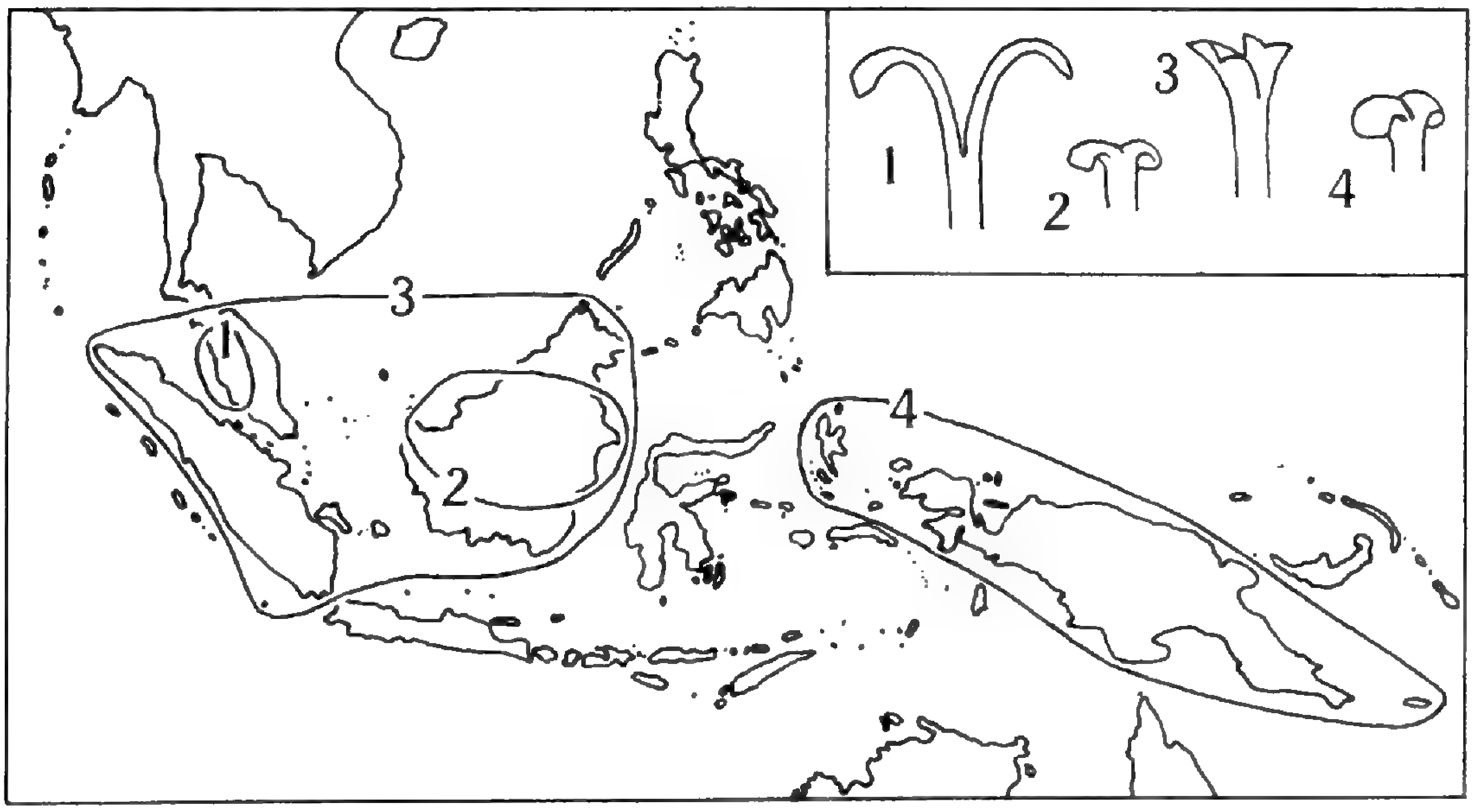

FIG. 10. Distribution of the species of *Prainea*, with inset showing styles; 1, *P. scandens;* 2, *P. frutescens;* 3, *P. limpato;* 4, *P. papuana.*

Renner's reduction of the genus in 1907 to the status of a section under *Artocarpus* has been discussed fully in the introductory paper of this series and rejected on the grounds that the resemblance in leaf structure to subg. *Artocarpus* and in leaf and stipular arrangement to subg. *Pseudojaca* is of less significance than the difference between the free perianths of the female inflorescence of *Prainea* and the syncarpium of *Artocarpus*. In uniting *Prainea* with *Artocarpus*, Renner correctly identified Beccari's *Prainea cuspidata* with Miquel's *Artocarpus limpato* (1861) and listed four species which are equivalent to those recognized here. He found the ovule to be pendulous in *Prainea frutescens* and thus the only species in which this character has not been established is *P. scandens*.

The species are readily separable and the characters used may be seen from the key. No marked variation occurs within the genus, although *P. scandens* and *P. frutescens*, on the one hand, and *P. limpato* and *P. papuana*, on the other, are somewhat more closely allied to each other by leaf characters and the length of the peduncle.

The genus *Prainea* is entirely restricted to Malaysia, with three species in western Malaysia, of which one is endemic to Malaya, and another to Borneo, and a single species in the Moluccas and New Guinea. Van Steenis, in discussing the distribution of the Styracaceae in 1932, cited *Prainea* as an example of a genus which, like that family, occurs in both the western and the eastern parts of Malaysia, but not in the Philippines. The absence of *Prainea* from the Philippines has been confirmed thus far and, moreover, the genus is apparently lacking from nearly all of the geologically unstable area between the Sunda and Sahul continental shelves. Species of *Artocarpus* showing a similar pattern of distribution will be noted in a discussion of the geographical distribution of this group of genera at the conclusion of this series of papers.

KEY TO THE SPECIES OF PRAINEA

1. Male peduncles 5–15 mm.; female peduncles 10–25 mm.; twigs c. 1.5 mm. thick; leaves with 6–12 pairs lateral veins.
    2. Male heads to c. 15 mm. across; female heads to c. 35 mm. across with fruiting perianths projecting up to 25 mm.; stylar branches 2 mm. long, acute. .... 1. *P. scandens.*
    2. Male heads 4–6 mm. across; female heads to c. 10 mm. across with fruiting perianths projecting less than 10 mm.; stylar branches 0.5 mm. long, truncate. .... 2. *P. frutescens.*
1. Male peduncles 15–60 mm.; female peduncles 35–110 mm.; twigs 2–5 mm. thick; leaves with 9–24 pairs lateral veins.
    3. Male heads to c. 15 mm. across; female heads to c. 35 mm. across with fruiting perianths projecting up to 15 mm.; stylar branches forked; mature leaves with lateral veins distinctly prominent beneath, areolae bullate above only, or not at all. .... 3. *P. limpato.*
    3. Male heads 3–8 mm. across; female heads to 20 mm. across with fruiting perianths projecting up to 10 mm.; stylar branches obtuse; mature leaves with lateral veins not or shallowly prominent beneath, areolae often bullate on both surfaces. .... 4. *P. papuana.*

1. **Prainea scandens** King in Hook. f. Fl. Brit. Ind. **5**: 547. 1888; King, Ann. Bot. Gard. Calcutta **5**(2): 162. *t. 196.* 1896; Ridley, Fl. Malay Penin. 3: 358. 1924. Syntypes, Malaya, *King 3549, 3693* (CAL, not seen); duplicates examined (BM, K).

Artocarpus scandens Renner, Bot. Jahrb. **39**: 367. 1907.

Climber(?), height to 20 m. *Twigs* c. 1.5 mm. thick, finely rugose, minutely appressed pubescent, soon glabrescent. *Leaves* 9–17 × 3.5–7 cm., obovate-elliptic, varying elliptic or oblong-elliptic, abruptly contracted into a narrow acumen to 1.5 cm. long, base cuneate, margin entire; midrib prominent beneath, lateral veins slightly so; lateral veins 9–12 pairs, curved, inarching at margin, often with secondary loops; intercostals not parallel; glabrous, dark green, drying greenish above, pale to reddish brown beneath, petiole 5–15 mm. long.

Inflorescences solitary in leaf-axils. *Male head* (not at anthesis) to 15 mm. across, short-obovoid; perianths tubular, bilobed above, 1 mm. long; stamen immature, filament cylindric, anther oblong, 0.3 mm. long; bracts slenderly stalked, heads peltate, 0.4 mm. across; peduncle to 15 × 1.5 mm., velutinous; *female head* at anthesis with bifid styles exserted, branches 2 × 0.2 mm., acute. *Mature female head* to 35 mm. across (excluding fruiting perianths), globose, loosely covered by numerous flowers and bracts, yellow, drying brown; fruiting perianths 1–7, projecting to 25 mm., ellipsoid, 15 mm. across, broadly and obtusely attenuate; remaining perianths 12–15 mm. long, apices clavate, perforate, minutely pubescent, 0.8 mm. across; bracts numerous, slenderly stalked, heads clavate, 0.8 mm. across, pubescent; peduncle 20–25 × 2.5 mm., puberulent.

DISTRIBUTION: in lowland evergreen forest to 2500 ft., endemic to Malaya.

Malaya. PERAK: Larut, *King 3549*, Nov. 1882 (BM, K, ♂), *King 3693* Dec. 1882 (BM, K, ♀). SELANGOR: bridge where Gap road crosses Sungei Semangko, *Strugnell Kepong FN 49703* (SING, ♀, detached inflorescence with leaves of *Artocarpus rigidus*).

The material of this species is inadequate, but King's collections agree well on vegetative characters and the mature female head on *Strugnell Kepong FN 49703* matches that of *King 3693*.

This species appears to differ from all others in *Prainea* and *Artocarpus* in being a climber instead of a tree. The labels on both King's collections describe the plants as "creepers." *King 3693* originally read "a tree with slender hanging branches 50–60 ft. high . . . clinging to another tree" and was altered later.

2. **Prainea frutescens** Becc. For. Borneo 635. 1902. Holotype, Borneo, *Beccari PB 667* (FI); isotypes (FI, K, P).

Parartocarpus sp. Benth. & Hook. f. Gen. Pl. **3**: 375. 1880.
Artocarpus frutescens Renner, Bot. Jahrb. **39**: 367. 1907.

Trees, height to 30 m. *Twigs* c. 1.5 mm. thick, finely and acutely rugose, appressed puberulent, soon glabrescent. *Leaves* 5–16 × 3–7 cm., obovate-elliptic to obovate- or elliptic-oblong or elliptic, abruptly contracted into a narrow acumen to 2 cm. long, base cuneate, rarely oblique with one side rounded, margin entire; midrib prominent beneath, lateral veins slightly so; lateral veins 6–10 pairs, curved, inarching at margin; intercostals not parallel; glabrous, drying greenish to pale or reddish brown; petiole 7–12 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 4–6 mm. across, subglobose to short-obovoid; perianths tubular, 0.8 mm. long, minutely pubescent; stamen 1.2 mm. long, filament cylindric, anther oblong, 0.15 mm. long; bracts slenderly stalked, heads peltate, 0.3 mm. across, ciliate; peduncle 5–12 × 1 mm., velutinous; *female head* with bifid styles exserted, branches 0.6 × 0.2 mm., truncate. *Mature female head* to 10 mm. across (excluding fruiting perianths), globose, compactly covered by 20–30 flowers and numerous bracts; fruiting perianths 2 (in only mature head seen) projecting to 7 mm., ovoid, 6 mm. across, obtuse; remaining perianths c. 2.5 mm. long, apices obtuse, minutely pubescent, 1.5 mm. across, mouth shortly bilobed; bracts coherent in groups, slenderly stalked, heads narrowly peltate, 0.25 mm. across, pubescent; peduncle 13–16 × 1.5 mm., short-pubescent.

DISTRIBUTION: in lowland evergreen forest to 200 ft., endemic to Borneo.

Borneo. SARAWAK: near Kuching, *Beccari PB 667*, Nov. 1865 (FI, K, P, ♂, ♀), *Haviland 3111* (BM, BO, ♀). EAST AND NORTHEAST BORNEO. W. Kutei: *bb 16183* (A, BO); Longbleh, Sungei Pekan, *bb 29606* (A, BO, L, SING, ♂); Mujup, *bb 16785*, *bb 16911* (A, BO, L).

3. **Prainea limpato** (Miq.) Beumée ex Heyne, Nutt. Pl. Ned.-Ind. ed. 2. 1: 579. 1927.

Artocarpus limpato Miq. Fl. Ind. Bat. Suppl. 421. 1861; Renner, Bot. Jahrb. **39**: 367. 1907. Syntypes, Sumatra, *Diepenhorst HB 2092*, *HB 2500* (U); lectotype, *Diepenhorst HB 2092* (U).

Urostigma diepenhorstii Miq. Fl. Ind. Bat. Suppl. 439. 1861. Holotype, Sumatra, *Teysmann HB 716* (U); isotype (BO).

Ficus diepenhorstii (Miq.) King, Ann. Bot. Gard. Calcutta **1**: 181. 1888.

Prainea cuspidata Becc. For. Borneo 636. 1902. Holotype, Borneo, *Beccari PB 2825* (FI); isotypes (FI, K, P).

Prainea multinervia Merr. Philip. Jour. Sci. **29**: 364. 1926, Pl. Elmer. Born. 46. 1929. Holotype, Borneo, *Castro and Melegrito 1610* (UC, not seen); isotypes (A, BO, K).

Trees, height to 30 m. (60 m. fide *Gusdorf 115*), buttressed, bark dark red-brown, peeling off in flakes. *Twigs* 2–5 mm. thick, finely rugose, appressed puberulent, soon glabrescent. *Leaves* 10–33 × 4–13 cm., oblong, varying oblong- or obovate-elliptic, or elliptic, apex abruptly contracted or often subtruncate below a narrow acumen to 1.5 cm. long, base cuneate, or often oblique with one side subcordate, margin entire; midrib and lateral veins prominent beneath, intercostals slightly so, areolae often slightly bullate above; lateral veins 11–24 pairs, straight or slightly curved, inarching at margin conspicuous; intercostals forming rectangular net; glabrous, drying dark to pale reddish brown; petiole 8–22 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis: male head* c. 15 mm. across, globose; perianths tubular, perforate, 1.4 mm. long, minutely pubescent; stamen 1.8 mm. long, filament cylindric, anther oblong, 0.4 mm. long; bracts slenderly stalked, heads peltate, 0.3 mm. across, ciliate; peduncle 30–40 × 2 mm., glabrous to short-pubescent; *female head* with bifid styles exserted, branches 0.5 × 0.2 mm., forked at the tips. *Mature female head* to 35 mm. across (to 55 mm. including fruiting perianths), globose, loosely covered by numerous flowers and bracts, yellow-green, drying brown; fruiting perianths 8–20, projecting to

15 mm., ellipsoid, 10 mm. across, obtuse or broadly and obtusely attenuate; remaining perianths c. 4 mm. long, apices clavate, perforate, minutely pubescent, 1.5 mm. across; bracts slenderly stalked, heads spathulate, 0.3 mm. across, ciliate; peduncle 75–110 × 2–3 mm., puberulent.

VERNACULAR NAMES: *Tampang* (Malay), Sumatra, Borneo; *Limpato*, Sumatra.

DISTRIBUTION: in lowland evergreen forest to 1700 ft., Malaya, Sumatra, Borneo.

Malaya. KEDAH: Weng road, near Baling, *Best SFN 21266* (K, SING, infl.). **Sumatra.** ATJEH: Bivak Aer Putih, waterfall near Pendeng, Gajolanden, *Van Steenis 9270* (BO, L, ♀). WEST COAST: Fort Elout, *Teysmann HB 716* (BO, U); Priaman, *Diepenhorst HB 2092* (BO, L, U, ♀), *HB 2500* (BO, L, U, ♂), *HB 2914* (BO). INDRAGIRI: Batang Peranap, *bb 30095* (BO, L); Muara Serangge, *bb 30066* (BO, L); Peranap, *bb 30105* (A, BO, L). DJAMBI: Danau Lama, *bb 13639* (BO). PALEMBANG: Lematang Ilir, Gunong Megang, *NIFS T 340* (BO, L ♂), *NIFS T 521* (BO, K, L, U, ♀); Lematang Ilir, Semangus, *bb 32063* (A, BO, L, SING, ♂), *bb 32085* (A, BO, L, SING); Mulak Ulu, *Grashoff 323* (BO, L). LAMPONGS: Manggala, *Gusdorf 115* (BO, ♀). ENGGANO: forest near Bua bua, *Lutjeharms 4558* (A, BO, K, L, P, SING). **Borneo.** SARAWAK: Gunong Braam, near Sabungo, *Beccari PB 2825*, Nov. 1866 (FI, K, P, ♂, ♀). SOUTH AND SOUTHEAST BORNEO: Tanah Bumbu, Kampong Baru, *bb 13364* (BO). EAST AND NORTHEAST BORNEO: Berouw, Domaring, *bb 18817* (A, BO, L); Bulungan, Mara, *bb 10809* (BO); Upper Mahakam, D. Parei, *bb 20743* (A, BO, L). BRITISH NORTH BORNEO: Limanis, *Wood 1790* (BO, ♂); Tawao, Elphinstone Prov., *Elmer 21799* (A, BM, BO, GH, K, L, P, SING, U, ♀). BANGUEY ISLAND: *Castro & Melegrito 1610*, July–Sep. 1923 (BO, K, ♂).

The appearance of the mature female head is rather variable, owing to differences in the number of fruiting perianths and in the extent to which the other perianths elongate after anthesis. The leaf form in which the apex is subtruncate below the acumen is distinctive and is found only in this species of the genus.

4. **Prainea papuana** Becc. For. Borneo 635. 1902. Holotype, New Guinea, *Beccari PP 675* (FI); isotypes (FI).

Artocarpus papuanus Renner, Bot. Jahrb. **39:** 367. 1907, non Diels, 1936.

Prainea microcephala J. J. Smith, Bull. Jard. Bot. Buitenzorg III. **6:** 80. 1922. Syntypes, Ternate, *Beguin 691*, Halmaheira, *Beguin 1919, 1980, 2242* (BO); lectotype, *Beguin 1980* (BO).

Parartocarpus papuanus S. Moore, Jour. Bot. **61** Suppl. 52. 1923, non Becc. 1902; Diels, Bot. Jahrb. **67:** 175. 1936. Syntypes, New Guinea, *Forbes 331, 411* (BM); lectotype, *Forbes 411* (BM).

Trees, height to 35 m., bark brown, peeling off in flakes. *Twigs* 2–3 mm. in diameter, finely rugose, appressed puberulent, soon glabrescent. *Leaves* 8–26 × 4–12 cm., oblong, varying elliptic, abruptly narrowed into an acumen to 1.5 cm. long, base cuneate or rounded, often oblique with one side subcordate, margin entire; midrib prominent beneath, lateral veins slightly so, areolae often bullate on both surfaces; lateral veins 9–20 pairs, straight or slightly curved, inarching at margin conspicuous; intercostals not parallel; glabrous, drying red-brown, grey or green above, dark to pale brown beneath; petiole 8–18 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* 3–8 mm. across, globose; perianths tubular, clavate, shortly bilobed above, 1.8 mm. long, minutely pubescent; stamen 2.5 mm. long, filament slender, cylindric, anther oblong, 0.4 mm. long; bracts slenderly stalked, heads clavate, 0.4 mm. across; peduncle 15–60 × 2 mm., velutinous; *female head* olive green, with bifid styles exserted, branches 0.7 × 0.5 mm., obtuse. *Mature female head* 10–20 mm. across (excluding fruiting perianths), globose, loosely to compactly covered by c. 25–100 flowers and numerous bracts, orange, drying brown; fruiting perianths 2–12(–25), projecting to 10 mm., subglobose to conical, 10 mm. across, mucronate; remaining perianths c. 2.5 × 1 mm., clavate, mouth contracted, obtusely 4-lobed; bracts slenderly stalked, heads clavate, 0.5 mm. across, often coherent in groups; peduncle 30–90 × 2 mm., velutinous.

DISTRIBUTION: in lowland evergreen forest to 3500 ft., Moluccas (Halmaheira group), New Guinea.

Moluccas. MOROTAI: Gunong Moku, *Anang 263* (L); Mt. Permatang, along the Sangowo River, *Kostermans 959* (L, SING); Tjaw, *Kostermans 836, 837* (L). HALMAHEIRA: Galela, Soa Tobaru, *Beguin 1919*, Dec. 1921 (BO, K, L, U, ♀), *1926* (BO, L, ♀), *1980*, May 1922 (BO, L, P, SING, U, ♀); Kampong Toliwang, *Idjan/Moehtar 364* (K); W. Pitu, *Beguin 2242*, Nov. 1922 (BO, K, L, P, U). TERNATE: Laguna, *Beguin 691*, May 1920 (BO, L, ♀). BATJAN: Masurung, *bb 23133* (BO, L).

New Guinea. VOGELKOP: Andai, *Beccari PP 675*, 1872 (FI, ♂, ♀); Manokwari, Pomi, Kolonisatie, *bb 15897* (BO, ♀); n. of Ransiki, 80 km. s. of Manokwari, *Kostermans 4746* (A, K, L, SING, ♀); Sorong, *Beccari s.n.* (FI). DUTCH NORTH NEW GUINEA: Bernhard Camp, Idenburg River, *Brass & Versteegh 13167, 14122* (A, ♀). PAPUA. Central Division: Boridi, *Carr 14976* (SING, ♀); Koitaki, *Carr 12213* (BM, K, L, SING, infl.), *12586* (BM, K, SING, infl.), *12886* (BM, K, L, SING, ♀); Sogeri, *Forbes 331, 411*, 1885–6 (BM, K, L, ♀). Milne Bay District, Cape Vogel Peninsula: near Medino village on n. coast, *Hoogland 4666* (A, ♀); Menapi, *Brass 22000* (A, ♀). MANDATED TERRITORY OF NEW GUINEA. Morobe District: *Womersley NGF 2994* (A, BO K, L, ♀); Quembung, Sattelberg, *Clemens 8099* (A, ♀). D'ENTRECASTEAUX Is. Normanby I.: Lebudowa River, *Brass 25517* (K, L, ♀); Waikaiuna Bay, *Womersley & Brass NGF 8674* (A, K, ♀); near Waikaiuna Plantation, *Jackson NGF 4109* (A, K, L, SING, ♀). JAPEN: Serui, *bb 30434* (BO, L), *bb 30655* (L). LOUISIADE ARCHIP.: Misima I., Mt. Sisa, *Brass 27523* (K, L, ♀).

In his description of *Parartocarpus papuana*, S. Moore cited a third specimen, *Forbes 503*, but this has not been found either at the British Museum (Natural History) or elsewhere.

The female head in *Prainea papuana* shows a variability similar to that of *P. limpato* in the number of seeds formed and in the degree of elongation of the perianths after anthesis. The latter is partially correlated with a geographical variation in the diameter of the head at anthesis. In eastern New Guinea the female head then has a diameter of 10–15 mm. and the surface generally remains compact at maturity, but in the Vogelkop and the Moluccas the diameter is only about 5 mm. at anthesis and later all the flowers usually elongate somewhat so that at maturity the surface becomes loose. A parallel variation occurs in the size of the male head. However, the collections from Dutch North New Guinea are intermediate, with a diameter of 8–10 mm. at anthesis and with the surface remaining fairly compact. The creation of subspecies is therefore not regarded as justifiable.

SPECIES EXCLUDENDA

Prainea rumphiana Becc. For. Borneo 636. 1902 = **Artocarpus fretissii** Teysm. & Binnend. Abh. Naturf. Ges. Halle **9**: 189. 1866.

A DISCUSSION OF THE PACIFIC RAILROAD REPORTS AS ISSUED IN THE QUARTO EDITION

SUSAN DELANO MCKELVEY

THE VOLUMES CONSIDERED in these pages contain the findings of those who participated, both in field and in laboratory, in the first systematic examination by the United States government of the immense area extending from the Mississippi River to the Pacific Ocean and from Canada on the north to Mexico on the south, and which, in the half century from 1803 to 1853 had become part of our national domain.

The only official expeditions yet to have crossed the region, those of Lewis and Clark and of Frémont, had acquired, everything considered, some interesting scientific facts, but these were inadequate when it became necessary to determine "the most practicable and economical route" for a railroad.

For the factor of practicability, concerned with such matters as grades, distances, and weather conditions, demanded trained topographers, astronomers and meteorologists; while the factor of economy, interlocked to be sure with the practicable, but even more intimately related to a railroad's construction and maintenance as well as to the subsistence of prospective settlers along its line of march, necessitated knowledge, in terms of identification, of rocks, minerals, soils, timber, plants and all forms of animal, bird, fish and reptilian life, as well as estimates of their abundance and availability. Such facts could only be supplied by geologists, mineralogists, botanists, zoologists and others proficient in the natural sciences, at that time a covering term for all that related to the systematic study of nature as a whole, whether animal, vegetable or mineral.

On earlier official expeditions the government had demonstrated little enthusiasm when asked to include men interested in such matters. Now the expert knowledge which only they could supply had become vital and the Smithsonian Institution and its members were called upon to provide instructions in the technicalities of field collecting — the making of the specimens and the keeping of the records upon which the reports of the scientists must of necessity be based — and to enumerate the equipment necessary for its accomplishment. This they did, wholeheartedly, even specifying red pencils and stressing the importance of adding tartar emetic to all alcohol — "besides adding to its preservative powers, [this] will remove any temptation to drinking it on the part of unscrupulous persons."

Because the expeditions were to cross the trans-Mississippi West at, or near, four widely separated parallels of north latitude, a comprehensive coverage was assured as far as natural history collections were concerned and the scientific reports, some including fine plates, which eventually were appended to those descriptive of the routes and which were written by such authorities as S. F. Baird, W. P. Blake, J. S. Newberry, J. Torrey, Asa Gray and many others, constituted and still must be regarded as invaluable records.

Although publications dealing with special aspects of the surveys never fail to mention that important scientific work was accomplished, they do not elaborate upon the statement. Long interested in collectors — often ignored to the point of anonymity — I determined, with the optimism of ignorance, to "run through" the series of reports, twelve volumes in thirteen, and see what could be learned of the men upon whose accomplishments in the field the scientific edifice was erected. The great quarto edition, occupying three to four feet of standing room, has been characterized as "monumental," "sumptuous" — it has been stated [1] that its publication cost the government over one million dollars, the surveys themselves four hundred and forty-five thousand — and, although its pristine magnificence is no longer in evidence, its very dimensions may have contributed to my confidence that the content would be well organized, clearly presented and easily digested. This did not prove to be the case and any "running through" was reduced to a walk and eventually a full stop, for, with a mental preference to understand one thing before proceeding to another, I was soon "bogged down" in the fine points of military terms and distinctions, as well as in far deeper swamps.

It finally became clear that, before attempting any study of the reports, three preliminary tasks must be faced: first, the government documents in which they were issued must be understood; second, the content of all volumes of the series must be analysed in order to be able to cite accurately from their pages; and, third, a satisfactory means of locating the data contained in the analyses must be devised. These tasks were completed for my own enlightenment and convenience. But, convinced that anyone approaching the reports for the first time must be faced with similar needs to mine, it is possible that my findings may have a wider usefulness. I shall comment upon what these three tasks involved before turning to their solution which constitutes my paper proper.

(1) The issues of the quarto edition have been enumerated before now. But because enumerations vary greatly in form of presentation, it was necessary to compare and to check, one against the other, a number of authoritative bibliographies in order to feel certain that an accurate and complete picture had been obtained — a slower task than the brevity of my summary might indicate.

Especially helpful to this end were the presentations contained in Mr. George Leslie Albright's "Official explorations for Pacific railroads 1853–1855," issued in 1921 (*University of California Publications in History*, Volume X), in a *Catalog of books represented by Library of Congress printed cards*, published in 1948 (Ann Arbor, Michigan, Volume 154, 634–635), and in Professor Howard Taft's *Artists and illustrators of the Old West 1850–1900*, published in 1953 (Charles Scribner's Sons, New York). Another volume, the *Checklist of United States public documents* (edition

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[1] *See* Taft, H., *op. cit.* this page, (5 & *fn.* 13).

3. 1: 1274–1275), published in 1911, which distinguishes all numbered Congressional Documents by Serial Set and Serial Number, served as a final check. These authorities are occasionally referred to in my paper.

(2) Examining the quarto edition for the first time, problems inherent in its makeup became apparent immediately. I mention some of the more baffling:

There is no index covering the content of the entire series, and understandably so. For, with the exceptions of Volumes VIII, IX and XI, none has pages numbered consecutively throughout — Volumes II and X, for examples, have seven sets of page numbers each — and it is therefore necessary, and I believe always will be necessary, to "leaf through" a volume to locate an included report. Although page numbers in individual reports are for the most part clear, seemingly endless blank or only occasionally numbered pages, in front or back matter especially, are, at best, an annoyance if one needs to cite therefrom.

Because it had been impossible, obviously, to assemble on time for a waiting printer, the great amount of material due from widely scattered sources, reports are not always present where a volume's table of contents indicates and subsidiary papers, usually scientific, are not always found in proximity to the report to which their content relates. A note on an inserted page or an easily overlooked footnote states that such and such a paper will appear later, although when or where is not predicted. Only by time-consuming search through later volumes — involving in all instances the "leafing through" procedure already mentioned — can matter delayed in publication be located; it should be added that, when found, it is usually referred to its appropriate place in an earlier volume!

And what is true of belatedly published papers is also true of matter elucidating the content of reports, whether this be in the form of plates of all sorts, of maps, of profiles, etc. Such material is usually enumerated in a report's list of illustrations, but checking often proves that certain items are lacking, or missing at the point indicated. To enumerate the discrepancies in illustration-content existing in the many issues of any one volume — they appear to have been dictated by the convenience, or perhaps necessity of a volume's compiler — was clearly impossible. One could not hope to do more than supply the total number included in the report under scrutiny and, when such existed, their numerical captions.

Attempts to record the whereabouts of a report's scattered but affiliated content, textual and illustrative, resulted in the analyses contained in this paper. That they were essential became evident when cross-references necessitated accurate citation. Furthermore, although analyses could not do away with the broken pagination of the volumes, an irremediable problem, they could lessen some of the other difficulties inherent in the makeup of the series; for to be able to ascertain, within the compass of a few pages, the content of its volumes, would certainly be far more convenient than to search repeatedly through the ponderous tomes themselves.

Two other matters related to the compilation of the volumes had best be mentioned here — others will be referred to at appropriate places in my analyses.

The first concerns dates of publication. The printers were obliged to proceed with their tasks; consequently the year supplied on the main title page of a given volume may be earlier than one recorded on an included letter, report, etc. When, in my analyses, later years than those which appear on the title pages are recorded, they are based on this internal evidence and merely represent the year before which, it may be assumed, a given volume could not have been issued. For one example see under Volume II.

To scientists dates of publication can be immensely important. Dr. I. M. Johnston's paper, "Publication dates for botanical parts of the Pacific Railroad Reports" (*Journal of the Arnold Arboretum*, Volume XXIV, 237–242, 1943), assigns, on the strength of records found in old letters, contemporary publications and the like, "Reasonably exact dates to the various botanical reports, accurate in most cases to within a month or two." Dr. Johnston also takes into consideration the first, or octavo edition of the reports, an issue not discussed in this paper. (*See* my *fn.* 3.) His conclusions are summarized in tabulated form at the end of his paper.

Only in rare instances do the authors of scientific reports included in the quarto series mention the publication date of their papers. When they do so the fact is noted in my analyses.

The second matter relates to the manner in which certain illustrations are incorporated in the volumes. Because of the great number contained in Volume XI the unfortunate results are especially apparent and my comments are confined to that volume, although to a lesser degree the criticism is applicable wherever similar illustrations are included.

Volume XI is, in text, perhaps the most generally useful in the entire series of *Pacific Railroad Reports*. It is regrettable, therefore, that its associated and very fine maps, profiles, panoramic views, etc., representing the graphic results of the topographers' arduous task, should have been included in a manner which makes their manipulation impossible and is destructive of the illustrations themselves. Most are extremely large and many-times-folded. Bound tightly in with and outbalancing the text which constitutes the first half of the volume, to unfold them, to keep any single one spread out for study or any two for comparison, and to execute the even more difficult refolding without tearing, are all impossibilities. Yet, because none bears any exterior notation, they must be opened to full size for identification — the placement of the beautifully lettered and explicit captions seems to have been selected to that very end! Even in copies of Volume XI which have obviously stood unused, many of the illustrations have already disintegrated along their exposed, uneven folds; lack of dusting or the reverse may have been responsible, or possibly the paper was not suitable in the first place. Had they been mounted on linen (*see fn.* 4), visibly captioned to conform to the enumeration found in the volume's "Contents," and supplied loose in a container, their usefulness would have been assured and their life expectancy prolonged; as issued, they symbolize endless labor and much money spent to little purpose. It is possible that in some instances these valuable records might still be mounted although in others it could not be done now.

(3) The Ann Arbor *Catalog*, cited on p. 39, supplies two synopses which serve as guides to the content of the quarto edition. The first, "Contents (Outline)," condenses into some 15 lines the routes described in its volumes, usually according to the parallels which they followed. The second, "Contents (By authors)," supplies an alphabetical list of the men who contributed reports, and then records, for the most part by a descriptive term, the subject matter of their papers, followed by the volume or volumes in which they are to be found. Presumably intended to supplement each other, these synopses presuppose a very great familiarity with the content of the series and, in my opinion, are not sufficiently explicit to offer much assistance to anyone approaching the reports for the first time. Moreover, necessitating frequent reference to the volumes themselves, they present many of the already mentioned difficulties inherent in the edition's makeup.

The "Alphabetical index of authors" which concludes this paper supplies, I believe, a more complete roster of contributors than does the somewhat similar list of the *Catalog*. And, when used in conjunction with my analyses, it provides, without reference to the volumes themselves, the precise association of every report as well as an outline of that report's entire subject matter and the pagination thereof. In possession of these facts one should be sufficiently informed to be able to turn immediately to the appropriate volume as well as to the information sought in any given report.

REPORTS OF EXPLORATIONS AND SURVEYS TO ASCERTAIN THE MOST PRACTICABLE AND ECONOMICAL ROUTE FOR A RAILROAD FROM THE MISSISSIPPI RIVER TO THE PACIFIC OCEAN[2]

An enumeration of the Congressional Documents containing the reports. An analysis of the content of the twelve volumes, in thirteen, of the quarto edition in which the reports were issued in final form. An alphabetical index of authors to be used in conjunction with the analyses.

CONGRESSIONAL DOCUMENTS CONTAINING THE REPORTS

Although a few of the *Pacific Railroad Reports* enumerated below were issued in an octavo edition,[3] the revised, complete and authoritative

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[2] Present on the title-page of every volume in the series as well as on the title-pages of included reports, this is inconveniently long for repeated citation and is usually shortened to *Pacific Railroad Reports*, an abbreviation which G. K. Warren used as early as 1859 in his table of contents of Volume XI, [5].

[3] The *Checklist of United States public documents* states, "Some of the . . . reports first appeared in 8° in House Document 129, 33d Congress, 1st session, in serial nos. 736, 737, and 739. Serial no. 738, the projected v. 3 of this edition, was never printed." *See* p. 39.

reports, the ones usually cited and the ones most often found in libraries, were prepared under the direction of the War Department and were issued for both Senate and House of Representatives in a quarto edition of twelve volumes, in thirteen, under the long descriptive title cited above.

The quarto edition is found as follows:

Volumes I through XI: *33d Cong., 2d Sess., Senate Ex. Doc. No. 78* [Serial Nos. 758 through 768 [4]]; *33d Cong., 2d Sess., House Ex. Doc. No. 91* [Serial Nos. 791 through 801].

Volume XII: *35th Cong., 3d Sess., Senate Ex. Doc. No. 46* [Serial No. 992 [5]]; *36th Cong., 1st Sess., House Ex. Doc. No. 56* [Serial Nos. 1054, 1055 [6]].

All the issues cited above are numbered Executive Documents and are included in the Serial Sets.

There are, in addition, two printings, one of Volume XI, one of Volume XII, which lack document numbers and are not included in the Serial Sets. These are:

Volume XI: *36th Cong., 2d Sess., Senate Ex. Doc.*[7]
Volume XII: *36th Cong., 1st Sess., Senate Ex. Doc.*[8]

There may be variations in these unnumbered issues, related primarily to such matters as the date of publication on a volume's title-page, their illustration-content or illustration-placement and so on, but as far as text is concerned, all issues, whether numbered or unnumbered documents, appear to be accepted as the same.

AN ANALYSIS OF THE CONTENT OF THE THIRTEEN VOLUMES OF THE QUARTO EDITION

Volume I — 1855

33d Cong., 2d Sess., Senate Ex. Doc. No. 78 [Serial No. 758 [9]]

The title-page of *Pacific Railroad Reports*, Volume I, is dated 1855. No included matter bears a later date.

Some parts, certainly, of the reports must have been issued for the Senate in this octavo, unillustrated, and preliminary edition; for example: *33d Cong., 1st Sess., Senate Ex. Doc. No. 52* [Serial No. 698]. *See* Albright (45, *fn.* 1; 160), and Taft (255, *fn.* 13).

[4] Taft (255, *fn.* 2) records: ". . . The maps in the Senate Serial Set (768^1 and 768^2) of volume 11 are mounted on linen . . . requiring two books (parts 1 and 2) to contain them." It has not been possible to locate a copy of Volume XI with mounted maps in the libraries of Boston or of Cambridge and the issue must be rare.

[5] Taft (255, *fn.* 4) states: "This volume (Serial No. 992) duplicated in a single book the material in Serial Nos. 1054, 1055 [see below] but is designated on the title page as 'Supplement to Volume 1' ". Card 2 of the Ann Arbor *Catalog* notes that this "Supplement to vol. I," was issued in 1859, W. A. Harris, printer.

[6] The two volumes of this issue are distinguished on the respective title-pages of *Pacific Railroad Reports* as Volume XII. Book I, Volume XII. Book II.

[7] The title-page records that this was printed in Washington by George W. Bowman and is dated 1861. The maps are bound in with the text. *See* Taft (255, *fn.* 2).

[8] The title-page records that this was printed in Washington by Thomas H. Ford and is dated 1860. As in *House Ex. Doc. No. 56* its two parts (Book I and Book II) are bound separately, making two volumes. *See* Taft (255, *fn.* 3).

[9] Because my analyses have been based upon a mixed set of the quarto edition, the

"Contents of Volume I," [iii], lists five papers. The subject matter of the first four, distinguished here as (1) through (4), is enumerated in the "Index to Report of the Secretary of War and Office Reports," [v]–viii, and that of the fifth, (5) below, in the "Alphabetical Index to Governor Stevens's Report," [637]–651. Page numbers run consecutively in (1) through (4); in (5) they are independently numbered.

The title-pages of (1) through (5) read respectively:

(1) Report of the Secretary of War on the several railroad explorations. [1]–35.

For reprintings of portions of this report *see* "Explanatory note" quoted under Volume III, *fn.* 18.

(2) An examination by direction of the Hon. Jefferson Davis, Secretary of War, of the reports of explorations for railroad routes from the Mississippi to the Pacific, made under the orders of the War Department in 1853–'54, and of the explorations made previous to that time, which have a bearing upon the subject: by Capt. A. A. Humphreys & Lieut. G. K. Warren, Corps of Topographical Engineers. [35]–111.

CONTENTS: Table of contents, [35]; An examination of the reports of explorations for railroad routes from the Mississippi to the Pacific, [37]–38; Humphreys & Warren report (6 chapters), [39]–111.

For reprintings of portions of this report *see* "Explanatory note" quoted under Volume III, *fn.* 18.

(3) Memoranda on railways, prepared Office of Pacific Railroad Surveys; by Capt. Geo. B. McClellan, Corps of Engineers, under instructions from Hon. Jefferson Davis, Secretary of War. [113]–130.

(4) Report upon the cost of transporting troops and supplies to California, Oregon, New Mexico, etc., etc. By Major General Thomas S. Jesup, Quartermaster General, U.S. Army. [131]–134.

(5) Report of explorations for a route for the Pacific railroad, near the forty-seventh and forty-ninth parallels of north latitude, from St. Paul to Puget Sound. By I. I. Stevens, Governor of Washington Territory. [i]–vii; [1]–651.

CONTENTS: Table of contents, [iii]–vii; Part I. Reports from the field, [1]–72; Part II. Report (18 chapters), [73]–159; Miscellaneous documents related to special aspects of the survey,[10] 160–635; Note, [636]; Alphabetical index to Governor Stevens's report. Prepared by E. B. Hunt, U.S.A., [637]–651.

For maps and profiles *see* under Volume XI.

A "Note," [636], states: "The Narrative of the Explorations, accompanied by Views, illustrating the Features of the country, the Natural History, Botanical and other Scientific Reports, with Illustrations, will be found in a Subsequent Volume." *See* under Volume XII, Books I and II.

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one in the Arnold Arboretum Library, the printing is cited in every instance to facilitate checking should such be desired.

[10] For authors of certain of these documents *see* *fn.* 56.

Volume II — 1857

33d Cong., 2d Sess., House Ex. Doc. No. 91 [Serial No. 792]

The title-page of *Pacific Railroad Reports*, Volume II, is dated 1855, but Pope's "Explanatory note" to Blake's geological report, inserted before the title-page of (4A) below, is dated February 18, 1857.

"Contents of Volume II," [iii], lists six papers, distinguished here as (1) through (6); a seventh, (4A) below, is not listed. Each of these seven papers has its own set of page numbers. They are cited on their respective title-pages as follows:

(1) Report of explorations for a route for the Pacific railroad, by Capt. J. W. Gunnison, Topographical Engineers, near the 38th and 39th parallels of north latitude, from the mouth of the Kansas River, Mo., to the Sevier Lake, in the Great Basin. Report by Lieut. E. G. Beckwith, Third Artillery. [1]–128. 13 Plates (captioned but not numbered).

CONTENTS: Introductory letter, [3]; Contents, [5]–8; Report (10 chapters), [9]–118; Appendix A. Letters relating to the progress of the survey of the route near the 38th and 39th parallels, in charge of Captain Gunnison, [119]–124; Appendix B. Explanations of the map and illustrations, [125]–128.

For associated botanical report *see* under (2) below. For associated zoological reports *see* under Volume X. For maps and profiles *see* under Volume XI.

(2) Report of explorations for a route for the Pacific railroad, on the line of the forty-first parallel of north latitude. By Lieut. E. G. Beckwith, Third Artillery. [1]–132.

CONTENTS: Introductory letter, [3]; Contents,[11] [5]–8; Report (10 chapters),[12] [9]–112; Appendix. Instructions from the Secretary of War, [113]–114; Botanical report, [115]–132.

For zoological reports *see* under Volume X. For plates, maps, profiles, *see* under Volume XI.

The title-page of the included Botanical report reads:

Report on the botany of the expedition: by John Torrey and Asa Gray. [115]–132. 10 plates (Nos. I–X).[13]

CONTENTS: Contents, [117]; Botanical report, Part I, [119]–125; Part II,[14] 125–131; Explanation of the plates, 131–132.

(3) Synopsis of a report of the reconnaissance of a railroad route from

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[11] For "Errata" see p. 8, and for "Additional errata" *see* sheet inserted between pp. 8 and [9].

[12] Of these Chapter X, "Geology," includes 4 plates of fossils (Nos. 1–4) and 3 woodcuts.

[13] Of these, No. I is associated with (2), Nos. II–X with (1).

[14] Part I describes collections made under (2) and Part II collections made under (1). For the wording of the long descriptive headings of Parts I and II, *see Pacific Railroad Reports*, Volume II, where the heading of Part I appears on pp. 117, 119, and that of Part II on pp. 117, 119, 125.

Puget Sound via South Pass to the Mississippi River: by Fred W. Lander, Civil Engineer. [1]–45.

CONTENTS: Contents, [3]; Legislative and executive action in reference to this exploration and report, [5]–6; Introduction, [7]–28; Report, [29]–45.

(4) Report of explorations of a route for the Pacific railroad, near the thirty-second parallel of north latitude, from the Red River to the Rio Grande, by Brevet Captain John Pope, Corps of Topographical Engineers. [i]–iv; [1]–185.

CONTENTS: Pope letter transmitting report, [ii]; Contents, [iii]–iv; Report (8 chapters), [1]–50; 12 Appendices (A through L),[15] [51]–156; Botanical report, [157]–178; Index, [179]–185.

For map and profile *see* under Volume XI.

The title-page of the included Botanical report reads:

> Report on the botany of the expedition: by John Torrey and Asa Gray. [157]–178. Index,[16] [179]–185.

Associated with the route described in (4) but with its own set of page numbers is:

(4A) Report on the geology of the route, near the thirty-second parallel: prepared from the collection and notes of Capt. Pope, by William P. Blake, Geologist of the Office of the United States Pacific Railroad Surveys. [1]–50. Geological map. Geological section.

CONTENTS: Explanatory note to geological report[17] [inserted before title-page]; Blake letter submitting his report, [3]; Contents, [5]–6; Report (6 chapters), [7]–40; Catalogue of the geological collection made by Brevet Captain John Pope, 1853, [41]–42; Note in explanation of the map and section, [43]–44; Index to the report on the geology of the route near the thirty-second parallel, [45]–50.

(5) Report of explorations for that portion of railroad route, near the thirty-second parallel of north latitude, lying between Dona Ana, on

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[15] Most of these are highly technical. Four, however, have a general interest:

"Appendix A. Diary of the expedition, by J. H. Byrne, Assistant Computer," [51]–95, and "Appendix E. Table of camping places along the direct line of survey," [98]–99, are both helpful guides to Pope's route.

"Appendix B. Preliminary report on the natural history," [94], signed by Spencer F. Baird, refers to the scope and importance of Pope's zoological collection, and to anticipated publications thereon.

"Appendix D. Note upon the geological report," [98], concerns the delayed publication of Blake's report upon the geological collection, and the preliminary report of Jules Marcou in the octavo edition of *Pacific Railroad Reports*. *See* under (4A) below.

[16] This covers matter contained in Pope's report proper as well as in the botanical report.

[17] Pope wrote: "The mineralogical collections made by me were placed in the hands of M. Jules Marcou for examination, and carried by him to France. They were subsequently returned in a confused condition, and with many of the labels displaced. This fact will account for many errors in the report, map, and section prepared by Mr. Blake." This is dated Washington, February 18, 1857.

the Rio Grande, and Pimas Villages, on the Gila. By Lieut. John G. Parke, Corps of Topographical Engineers. [1]–28.

CONTENTS: Report, [3]–24; Appendix (in two parts, A and B), [25]–26; Index, [27]–28.

For Parke's later report *see* under Volume VII.

(6) Extract from report of a military reconnaissance, made in 1846 and 1847, by Lieut. Col. W. H. Emory. [1]–22.

CONTENTS: Humphreys letter explaining the inclusion of this earlier report, [3]; Extract from Lt. Col. Emory's report, [5]–20; Index, [21]–22.

Volume III — 1856

33d Cong., 2d Sess., House Ex. Doc. No. 91 [Serial No. 793]

The title-page of *Pacific Railroad Reports,* Volume III, is dated 1856. No included matter bears a later date.

Volume III has five sets of page numbers.

"Contents of Volume III," [1], divides the subject matter into two parts, distinguished here as (1) and (2). The first bears the heading:

(1) Extracts from the (preliminary) report of explorations for a railway route, near the thirty-fifth parallel of north latitude, from the Mississippi River to the Pacific Ocean, by Lieutenant A. W. Whipple, Corps of Topographical Engineers. [3]–36.

CONTENTS: Explanatory note,[18] [3]; Extracts, [3]–32; [Portion of] Appendix B. Table containing the distances, altitudes, * * * * of each camp from Fort Smith to the Pacific Ocean, 33–36.

The title-page of the second reads:

(2) Report of explorations for a railway route, near the thirty-fifth parallel of north latitude, from the Mississippi River to the Pacific Ocean: by Lieutenant A. W. Whipple, Corps of Topographical Engineers; assisted by Lieutenant J. C. Ives, Corps of Topographical Engineers.

CONTENTS: [19] Letter to the Secretary of War, [vii]–viii; General

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[18] Signed by Humphreys, the "Explanatory note" reads: "The reports of the Secretary of War and the revising officer, which appear in volume one, were founded, so far as they relate to the route near the 35th parallel, upon the preliminary report of Lieutenant Whipple. The following chapters, being those which are principally referred to in those revisory reports, are, therefore, republished. They are chapters two, three, four, five, and eleven, with a portion of appendix B. The preliminary profiles are also reprinted."

For "preliminary report of Lieutenant Whipple," *see* octavo edition of *Pacific Railroad Reports* (*House Ex. Doc. No. 129*). For "reports of the Secretary of War and the revising officer which appear in volume one" *see* under that volume. Reprintings of the "preliminary profiles" have not been located in the printings of the quarto series examined.

[19] Page numbers in front matter preceding Part I appear to be confused but are cited as given.

table of contents,[20] [ix]–x; Part I, [i]–viii; [1]–136; Part II, [1]–77; Part III, [1]–127; Part IV, [iii]–xiii, [1]–175.

The title-pages of Parts I, II, III and IV read respectively:

Part I. Itinerary. [i]–viii, [1]–136. 10 plates (captioned but not numbered). 10 woodcuts.

CONTENTS: Errata, [iv]; Contents, [v]–vii; Illustrations, [viii]; Introduction, [1]–4; Itinerary (16 chapters), [5]–136.

Part II. Report of the topographical features and character of the country. [3]–77. 2 plates (captioned but not numbered). 2 woodcuts. 8 plates (diagrams, Nos. 1–8).

CONTENTS: Contents, [5]; Illustrations, [6]; General sketch of the route, [7]; Sections I through VII (of the route), [8]–45; General remarks upon various subjects, [45]–77.

For Maps and profiles *see* under Volume XI.

Part III. Report upon the Indian tribes, by Lieut. A. W. Whipple, Thomas Ewbank, Esq., and Prof. Wm. W. Turner, [1]–127. 7 plates (captioned but not numbered). 30 woodcuts. 3 maps (Nos. 1, 2, 3; inserted in text).

CONTENTS: Contents, [3]; Illustrations, [5]; Report (7 chapters), [7]–127.

Part IV. Report on the geology of the route, [i]–[xiii]; [1]–175. 3 plates (1 in text, unnumbered; for Nos. I, II, fossils, *see fn.* 21); 18 woodcuts. Geological map. 2 Geological sections. 9 small Geological sections (included in No. 2 below).

CONTENTS: Contents, [v]–vii; Illustrations, [viii]; Errata and addenda, [ix]; Additional errata, [xi]; Introductory letter (to No. 1), [xiii]; No. 1. General report upon the geological collections. By William P. Blake, Geologist of the Office of the United States Pacific Railroad Explorations and Surveys (10 chapters),[21] [xiii]; [1]–116; Catalogue of the geological collection, [117]–119; No. 2. Resumé and field notes, by Jules Marcou,[22] Geologist and Mining Engineer to the expedition; with a translation by William P. Blake, [121]–164; Resumé of a geological reconnaissance, extending from Napoleon, at the junction of the Arkansas with the Mississippi, to the Pueblo de los Angeles, in California. By Jules Marcou, Geologist and Mining Engineer,[23] [165]–175.

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[20] This covers the subject matter of the entire Whipple report, Parts I through VI and its 13 Appendices (A through I, K through N), but only Parts I through IV are included in Volume III. For Parts V, VI and Appendices *see* under Volume IV.

[21] Chapter IX, [99]–105, is headed: "Descriptions and notices of the fossils collected upon the route. By Professor James Hall." It contains 2 plates (Nos. I, II).

[22] A "Note," [121], reads: "This paper is a copy of Mr. Marcou's field-book, and is an exact transcript of the original rough notes as they were taken while on the road or in camp."

[23] *Fn.* 1, [165], states: "This resumé is reprinted from the preliminary or first report of Lieutenant Whipple, in 8vo., Chap. VI, p. 40. (Reports of Pacific Railroad Surveys, House Doc. 129: Washington. 1855.)"

Volume IV — 1857

33d Cong., 2d Sess., House Ex. Doc. No. 91 [Serial No. 794]

The title-page of *Pacific Railroad Reports*, Volume IV, is dated 1856, but the "Introduction" to Part V, No. 4, [59], is dated January 12, 1857.[24]

Volume IV has three sets of page numbers.

It is a continuation of the Whipple report begun in Volume III and includes Part V, Part VI, No. 1, and "Appendices to report." These subdivisions are distinguished here as (1), (2) and (3) and their title-pages read:

(1) Part V. Report on the botany of the expedition. [i]–vii; [1]–195.

CONTENTS: Contents, [v]–vii; Nos. 1, 2, 3, 4, [1]–167; Index to botany, [169]–182; No. 5, [185]–193.

For included botanical profile and for plates *see* under Nos. 2, 3, 4, 5, below.

Part V includes five papers, headed respectively:

No. 1. General description of the botanical character of the country. By J. M. Bigelow, M.D. [1]–16.

No. 2. Description of forest trees. By J. M. Bigelow, M.D. [17]–26. Botanical profiles.

No. 3. Description of the Cactaceæ. By George Engelmann, M.D., of St. Louis, and John M. Bigelow, M.D. [27]–58. 24 plates (Nos. I–XXIV).

CONTENTS: No. 3, [27]–53; Explanation of the plates of Cactaceæ, [54]–58.

No. 4. Description of the general botanical collections. By John Torrey. [59]–182. 25 plates (Nos. I–XXV).

CONTENTS: Introduction, [59]; No. 4, [61]–161; Explanation of the plates, [163]–167; Index to botany, [169]–182.

No. 5. Description of the mosses and liverworts. By W. S. Sullivant. [185]–193. 10 plates (Nos. I–X).

CONTENTS: No. 5, [185]–191; Explanation of the plates, 192–193.

(2) Part VI. Report on the zoology of the expedition. [1]–17.

This includes one paper, headed:

No. 1. Field notes and explanations. By C. B. R. Kennerley, M.D., Physican and Naturalist to the expedition. [5]–17.

An inserted sheet, following p. 17, bears a "Note," reading: "*The remainder of the Zoological Report will appear in a subsequent volume, it being impossible to prepare it in time for publication in connexion with the other portions of this report.*"

For Part VI, Nos. 2, 3, 4, 5, *see* under Volume X.

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[24] *See* under Whipple report, *Part VI. Zoological report* (Volume X, [7], *fn.*), where it is stated — it would seem incorrectly — that No. 1 ". . . appeared in Vol. IV, 1856."

(3) Appendices to report. [1]–288.

These 13 appendices are distinguished by the letters A through I, K through N, and consist, according to a "Note" [3], of ". . . the original unreduced records of the astronomical, magnetic, and meteorological observations. . ."

Volume V — 1857

33d Cong., 2d Sess., Senate Ex. Doc. No. 78 [Serial No. 762]

The title-page of *Pacific Railroad Reports,* Volume V, is dated 1856, but the title-page of Part II. Geological report, is dated 1857 and Blake's letter transmitting that report is dated April 6, 1857.

Volume V has four sets of page numbers.

The title-page, covering the content of Volume V, reads:

Report of explorations in California for railroad routes, to connect with the routes near the 35th and 32d parallels of north latitude, by Lieutenant R. S. Williamson, Corps of Topographical Engineers.

Front matter preceding and following this title-page and related to Williamson's report in its entirety appears on 12 unnumbered pages and includes the following: Contents of Volume V; Letter to the Secretary of War; General table of contents; Introduction. Instructions from the War Department.

The "General table of contents" divides the report into Parts I, II, III and IV, and three Appendices (A, B, C). These subdivisions, distinguished here as (1), (2), (3), (4) and (5), are cited on their respective title-pages as follows:

(1) Part I. Report. [1]–43. 12 plates (Nos. I–XII). 12 wood engravings.

CONTENTS: Contents, [5]; Illustrations, [5]; Report, [7]–43.

For maps and profiles *see* under Volume XI.

(2) Part II. Geological report, by William P. Blake, Geologist and Mineralogist to the expedition. [i]–xvi; [1]–370; [i]–xiii.

CONTENTS: Blake letter submitting the report, [v]; Contents, [vii]–xii; [Contents of] Appendix, [xiii]; Illustrations, xiv–xvi; I. Itinerary, [1]–130; II. Geology of portions of the route, [131]–310; Appendix (Articles I through VII), [311]–370; Index, [i]–xiii.

For maps, sections, plates, wood engravings, *see* under I. Itinerary; II. Geology of portions of the route; and Appendix (Articles I, II, III, V and VII).

The three subdivisions of the Geological report are cited on their respective title-pages as follows:

I. Itinerary, or notes and general observations upon the geology, mineralogy, and agricultural capabilities of the route (10 chapters, I–X), [1]–130. 9 plates (Nos. I–IX). 53 wood engravings.

II. Geology of portions of the route (10 chapters, XI–XX). [131]–310. 8 plates (3 maps, 4 views, section). 34 wood engravings. Geological sections. Geological map.

Appendix. [311]–370.

For plates *see* under Articles I, II, III, V, VII, below.

The Appendix includes seven Articles (of a contemplated eight) which are headed respectively:

Article I. Notice of fossil fishes. By Professor Louis Agassiz. [313]–316. 1 plate (No. 1).

Article II. Description of the fossil shells.[25] By T. A. Conrad. [317]–329. 8 plates (Nos. II–IX).

Article III. Catalogue of the recent shells, with descriptions of the new species. By Augustus A. Gould, M.D. [330]–336. 1 plate (No. XI).

Article IV. Letter from Professor J. W. Bailey, describing the structure of the fossil plant from Posuncula River. [337].

For plate (No. XII, figs. 1, 2) *see* under Article V.

Article V. Description of the fossil wood from the Colorado Desert. By Prof. Geo. E. Schaeffer. [338]–339. 1 plate (No. XII, figs. 1–4).

Article VI. Chemical examination of soils and incrustations. By J. D. Easter, Ph.D. [340]–358.

CONTENTS: Article VI, 340–343; Catalogue of the geological collection with descriptions of several of the specimens, [343]–358.

Article VII. Description of plants collected along the route, by W. P. Blake, and at the mouth of the Gila.[26] By John Torrey. [359]–370. 10 plates (Nos. I–X).

CONTENTS: Article VII, [359]–367; Description of the plates, [368]–370.

Article VIII.[27]

(3) Part III. Botanical report: by E. Durand and T. G. Hilgard, M.D. [1]–15. 18 plates (Nos. I–XVIII).

(4) Part IV. Zoological report.[28]

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[25] A *fn.* states: "These descriptions were published in 1855. See Appendix to the Preliminary Geological Report, 8vo; Washington, 1855."

[26] An introductory paragraph, [359], signed by Torrey, mentions that the collection included, in addition to those of Blake, plants ". . . collected near Fort Yuma, by Major Thomas and Lieutenant Du Barry, of the United States army . . ."

[27] A page inserted at this point bears a "Note" reading: "Article VIII was not received in time for publication with the other portion of this report."

Article VIII has been cited in the contents of the Appendix (Part II. Geological report, [xiii]), as: "Description of fossil microscopic organism, from Monterey: By Professor J. W. Bailey." It has not been found in the series of *Pacific Railroad Reports* examined.

[28] A "*Note*" following the above title-page states: "The Zoological Report will appear in a subsequent volume, it being found impossible to prepare it in time for publication in connexion with the other parts of this report."

According to the "General table of contents" of Volume V, Part IV should have included the following papers: "No. 1. Mammals, by Professor S. F. Baird"; "No. 2. Birds, by Dr. A. L. Heermann, Physician and Naturalist to the expedition"; "No 3.

(5) Appendices. [1]–14.

CONTENTS: Appendix A. Distances and altitudes, [3]–4; Appendix B. Latitudes and longitudes, [5]; Appendix C. Data for profiles, [6]–14.

Volume VI — 1857

33d Cong., 2d Sess., Senate Ex. Doc. No. 78 [Serial No. 763]

The title-page of *Pacific Railroad Reports*, Volume VI, is dated 1857. This date is corroborated in a footnote to "Contents" of Abbot's zoological report, (Volume X, [7]), which reads: "Numbers 1, 2, and 3 [of Part IV. Zoological report, my (4) below] will be found in Vol. VI of the Pacific Railroad Surveys, printed and published in 1857 . . ."

Volume VI has five sets of page numbers.

The title-page covering the content of Volume VI reads:

Report of Lieut. Henry L. Abbot, Corps of Topographical Engineers, upon explorations for a railroad route, from the Sacramento Valley to the Columbia River, made by Lieut. R. S. Williamson, Corps of Topographical Engineers, assisted by Lieut. Henry L. Abbot, Corps of Topographical Engineers.

CONTENTS (front matter): Letter to the Secretary of War,[29] [3]–4; General table of contents, [5]; Introduction. Instructions from the War Department, [7]–15.

The Abbot report has five main subdivisions, distinguished here as (1), (2), (3), (4) and (5). Their respective title-pages read:

(1) Part I. General report. [17]–134. 12 plates (Nos. I–XI, XIII). 3 woodcuts.

CONTENTS: Contents, [21]–23; List of illustrations, [24]; General report (7 chapters), [25]–129; Index to General report, [130]–134.

For maps and profiles *see* under Volume XI.

(2) Part II. Geological report, [1]–85.

CONTENTS: Contents, [5]–7; List of illustrations, [8]; Nos. 1, 2, 3, and 4 of Geological report, [9]–85.

Part II contains four papers, headed respectively:

No. 1. Report upon the geology of the route. By J. S. Newberry, M.D., Geologist of the expedition (8 chapters), [9]–68. 1 plate (No. I). 11 woodcuts.

No. 2. Description of the tertiary fossils collected on the survey. By T. A. Conrad. [69]–73. 4 plates (Nos. II–V).

No. 3. Report upon an analytical examination of water and

Reptiles, by Dr. Edward Hallowell"; "No. 4 Fishes, by Dr. Charles Girard." For these papers *see* under Volume X.

[29] The Hon. Jefferson Davis held the post of Secretary of War from March, 1853, to March, 1857. The letter is addressed to the Hon. John B. Floyd who had been appointed to that office by President Buchanan in March, 1857.

minerals from the Hot Springs in Des Chutes Valley. Conducted under the direction of Prof. E. N. Horsford.[30] [74]–78.

No. 4. Catalogue of the minerals and fossils collected on the survey. [79]–85.

(3) Part III. Botanical report. [1]–102.

CONTENTS: Contents, [5]; List of illustrations, [7]–8; Nos. 1 and 2 of Botanical report, [9]–94; Index to Botanical report, [97]–102.

For plates and woodcuts *see* under Nos. 1 and 2 below.
Nos. 1 and 2 are headed respectively:

No. 1. Report upon the botany of the route. By John S. Newberry, M.D., Botanist of the expedition (2 chapters), [9]–64.
Chapter I. Geographical botany. [9]–19.
Chapter II. Description of the forest trees of northern California and Oregon. [20]–64. 10 plates (Nos. I–X). 28 woodcuts.

No. 2. General catalogue of the plants collected on the expedition. By J. S. Newberry, assisted by Asa Gray and John Torrey, as specified in the proper places, [65]–94.

No. 2 has four subdivisions:

I. Exogenous plants.[31] [65]–90. 6 plates (Nos. XI–XVI).
II. Endogenous plants. By John Torrey, [90]–92.
III. Mosses and liverworts. By W. S. Sullivant, 93–94.
IV. Lichens. By Edward Tuckerman, 94.

(4) Part IV. Zoological report. [1]–114.

CONTENTS: Contents, [5]; List of illustrations, [6]; Prefatory note to Part IV, [7]; Nos. 1, 2, and 3 [32] of Zoological report, [9]–114; Index to Zoological report, [i]–iv.

The subdivisions included in the Zoological report are the following:

No. 1. Report upon fishes collected on the survey. By Charles Girard, M.D. [9]–34. 11 plates. (Nos. XXIIa, XXIIb, XXVa, XXVb, XLa, XLVI, LXII, LXVI, LXVIII, LXX, LXXIV).

No. 2. Report upon the zoology of the route. By J. S. Newberry, M.D.[33] (2 chapters), [35]–110.

For allocation of included plates *see* under Chapters I, II, below.
The chapters are headed:

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[30] A Horsford letter, [74], refers to this as ". . . the report of my assistant, Mr. L. M. Dornbach. . ."

[31] In "Contents," [5], of Botanical report, the authors of "Exogenous plants" are named as Asa Gray, John Torrey, and J. S. Newberry.

[32] For omission of Part IV, No. 4, which had been cited in "Contents," [5], *see* "*Note*" following No. 3 below.

[33] A *fn.*, [38], states: "The species enumerated in this report have been determined, and their diagnoses prepared, by Prof. S. F. Baird, Assistant Secretary of the Smithsonian Institution."

Chapter I. Report upon the mammals: [35]–72. 3 plates (Nos. I, III, XXII).

Chapter II. Report upon the birds.[34] [73]–110. 2 plates (Nos. XXVI, XXXIV.

No. 3. Report upon the land shells collected on the survey. By W. G. Binney, Member of the Academy of Natural Sciences of Philadelphia. [111]–114.

A "Note" on an inserted page, following p. 114, states: "*No. 4 has not been completed in time for publication with the rest of this Report. It will appear in a subsequent volume.*" No. 4 had been cited in the "Contents," [5], of Part IV. Zoological report as: "Report upon reptiles collected on the survey. By S. F. Baird, Assistant Secretary of the Smithsonian Institution." For this *see* under Volume X.

(3) Appendices. [1]–64.

Distinguished by letters A through F, these 13 Appendices relate to astronomical observations and the like. They are enumerated in "General table of contents," [5], of the Abbot report.

An inserted page following the Appendices lists "Errata for Volume VI."

Volume VII — 1857

33d Cong., 2d Sess., Senate Ex. Doc No. 76 [Serial No. 764]

The title-page of *Pacific Railroad Reports*, Volume VII, is dated 1857. No included matter bears a later date.

Volume VII has five sets of page numbers.

"Contents of Volume VII," [3], records two subdivisions, distinguished here as (1) and (2). The title-page of the first reads:

(1) Report of explorations for railroad routes from San Francisco Bay to Los Angeles, California, west of the Coast Range, and from the Pimas Villages on the Gila to the Rio Grande, near the 32d parallel of north latitude, by Lieutenant John G. Parke, Corps of Topographical Engineers, assisted by Albert H. Campbell, Civil Engineer.

CONTENTS: Letter to the Secretary of War, (7); General table of contents, [9]; Introduction. Instructions from the War Department, [11]–15; Part. I. General report, [17]–[23],[35] [1]–12; Part II. Geological report, [1]–204; Part III. Botanical report, [1]–28; Appendices (A through E), [1]–118.

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[34] A *fn.*, [73], reads: "As the final determination of the species of birds collected by the expedition has not yet been completed by Prof. Baird, the names here given are to be considered as temporary. In his general report upon the birds of the Pacific Railroad Surveys, hereafter to appear, the names and pages of the species in this article will be carefully quoted, and any errors of determination thus rectified." For Baird's "general report upon the birds" see under Volume IX.

[35] The 23 pages (8 blank) which precede the text proper of Part I. General report, are, with the exceptions of pages 14, 15, 22, unnumbered. The content of some relate to Parke's report as a whole, while others represent front matter to Part I. I have inserted the missing page numbers and have allocated the subject matter to accord with my understanding of its proper association.

For maps and profiles *see* under Volume XI.

Parts I, II, III, and Appendices are cited on their respective title-pages as follows:

Part I. General report. [17]–[23]; [1]–42. 8 plates.

For allocation of the plates *see* under Nos. 1 and 2 below. For maps and profiles *see* under Volume XI.

CONTENTS: Contents, [21]–[23]; [1]–23; List of illustrations, [23]; Nos. 1 and 2, [1]–42.

The two subdivisions of the General report are headed:

No. 1. Report of explorations from San Francisco Bay to Los Angeles. [1]–18. 3 plates (Nos. I, II; the third not numbered).

No. 2. Report of explorations from Pimas Villages to Rio Grande. [19]–42. 5 plates (Nos. VI [= IV], V, VI, VII, VIII).

Part II. Geological report, by Thomas Antisell, M.D., Geologist of the expedition. [1]–204. 2 maps (geological). 24 plates.

For allocation of plates *see* under Chapters XXIX and XXX below.

CONTENTS: Contents, [5]–10; List of illustrations, [11]–13; Geological report (30 chapters), [15]–197; Description of the plates, [19]–204.

Of the 30 chapters of the Geological report, Chapter XXIX ("Report upon the palaeontology of the survey. By T. A. Conrad"), [189]–196, contains 10 plates (Nos. I–X); and Chapter XXX ("Order of position of Californian strata"), [197], contains 14 plates (Nos. I–XIV).

Part III. Botanical report: by John Torrey. [1]–28. 8 plates.

For allocation of plates *see* under Chapter I below.

CONTENTS: Contents,[36] [5]; Chapters I, II, III, [7]–28.

The subdivisions of the Botanical report are headed respectively:

Chapter I. List and descriptions of the plants collected. By John Torrey, M.D. [7]–22. 8 plates (Nos. I–VIII).

Chapter II. Synoptical tables of botanical localities. By Thomas Antisell, M.D. [23]–26.

Chapter III. Description of the plates. By John Torrey, M.D. [27]–28.

Appendices. [1]–116. 11 plates.

For allocation of plates *see* under Appendix A.

The five Appendices are headed respectively:

Appendix A. Remarks on meteorology and barometic results, with meteorological plates. By Albert C. Campbell, A.M. Civil Engineer to the expedition. [3]–14. 11 plates (Nos. I–XI).

Appendix B. Report upon the route from San Diego to Fort

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[36] This contains a list of plates.

Yuma via San Diego River, Warner's Pass, and San Felipe Canon. By Charles M. Poole, Chief Engineer. [15]–28.

Appendix C. Translation of an archive from Tucson. [29]–30.

Appendix D. Description of maps and profiles, with table of latitudes. [31]–34.

Appendix E. Table of distances, and barometric and meteorological observations and results. By Albert H. Campbell, A.M., Civil Engineer to the expedition. 35–116.

The title-page of the second subdivision of Volume VII reads:

(2) Conclusion of the official review of the reports upon the explorations and surveys for railroad routes from the Mississippi River to the Pacific Ocean. [1]–37.

For General map and General profiles *see* under Volume XI.

CONTENTS: Contents, [3]; Prefatory note, [5]; Nos. 1, 2, 3, 4, 5, [7]–37.

The five subdivisions of the "official review" are headed respectively:

No. 1. Extract from the annual report of the Secretary of War. December, 1855. [7]–10.

No. 2. Report upon the progress of the Pacific Railroad explorations and surveys. November, 1855. By Captain A. A. Humphreys, Corps of Topographical Engineers. [11]–18.

No. 3. Extract from the annual report of the Secretary of War, December, 1856. [19]–22.

No. 4. Report upon the progress of the Pacific Railroad explorations and surveys. November, 1856. By Captain A. A. Humphreys, United States Topographical Engineers. [23]–34.

No. 5. Table exhibiting the comparative lengths, cost, etc., of the different routes, with explanatory remarks. By Captain A. A. Humphreys, Corps Topographical Engineers. [35]–37.

Volume VII ends with an inserted page: "Errata for Volume VII."

Volume VIII — 1857

33d Cong., 2d Sess., Senate Ex. Doc. No. 79 (Serial No. 765)

The title-page of *Pacific Railroad Reports*, Volume VIII, is dated 1857. This date is corroborated in the "Preface" to Part II. Birds (Volume IX, [xiii]) which refers to the account of the mammals (Part I. below) as ". . . having been published in 1857. . ."

The pages of Volume VIII are numbered consecutively throughout.

Following "Contents of Volume VIII," [iii], is a title-page reading:

General report upon the zoology of the several Pacific Railroad routes.

CONTENTS: Letter to Captain Humphreys, Topographical Engineers,

[vii]; General table of contents,[37] [ix]; Introduction. General sketch of lines explored,[38] [xi]–xvii.

The title-pages covering the content of Volume VIII read:

> Part I. Mammals: by Spencer F. Baird, Assistant Secretary of the Smithsonian Institution. [xix]–xlviii; [1]–757. 38 woodcuts. 43 plates. (Nos. XVII–XXVIII, XXX–LX).
>
> CONTENTS: Contents, [xxiii]; Preface, [xxv]–xxix; Table of the higher groups, xxx–xxxi; List of species, [xxxii]–xlviii; Introductory remarks, [1]; [Orders of mammals, I through VI], [3]–684; Appendix A. List of authorities referred to in the preceding report, [685]–703; Appendix B. Alphabetical list of localities referred to in the preceding report, [704]–715; Alphabetical index. I. Systematic index of common names, [717]–720; Alphabetical index. II. Systematic index of scientific names, [721]–735; Explanation of the plates,[39] [737]–750; List of wood-cut figures, 750–752; Systematic list of illustrations, 755–757.

Volume IX — 1858

33d Cong., 2d Sess., Senate Ex. Doc. No. 78 [Serial No. 766]

The title-page of *Pacific Railroad Reports*, Volume IX, is dated 1858. No included matter bears a later date.

The pages of Volume IX are numbered consecutively throughout.

It is a continuation of the "General report upon the zoology of the several Pacific Railroad routes" begun in Volume VIII.

Following "Contents of Volume IX," [iii], and "Letter to Captain Humphreys, Topographical Engineers," [v], are title-pages readings:

> Part II. Birds: by Spencer F. Baird. Assistant Secretary Smithsonian Institution. With the co-operation of John Cassin and George N. Lawrence. [vii]–lvi; [1]–1005.
>
> CONTENTS: Contents, [xi]; Preface,[40] [xiii]–xvi; I. Table of the

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[37] This cites the content of Volume VIII (Part I. Mammals); of Volume IX (Part II. Birds); and of Volume X (as to Part III. Reptiles and Part IV. Fishes).

[38] A valuable reference paper, enumerating collectors in natural history, not only along the main lines of the Pacific Railroad surveys but along routes "intimately connected" therewith. Included also are men who, working independently, made collections contributing to the report. For a somewhat similar paper *see* "Preface" (Volume IX, [xiii]–xvi).

[39] A *fn.*, [747] explains to which reports the plates of mammals enumerated in the list of illustrations supplied in the "Explanation of the plates" should be allocated: whether to the "General report upon the zoology of the several Pacific Railroad routes" (" . . . all that have been prepared for the present volume . . .") or to ". . . the special reports of the different railroad parties. . .", and tells how plates associated with special reports should be distinguished. A list of officers in command of the different lines of survey and the zoologists associated with them, is also supplied. Despite the explicit directions, attempts to check the plates were not successful.

[40] This useful enumeration of collectors is somewhat similar to the one supplied in "Introduction. General sketch of lines explored" (Volume VIII, [xi]–xvii) for the reason that some of the men collected in more than one branch of natural history. But it contains additional names and covers some different territory.

higher groups, [xvii]–xxiv; II. List of species, [xxx]–lvii; Introductory remarks, [1]–2; [Orders of birds, I through VI], [3]–920; Appendix A. Additional remarks on North American birds, [921]–925; Appendix B. Birds found at Fort Bridger, Utah, [926]–937; Appendix C. List of authorities referred to in the preceding report, [928]–954; Alphabetical index. I. Systematic index of common names, [955]–963; Alphabetical index. II. Systematic index of scientific names, [965]–1005.

Volume X — 1859

33d Cong., 2d Sess., Senate Ex. Doc. No. 78 [Serial No. 767]

The title-page of *Pacific Railroad Reports*, Volume X, is dated 1859. This date is corroborated in a footnote to the "Contents" of Abbot's report (Part IV. Zoological report, Volume X, [7]), which states: "No. 4 [Report on reptiles collected on the survey. By S. F. Baird] dates 1859." *See fn.* 49.

Volume X has seven sets of page numbers.

"Contents of Volume X," [3], names two subdivisions: first, Parts III and IV of the "General report upon the zoology of the several Pacific Railroad routes" (continued from Volumes VIII and IX); and, second, five groups of zoological papers which had not been ready when the reports with which they are affiliated has been published; they are distinguished here as (1), (2), (3), (4), and (5).

The title-pages of Parts III and IV read respectively:

Part III. Reptiles: by Spencer F. Baird, Assistant Secretary of the Smithsonian Institution. [7]–18. 13 plates (Nos. XXIV–XXXVI).

CONTENTS: Letter of Humphreys,[41] [11]; Explanation of the plates, [13]–16.

Part IV. Fishes: by Charles Girard, M.D. [i]–xiv; [1]–400. 21 plates (Nos. VII, VIII, XIII, XIV, XVII, XVIII, XXIIc, XXVI, XXIX, XXX, XXXIV, XXXVII, XL, XLI, XLVIII, LIII, LIX, LXI, LXIV, LXV, LXXI).

CONTENTS: Contents, [v]–xiv; Introductory remarks,[42] [1]–2; [Orders of fishes, I through X], [3]–284; List of the plates,[43] [385]–388; Alphabetical index, 389–400.

The title-pages of the five groups of reports forming the second subdivision of Volume X read respectively:

(1) Report of Lieut. E. G. Beckwith, Third Artillery, upon explorations for a railroad route, near the 38th and 39th parallels of north latitude,

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[41] This reads: "The General Natural History Reports having been extended so much beyond the limits originally contemplated, the War Department has considered it advisable to omit the publication of the Report on Reptiles. The plates to accompany this report having been prepared and printed, they, with a brief explanation of the figures composing them, are herewith given."

[42] These appear in two forms in the printing under analysis. One was presumably a preliminary draft and should have been omitted.

[43] A *fn.* states: "Plates XXIIa, XXIIb, XXVa, XLa, XLVI, XLVII, LXVI, LXVIII, LXX and LXXIV of this list will be found in vol. VI, part IV, of the present series. Other plates missing from this volume will be found in vol. X."

by Captain J. W. Gunnison, Corps of Topographical Engineers, and near the forty first parallel of north latitude, by Lieut. E. G. Beckwith, Third Artillery. Zoological report.[44] 20 plates.

For allocation of the plates see under Nos. 1, 2, 3, and 4 below.

Contents: Contents,[45] [5], List of illustrations, [6]; Nos. 1, 2, 3, and 4, [7]–27; Alphabetical index, [28].

The four included zoological reports are headed respectively:

No. 1. Report upon mammals collected on the survey. By S. F. Baird. [7]–9. 3 plates (Nos. IV, VI, X).

No. 2. Report upon birds collected on the survey. By S. F. Baird. [13]–16. 7 plates (Nos. XII, XIII, XIV, XV, XVII, XXXII, XXXV).

No. 3. Report on reptiles collected on the survey. By S. F. Baird. [17]–20. 4 plates (Nos. XVII, XVIII, XXIII, XXIV).

No. 4. Report on fishes collected on the survey. By Charles Girard, M.D. [21]–27. 6 plates (Nos. XXIII, XLIX, LIV, LVI, LXXIII, LXXV).

(2) Report of explorations for a railway route (near the thirty-fifth parallel of north latitude), from the Mississippi River to the Pacific Ocean. By Lieutenant A. W. Whipple, Corps of Topographical Engineers: assisted by Lieutenant J. C. Ives, Corps of Topographical Engineers. Part VI.[46] Zoological report. [1]–34. 34 plates.

For allocation of plates *see* under Nos. 2, 3, 4 and 5 below.

Contents: Contents,[47] [7]; List of illustrations, [9]–10; Nos. 2, 3, 4, and 5, [11]–59; Alphabetical index, [61]–64.

The four included zoological reports are headed respectively:

No. 2. Report on mammals collected on the survey. By C. B. R. Kennerley, M.D. [11]–18. 6 plates (Nos. VIII, XI, XII, XIII, XIV, XVI).

No. 3. Report on birds collected on the route. By C. B. R. Kennerley, M.D. [19]–35. 11 plates (Nos. XVIII, XIX, XX, XXII, XXVII, XXIX, XXX, XXXI, XXXIII, XXXVI, XXXVII).

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[44] A *fn.* states: "The report to which this article belongs will be found in Vol. II of this series."

[45] Of five zoological reports listed, only four are included. The missing report, named in "Contents" as "No. 5. Report on insects collected on the survey. By John L. Leconte, M.D.," has not been found in the quarto series.

[46] For Parts I, II, III and IV, *see* Volume III; for Part V, and Part VI, No. 1, *see* Volume IV.

[47] Of five zoological reports cited, only four are included. Of the missing report (No. 1. Field notes and explanations. By C. B. R. Kennerley, M.D.) it is stated in a *fn.*: "No. 1 has already appeared in Vol. IV, 1856." According to my analysis Volume IV was published in 1857, certainly not earlier. See Volume IV, Introduction to Part V, No. 4, [59], which is dated January 12, 1857.

No. 4. Report upon the reptiles of the route. By S. F. Baird. [37]–45. 3 plates (Nos. XXV, XXVI, XXVII).

No. 5. Report upon fishes collected on the survey. By C. Girard, M.D. [47]–59. 14 plates (Nos. III, IV, V, VI, IX, X, XXI, XXIV, XXV, XXXV, XLb, LII, LVII, LVIII).

(3) Report of explorations for a railroad route near the 32d parallel of north latitude, lying between Dona Ana, on the Rio Grande, and Pimas Villages, on the Gila, by Lieutenant John G. Parke, Corps of Topographical Engineers. Zoological report. [1]–24. 4 plates.

For allocation of plates *see* under Nos. 1 and 2 below.

CONTENTS: Contents, [5]; List of illustrations, [6]; Introductory letter, [7]; Nos. 1 and 2, [9]–24.

The two included zoological reports are headed respectively:

No. 1. Report upon the birds collected on the survey. By A. L. Heermann, M.D. [9]–21. 3 plates (Nos. I, IV, VI).

No. 2. Report upon reptiles collected on the survey. By Edward Hallowell, M.D. [23]–24. 1 plate (No. II).

(4) Report of explorations in California for railroad routes to connect with the routes near the 35th and 32d parallels of north latitude. By Lieutenant R. S. Williamson, Corps of Topographical Engineers. Part IV. Zoological report, [i]–[viii]; [1]–91. 26 plates.

For allocation of plates *see* under Nos. 1, 2, and 4 below.

CONTENTS: List of illustrations, [vi]; Contents,[48] [vii]; Introductory letter. By A. L. Heermann, M.D. [viii]; Nos. 1, 2, 3 and 4, [1]–91; Alphabetical index, [93]–97.

The four included zoological reports are headed:

No. 1. Report upon the reptiles collected on the survey. By Dr. Edward Hallowell. [1]–23; List of reptiles collected. By Dr. A. L. Heermann, Naturalist to the expedition, [24]–25; Explanation of the plates, [26]–27. 9 plates (Nos. I, III, IV, V, VII, VII [sic], VIII, IX, X).

No. 2. Report upon birds collected on the survey. By A. L. Heermann, M.D. [29]–77; List of birds collected between San Francisco and Fort Yuma, California, during the survey of railroad routes from the Mississippi to the Pacific Ocean, under the command of Lieutenant R. S. Williamson, Top. Engs. [79]–80. 7 plates (Nos. II, III, V, VII, VIII, IX, X).

No. 3. Report on mammals collected on the survey. By S. F. Baird. [81]–82.

No. 4. Report on fishes collected on the survey. By Charles Girard,

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[48] A *fn.* states: "The report to which the present part belongs will be found in volume V."

M.D. [83]–91. 10 plates (Nos. II, XII, XXII, XXVII, XXVIII, XXXI, XXXVI, XXXVIII, XXXIX, XLVII).

(5) Report of Lieut. Henry L. Abbot, Corps of Topographical Engineers, upon explorations for a railroad route, from the Sacramento Valley to the Columbia River, made by Lieut. R. S. Williamson, Corps of Topographical Engineers, assisted by Lieut. Henry L. Abbot, Corps of Topographical Engineers. Part IV. Zoological report. [1]–13. 4 plates.

For plates *see* under No. 4 below.

CONTENTS: Contents,[49] [7]; List of illustrations, [8]; No. 4, [9]–15.

The included zoological report is headed:

No. 4. Report on reptiles collected on the survey. By S. F. Baird. [9]–13. 4 plates (Nos. XI, XXVIII, XXX, XLIV).

Volume XI — 1859

33d Cong., 2d Sess., House Ex. Doc. No. 91 [Serial No. 801]

The title-page of *Pacific Railroad Reports*, Volume XI, is dated 1855, but the title-page of Warren's Memoir as well as the title-page preceding the maps, profiles, plates, etc., which form the last half of the volume, are dated 1859.

Following the "Contents of Volume XI," [3], and "Letter to the Secretary of War," [5], is a title-page reading:

Memoir to accompany the map of the territory of the United States from the Mississippi River to the Pacific Ocean, giving a brief account of each of the exploring expeditions since A.D. 1800, with a detailed description of the method used in compiling the general map. By Lieut. Gouverneur K. Warren, Corps of Topographical Engineers, U.S.A. [3]–120. 4 plates (Nos. I, II, III, IV).[50]

CONTENTS: Letter to Captain A. A. Humphreys, Topographical Engineers, [9]; Contents, [11]–12; List of illustrations, [13]; Introductory remarks, [13]–16; Memoir (6 chapters), [17]–115; Alphabetical index, [117]–120.

The remainder of Volume XI is preceded by a title-page reading:

Topographical maps, profiles, and sketches, to illustrate the various reports of surveys for railroad routes from the Mississippi River to the Pacific Ocean.

This is followed by "Contents," [iii]–iv, in which the illustrations, segregated under ten headings, are meticulously enumerated and described. These headings and the total number and type of illustration allotted to each in the "Contents" follow:

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[49] A *fn.* states: "Numbers 1, 2, and 3 will be found in Vol. VI of the Pacific Railroad Surveys, printed and published in 1857. No. 4 dates 1859."

[50] These are reduced copies of old maps, intended for insertion in the text.

Sketch of route of the 41st parallel — Beckwith's Report, Vol. II. 8 plates (views). 5 panoramas (views).

Official review of the reports — Vols. I and VII. General map. General profile.

Route of the 47th and 49th parallels — Stevens's Report, Vol. I. 3 maps (Nos. 1, 2, 3). Profiles.

Routes in Oregon and California — Abbot's Report, Vol. VI. 2 maps (Nos. 1, 2). 2 profiles (Nos. 1, 2).

Route near the 41st parallel — Beckwith's Report, Vol. II. 4 maps (Nos. 1, 2, 3, 4). Profiles of the route.

Route near the 38th and 39th parallels — Beckwith's Report, Vol. II. Profiles of the route. 4 maps (Nos. 1, 2, 3, 4).

Route near the 35th parallel — Whipple's Report, Vol. III. 2 maps (Nos. 1, 2). Profiles.

Routes in southern California — Williamson's Report, Vol. V. 4 maps. 2 profiles (sheets Nos. 1, 2).

Routes in California and on the 32d parallel — Parke's Reports, Vol. VII. 2 maps (Nos. 1, 2). Profiles.

Route of the 32d parallel — Pope's Report, Vol. II. Map and profile.

Volume XII. Book I [51] — 1860

36th Cong., 1st Sess., House Ex. Doc. No. 56 [Serial No. 1054]

The title-page of *Pacific Railroad Reports*, Volume XII, Book I, is dated 1860. No included matter bears a later date.

The volume has two sets of page numbers.

"Contents of Volume XII. Book I," [3], records two subdivisions: Part I and Appendices.[52]

Following "Contents of Volume XII. Book I" is a title-page reading:

Narrative and final report of explorations for a route for a Pacific railroad, near the forty-seventh and forty-eighth parallels of north latitude, from St. Paul to Puget Sound. By Isaac I. Stevens, Governor of Washington Territory.

This is followed by "Letter to the Secretary of War," by the "General table of contents" and by an "Introduction."

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[51] The first Stevens report appeared in Volume I. His second and final report and the scientific papers associated with it necessitated two volumes which are distinguished on the title-pages of *Pacific Railroad Reports* as "Volume XII. Book I" and "Volume XII. Book II."

[52] The subdivisions are in accord with the contents of Book I as issued. For the reason that, with one exception, none of the pages in Volume I preceding page 20 is numbered and the exception, page "18," bears no numerical relationship to those which precede or follow it, and for the reason that the "General table of contents," [9], places the Appendices after Part III. Zoological report (Volume XII. Book II), it seems probable that there were "last minute" changes in the compilation of Books I and II which were not incorporated in the introductory pages of Book I. *See* also *fn.* 54.

The title-page of the first subdivision of Volume XII, Book I reads:

Part I. General report. [15]–358. 70 plates (Nos. I–LXX). 2 maps. 1 sheet of profiles.

CONTENTS: Contents, [19]–27; List of illustrations, [29]–30; General report (18 chapters), [31]–358.[53]

The second subdivision of Volume XII. Book I is preceded by a title-page reading:

Appendices. [1]–25.[54]

CONTENTS: Appendix A. Heights and distances. [3]–12; Appendix B. Meteorological register, [13]–25.

Volume XII. Book II — 1860

36th Cong., 1st Sess., House Ex. Doc. No. 56 [Serial No. 1055]

The title-page of *Pacific Railroad Reports,* Volume XII. Book II, is dated 1860. No included matter bears a later date.

The volume has two sets of page numbers.

It is a continuation of the Stevens report begun in Volume XII. Book I. "Contents of Volume XII. Book II," [3], divides the subject matter into two Parts which are cited on their respective title-pages as follows:

Part II. Botanical report. [5]–76. 6 plates.

For allocation of plates *see* under Nos. 2 and 3 below.

CONTENTS: Contents, [9]; List of illustrations, [11]; Nos. 1, 2 and 3 of Botanical report, [13]–71; Index to Botanical report, [73]–76.

The three included papers are headed respectively:

No. 1. Report on the botany of the route. By J. G. Cooper, M.D. [13]–39.

No. 2. Catalogue of plants collected east of the Rocky Mountains. By Professor Asa Gray. [40]–49. 5 plates (Nos. I, II, III, IV, V).

No. 3. Catalogue of plants collected in Washington Territory. By J. G. Cooper, M.D. [50]–71. 1 plate (No. VI).

Part III. Zoological report. [i]–[ix]; [1]–399. 46 plates.

For allocation of plates *see* under Nos. 1, 2, 3, 4, 5 below.

CONTENTS: Contents, [v]–vi; List of illustrations,[55] [vii]–viii.

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[53] The "General report" is subdivided into Narrative of 1853 (Chapters I–X, [31]–195); Narrative of 1855 (Chapters XI–XII, [196]–225); Geographical memoir (Chapters XIII–XVI, [226]–331); Railroad report and estimate (Chapter XVII, [332]–351); Computation of altitudes from barometrical observations. Table of heights and distances. Meteorological register (Chapter XVIII, [352]–358).

[54] Following the Appendices and with pages in numerical sequence thereto is an Alphabetical index, [27]–41. Its content does not cover the Appendices and its existence is nowhere recorded in the volume. *See fn.* 52.

[55] This enumerates between 80 and 90 plates, more than half of which are referred to zoological reports contained in Volume XII. Book II, and the remainder to zoological reports published in earlier volumes of the series. Attempts to check the enumeration

Prefatory note to Part III, [ix]; Nos. 1 through 7 of Zoological report, [1]–389; Index to Zoological report, [391]–399.

Part III contains 7 papers, headed respectively:

No. 1. Report upon insects collected on the survey. By John T. Leconte, M.D. [1]–77. 2 plates (Nos. I, II).

No. 2. Report upon the mammals collected on the survey. [73]–138. 5 plates.

For allocation of plates *see* under Chapters I and II below.
No. 2 contains 3 reports headed respectively:

Chapter I. Report by J. G. Cooper, M.D. [73]–88. 4 plates (Nos. V, VII, IX, XV).

Chapter II. Report by Dr. Geo. Suckley, U.S.A. [89]–106. 1 plate (No. II).

Chapter III. Report of Dr. Geo. Suckley, U.S.A., and Geo. Gibbs, Esq. [107]–138.

No. 3. Report upon the birds collected on the survey. [140]–291. 8 plates.

For allocation of plates *see* under Chapters I, II, below.
No. 3 contains 2 subdivisions, headed respectively:

Chapter I. Land birds, by J. G. Cooper, M.D. [140]–226. 7 plates (Nos. XI, XVI, XXVIII, XXI, XXIII, XXIV, XXV).
Chapter II. Water birds, by Dr. G. Suckley, US.A. [227]–291. 1 plate (No. XXXVIII).

No. 4. Report upon the reptiles collected on the survey. By J. G. Cooper, M.D. [292]–306. 11 plates. (Nos. XII, XIII, XIV, XV, XVI, XIX, XX, XXI, XXII, XXIX, XXXI).

No. 5. Report upon the fishes collected on the survey. By Dr. G. Suckley, U.S.A. [307]–368. 21 plates (Nos. I, XI, XV, XVI, XIX, XX, XXXII, XXXIII, XLII, XLIII, XLIV, XLV, L, LI, LV, LX, LXIII, LXVII, LXIX, LXXII, LXXV).

No. 6. Report upon the Mollusca collected on the survey. By William Cooper. [369]–386.

No. 7. Report on the Crustacea collected on the survey. By J. G. Cooper, M.D. [387]–389.

ALPHABETICAL INDEX OF AUTHORS TO BE USED IN CONJUNCTION WITH THE ANALYSES[56]

ABBOT, H. L. (Sacramento Valley to Columbia River): Report, v. VI.
AGASSIZ, L. (Williamson route): Fossil fishes, v. VI.

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of this List with plates in the given reports have not been satisfactory, either as to the total number of plates or as to their allocation. *See fn.* 39.

[56] To the first Stevens report published in Volume I are appended (pp. 160–635),

Antisell, T. (Parke route): Geological report; Synoptical table botanical localities, v. VII.

*Arnold, R. 160–177, v. I.

Bailey, J. W. (Williamson route): Fossil plant Posuncula River, v. V.

Baird, S. F. (Pope route): Preliminary report natural history, v. II.
(General report on zoology): Mammals, v. VIII. Birds, v. IX. Reptiles, v. X.
(Beckwith and Gunnison routes): Mammals; Birds; Reptiles, v. X.
(Whipple route): Reptiles, v. X.
(Williamson route): Mammals, v. X. (Abbot route): Reptiles, v. X.

Beckwith, E. G. (41st parallel route): Report, v. II. (Gunnison route, 38th and 39th parallels): Report, v. II.

Bigelow, J. M. (Whipple route): Botanical character country; Forest trees, v. IV.

Bigelow, J. M. *See* Englemann, G.

Binney, W. G. (Abbot route): Land shells, v. VI.

Blake, W. P. (Pope route): Geology, v. II. (Whipple route): General report geological collections, v. III. (Williamson route): Geological report, v. V.

*Blodget, L. 566–571, v. I.

*Burr, F. H. 586–597, v. I.

Byrne, T. H. (Pope route): Diary, v. II.

Campbell, A. H. (Parke route): Table distances, barometric observations, v. VII.

Conrad, T. S. (Williamson route): Fossil shells, v. V. (Abbot route): Tertiary fossils, v. VI. (Parke route): Palaeontology, v. VII.

*Cooper, J. G. (Stevens route): Botany; Catalogue plants Washington Territory; Mammals; Land birds; Reptiles; Crustacea, v. XII. Book II. *See also*: 179–180; 219–221, v. I.

Cooper, W. (Stevens route): Mollusca, v. XII. Book II.

Davis, J. Report on the several railroad explorations, v. I.

*Donelson, A. J. 231–247; 269–279; 358–359; 360–363, v. I.

Dornbach, L. M. (Abbot route): Examination water, minerals, v. VI.

*Doty, J. 441–442; 442–445; 445–446; 543–553; 553–565; 572–584, v. I.

*Duncan, J. K. 203–219, v. I.

Durand, E. and Hilgard, T. G. (Williamson route): Botanical report, v. V.

Easter, J. D. (Williamson route): Chemical examination soils, incrustations, v. V.

Emory, W. H. Extract from report of a military reconnaissance made 1846, 1847, v. II.

Engelmann, G. and Bigelow, J. M. (Whipple route): Cactaceae, v. IV.

Ewbank, J. *See* Whipple, A. W.

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together with letters, etc., etc., a number of signed documents describing work done in connection with particular sections and aspects of his survey; some of these (pp. 160–449) were appended to the report when submitted; others (pp. 449–635) were added at a later date. In my analysis of the content of the report these papers are merely noted as "Miscellaneous documents related to special aspects of the survey, 160–635", and neither the authors nor the long descriptive titles of their papers are enumerated — in *fn.* 10, reference is made to the present statement.

In the "Alphabetical index of authors" the names of those who contributed these appended papers are preceded by an asterisk and the pages where their contributions appear in the Stevens report of Volume I are supplied. In instances where authors contributed papers which are cited in the analyses, and appended reports also, the first take precedence and the last are preceded by the notation *See also*.

*Gibbs, G. 402–434; 465–473; 473–486, v. I.

Gibbs, G. *See* Suckley, G.

Girard, C. (Abbot route): Fishes, v. VI. (General report on zoology): Fishes, v. X. (Beckwith and Gunnison routes): Fishes, v. X. (Whipple route): Fishes, v. X. (Williamson route): Fishes, v. X.

Gould, A. A. (Williamson route): Recent shells, v. V.

Gray, A. (Stevens route): Catalogue plants from east of Rocky Mountains, v. XII. Book II.

Gray, A., Torrey, J., and Newberry, J. S. (Abbot route): Exogenous plants, v. VI.

Gray, A. *See* Torrey, J.

*Grover, C. 222–223; 247–248; 396–398; 486–488; 488–498; 498–515, v. I.

Gunnison, J. W. For route of, *see* Beckwith, E. G.

Hall, J. (Whipple route): Fossils, v. III.

Hallowell, E. (Parke route): Reptiles, v. X. (Williamson route): Reptiles, v. X.

Heermann, A. L. (Parke route): Birds, v. X. (Williamson route): Birds, v. X.

Hilgard, T. C. *See* Durand, E.

Humphreys, A. A. Official review reports and explorations, 1855, 1856, v. VII.

Humphreys, A. A. and Warren, G. K. Examination of reports of explorations made 1853, 1854, and earlier, v. I.

Hunt, E. B. Index to Stevens report, v. I.

Jesup, T. S. Cost transporting troops, supplies, v. I.

Kennerley, C. B. R. (Whipple route): Zoological field notes, v. IV. (Whipple route): Mammals; Birds, v. X.

*Lambert, J. 160–177, v. I.

*Lander, F. W. Reconnaissance Puget Sound to Mississippi River, v. II. *See also*: 186–187; 224–225, v. I.

Leconte, J. T. (Stevens route): Insects, v. XII. Book II.

*Macfeeley, R. 286–290, v. I.

*McClellan, G. B. Memoranda on railways, v. I. *See also*: 180–183; 188–202, v. I.

Marcou, J. (Whipple route): Resumé, field notes; Geological reconnaissance Napoleon to Pueblo de los Angeles, v. III.

*Minter, J. F. 377–389, v. I.

*Mowry, S. 389–395; 602–613, v. I.

*Mullan, J. 301–319; 319–349; 349–352; 437–441; 516–527; 527–537; 538–540, v. I.

Newberry, J. S. (Abbot route): Geology; Botany (Geographical botany; Forest trees northern California and Oregon); Zoology (Mammals; Birds), v. VI.

Newberry, J. S. *See* Gray, A.

Parke, J. G. (32d parallel, Dona Ana to Pimas Villages): Report, v. II. (San Francisco Bay to Los Angeles and Pimas Villages to Rio Grande near 32d parallel): Report, v. VII.

Poole, C. M. (San Diego to Fort Yuma, Parke route): Report, v. VII.

Pope, J. (32d parallel route, Red River to Rio Grande): Report, v. II.

*Saxton, H. 249–250; 251–269, v. I.

Schaeffer, G. E. (Williamson route): Fossil wood, v. V.

*Stanley, J. M. 447–449, v. I.

Stevens, I. I. (47th and 49th parallels): Report, v. I. Narrative and final report, v. XII. Book I.

*SUCKLEY, G. (Stevens route): Mammals; Water birds; Fishes, v. XII. Book II. *See also*: 177–179; 291–301, v. I.

SUCKLEY, G. and GIBBS, G. (Stevens route): Mammals, v. XII. Book II.

SULLIVANT, W. S. (Whipple route): Mosses and liverworts, v. IV. (Abbot route): Mosses and liverworts, v. VI.

*TINKHAM, A. W. 184–186; 226–230; 276–281; 352–358; 399–400. v. I.

TORREY, J. (Whipple route): Description general botanical collections, v. IV. (Williamson route): Plants collected by W. P. Blake, v. V. (Abbot route): Endogenous plants, v. VI. (Parke route): Botanical report (Description of plants collected; Description of plates), v. VII.

TORREY, J. *See* GRAY, A.

TORREY, J. and GRAY, A. (Beckwith and Gunnison routes): Botany, v. II. (Pope route): Botanical report, v. II.

TUCKERMAN, E. (Abbot route): Lichens, v. VI.

TURNER, W. W. *See* WHIPPLE, A. W.

WARREN, G. K. Memoir of explorations since A.D. 1800, v. XI.

WARREN, G. K. *See* HUMPHREYS, A. A.

WHIPPLE, A. W. Extracts from preliminary report, v. III. (35th parallel route): Report, v. III.

WHIPPLE, A. W., EWBANK, T., and TURNER, W. W. (Whipple route): Indian tribes, v. III.

WILLIAMSON, R. S. (Route to connect with those near 35th parallel): Report, v. V.

STUDIES IN THE GENUS COCCOLOBA, VI. THE SPECIES FROM THE LESSER ANTILLES, TRINIDAD AND TOBAGO *

RICHARD A. HOWARD

THE PRESENT STUDY continues a series of papers on the genus *Coccoloba* as it occurs in the West Indies. A single study of the genus as a whole has been considered impossible for a number of reasons. Not only is the genus a large one, but reliable data based on field observations, particularly in relation to hybridity and possible apomixis, have been lacking. In addition, the application of many names is difficult, for too many species, including some only recently described, have been based on anomalous specimens (adventitious shoots, for example). Many names either have been misapplied or have passed unnoticed and many species are represented only by the type collection. A further difficulty is the lack of strong and easily defined characteristics which can be used in dividing the genus taxonomically. Some of these obstacles have been overcome in part, as has been pointed out in earlier papers of this series. However, other difficulties, such as our inadequate knowledge of the range of variation in these plants, still remain and much more field work will be needed.

The artificial geographical division which was the basis for my previous studies of the genus as it occurs in Cuba, Jamaica, Puerto Rico and the Bahamas, Hispaniola, and now the Lesser Antilles and Trinidad, has allowed progressive steps which will be the foundation for further work on the genus in South America, Central America and Mexico.

In 1950 I completed a field study of *Coccoloba* in the Lesser Antilles, Trinidad and Tobago which supplied much of the material and information used in this paper. I am grateful to the directors of the American Philosophical Society and the directors of the Milton Fund of Harvard University for grants which made the field work possible. Specimens used in this study have been borrowed from a number of herbaria and botanical institutions represented by the standard abbreviations given. I wish to express my grateful appreciation to the directors and the curators of these institutions for the use of these specimens.

The same difficulties encountered in earlier work apply to this study. Although field work in the Caribbean area has resolved many problems, many others remain and further studies will be necessary for a complete understanding of many of the species. The variation in leaf-form and -size when correlated with the growth habit of any particular plant should be incorporated into a general description of the species. In doing so, the

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*The preceding papers in this series will be found in Jour. Arnold Arb. **30**: 388–424. 1949; **37**: 317–339. 1956; **38**: 81–106. 1957; **38**: 211–242. 1957; **39**: 1–48. 1958.

construction of a key to species to cover all variations seen in the field and represented in the herbarium collections becomes more difficult. In some species only one sex is known; in some, the fruiting material is unknown or is inaccurately associated with the flowering material.

Fortunately, I have been able to see the type material of all of the more recently described species and all but a few of the older species. Many of Lindau's species from Trinidad were based on specimens in the herbarium of the Imperial College of Tropical Agriculture, Port of Spain, Trinidad. Fragments of these specimens were placed by Lindau in the herbarium of Krug and Urban in the Botanisches Museum in Berlin. The fragments remain in Berlin, but the more complete material in Trinidad has largely been destroyed by the tropical environment and by periods of neglect.

The geographic area considered in this paper is currently regarded as an unnatural one. The Lesser Antilles (the Leeward and Windward Islands from Antigua to Grenada) form a group of relatively young islands, mostly volcanic in origin. The natural vegetation of this area is presumed to have been derived by migrations southward from the Greater Antilles, by migrations northward from Trinidad and South America and by the *in situ* development of some endemic or localized species. Trinidad and Tobago, in contrast, appear floristically as well as geologically as a part of the South American mainland. Of the seventeen taxa considered in this paper, two (*Coccoloba uvifera* and *C. venosa*) are widespread, appearing along the seacoasts of the Antilles, Central America and South America. Four species and one form, *C. diversifolia*, *C. krugii*, *C. pubescens*, *C. swartzii* and *C. swartzii* f. *pubescens*, are found in the Greater Antilles and extend to varying degrees into the Lesser Antillean islands. Only one taxon, *C.* × *boxii*, representative of a hybrid population, occurs only in the Lesser Antilles. *Coccoloba dussii* occurs only in the Lesser Antilles and Trinidad, but is very similar to a species from South America. *Coccoloba ascendens* and *C. novogranatensis* occur in the Lesser Antilles and Trinidad and in South America, with the range of *C. novogranatensis* extending west and then north through Central America, while the range of *C. ascendens* continues south and east in Brazil. Five species (*C. cruegeri*, *C. fallax*, *C. latifolia*, *C. nitida* and *C. striata*) occur in Trinidad and South America but have not been found in the Lesser Antilles. One species, *C. nigrescens*, is currently known only from the Bocas Islands near Trinidad, but additional material will probably reveal its relationship or identity with other southern species.

Thus, in contrast to the Greater Antilles where the genus *Coccoloba* has evolved a great many endemic species, neither Trinidad nor the Lesser Antilles has experienced a parallel elaboration of the genus. The Lesser Antillean species of *Coccoloba* are predominantly Greater Antillean species which have migrated southward. The species found in Trinidad are basically South American and only a few species have migrated northward into the Lesser Antilles.

Following the key, the species are described and are listed in alphabetical order.

KEY TO THE SPECIES

A. Inflorescence paniculate, stems thick, striate-angled, hollow; leaves umbonate between the conspicuously reticulate veins. .... *C. latifolia.*

AA. Inflorescence racemose, solitary or fascicled.

B. Inflorescence generally fasciculate; ocreae large and flaring, conspicuously striate. .... *C. fallax.*

BB. Inflorescence solitary, rarely with a smaller one at the base.

C. Lianas or woody plants with scrambling branches.

D. Branches scandent or entire plant with flattened stems through bilateral cambial activity; flowers and fruit on pedicels longer than ocreolae. .... *C. dussii.*

DD. Branches uniformly thickened; pedicels scarcely, if at all, exceeding ocreolae in flower; fruit on conspicuous pedicels.

E. Leaves of normal shoots usually oblong-elliptic, coriaceous, shining when dry, flat, coarsely and conspicuously reticulate veined, the apex rounded to emarginate; fruit large, 1.8–2 cm. long, 1–1.2 cm. thick; fruiting hypanthium rugose when dry, thick and brittle. .... *C. ascendens.*

EE. Leaves of normal shoots not oblong-elliptic, thinner in texture, usually acute or acuminate at the apex; fruit smaller; hypanthium thin and vascular.

F. Leaves ovate, chartaceous, flat, the apex acuminate, the ultimate venation finely reticulate; stems hollow; inflorescence slender. .... *C. striata.*

FF. Leaves ovate to obovate-oblong on normal branches, the blades usually umbonate between the veins, the apex acute; branches solid; inflorescence stout. .... *C. nitida.*

CC. Trees or shrubs, branches not noticeably scandent.

G. Pedicels conspicuously longer than the ocreolae in flower and fruit.

H. Leaves basically orbicular, as broad as or broader than long, one or both basal lobes overlapping the petiole.

I. Leaves conspicuously rugose and pubescent; fruit globose or ovoid, 0.5–0.6 cm. long. .... *C. pubescens.*

II. Leaves conspicuously fleshy, not rugose, glabrate; fruit obpyriform, 1.2–2 cm. long. .... *C. uvifera.*

HH. Leaves basically ovate to elliptic, longer than broad, narrowed or rounded at the base. .... *C. diversifolia.*

GG. Pedicels shorter than or scarcely exceeding the ocreolae in flower and generally in fruit.

J. Plants deciduous; ocreae membranaceous, translucent and usually deciduous for all of its length (Trinidad species).

K. Leaves of normal shoots usually broadest above the middle, narrowed toward the base, the midrib not sharply keeled below, the blades turning black on drying. .. *C. nigrescens.*

KK. Leaves of normal shoots usually broadest below the middle, round to cordate at the base, the midrib sharply keeled, the blades at most darkening slightly on drying. .... *C. cruegeri.*

JJ. Plants not noticeably deciduous; ocreae not membranaceous, the base at least coriaceous and persisting.

L. Achene surrounded by the perianth lobes, the ocreolar sheath commonly elongating with the pedicels, the bracts usually black. . . . . *C. venosa.*

LL. Achene surrounded by the hypanthium, the perianth lobes appressed and imbricate or coronate on the achene, the bracts not conspicuously dark in color.

- M. Perianth lobes appressed and imbricate in fruit, the fruit triangular in cross section; leaves ovate to suborbicular, 2–5 cm. long, cordate at the base. . . . . *C. krugii.*
- MM. Perianth lobes coronate in fruit (fruit not known for *C. × boxii*), the fruit round in section; leaves larger.
  - N. Leaves cordiform-ovate, broadest below the middle, 11 × 6.5 to 27 × 17.5 cm. long and broad, the base obliquely auriculate-cordate or rounded and evenly cordate. . . . . *C. × boxii.*
  - NN. Leaves ovate to ovate-elliptic, smaller, generally narrowed below the middle.
    - O. Petioles arising above the base of the ocreae, the base of the blade auriculate at the junction with the petiole, the ultimate venation not conspicuous. . . . . *C. novogranatensis.*
    - OO. Petioles arising from the base of the ocreae, the base of the blade slightly decurrent on the petiole, the ultimate venation reticulate and slightly elevated. . . . . *C. swartzii.*

Coccoloba ascendens Duss ex Lindau, Engl. Bot. Jahrb. **13**: 156. 1890.

Coccoloba ascendens Duss mss. in herb. Krug & Urban; Ann. Inst. Col. Marseille 3: 168. 1897, in part.

Coccolobis quadrifida Britton, Bull. Torrey Bot. Club **53**: 467. 1926.

Coccoloba urbaniana Lindau, Engl. Bot. Jahrb. **13**: 155. 1890 (as to Trinidad specimens cited but not description).

Climbing shrub or liana, much branched, the branches to 50 feet long, glabrous, occasionally hollow; ocreae membranaceous, deciduous, cut to the base, 17–20 mm. long, acuminate at the apex, glabrous to lightly puberulent; petiole inserted below the ocrea, stout to slender, 1–2.5 cm. long, flattened adaxially with a narrow compressed groove, glabrous; leaf blades elliptic, obovate, oblong, rarely ovate, 11 × 6, 13 × 8 to 17 × 14.5 cm. long and broad, coriaceous, glabrous on both surfaces, the apex rounded, acute or emarginate, the base rounded to cordate, the midrib and primary veins prominent below, distinct but not prominent above, the primary veins 5–7 pairs, arcuate anastomosing near the margin, the ultimate venation reticulate and conspicuous on both surfaces; juvenile leaves of the current year's lateral shoots elliptic-lanceolate, 14 × 7 to 20 × 8.5 cm. long and broad, the apex acute to acuminate, the base acute; leaves of adventitious shoots on petioles 3–5 cm. long, the blades ovate to elliptic-ovate, 30 × 20 to 45 × 30 cm. long and broad, the apex acute, the base rounded to slightly cordate; inflorescence axillary or terminal, 13–17 cm. long, the basal ocrea

1 cm. long, densely ferrugineous puberulent, the rachis puberulent, the bracts broadly ovate, 2 mm. long and broad; ocreolae 2 mm. long, shallowly lobed; flowering pedicels to 2 mm. long; hypanthium 1.5 mm. long, the perianth lobes 1.5–2 mm. long and broad; stamens 8, the filaments to 2 mm. long, united at the base; pistil rudimentary, to 1.5 mm. long; staminate flowers 2–3 per nodule, the pistillate flower borne singly; hypanthium and perianth similar but stamens rudimentary, functional pistil to 2 mm. long; fruiting inflorescence to 30 cm. long, the rachis to 4 mm. diameter at the base, the mature pedicels 3–4 mm. long, the fruit conspicuously articulate; fruit 1.8–2.4 cm. long and 1–1.2 cm. in diameter; fruiting hypanthium thick, slightly woody, with 11 bundles, the achene chestnut brown, smooth and shiny when dry.

LOCAL NAMES: *liana baur* (Dominica), *liane cacao* (St. Lucia), *cuchape* (Trinidad).

DISTRIBUTION: Guadeloupe to Trinidad (and possibly South America).

Guadeloupe: Ravine Chaud, *Questel 752* (US), *Duss 2180* in part (C, US); Baines Jaunes, *Stehlé 388* (US), *1036* (NY), *1501* (US), *1989* (US), *Howard 11796* (GH), *11812* (A, GH); Fonfarabre, *Stehlé 3023* (NY); without location, *Duchassaing* (B). **Dominica:** Carib reserve on Castle Bruce trail, *W.H. & B.T. Hodge 3334* (GH); Between Pointe Ronde and Milton Estate, *W.H. & B.T. Hodge 2669* (GH); Between Riverdale and Deux Branches, *Howard 11758* (GH), *11771* (GH). **Martinique:** Fonds St. Denis, Morne Rouge, *Duss 36* (B, NY, US); Morne Juin, *Hahn 1005* (B-LECTOTYPE, GH, US). **St. Lucia:** Quilesse, *P. Beard 1089* (GH, MO, S), *Howard 11676* (GH); Barre d'Isle, *Howard 11388* (GH); Castries-Dennery Rd., *Howard 11336* (GH); Patience near Micoud, *Howard 11602* (GH). **Grenada:** Grand Etang, *Howard 10660* (GH); without location, *Broadway 1206* (FM). **Trinidad:** Arima valley near Simla, *A.C. Smith 10103* (A); Aripo Savannah at Waller Field, *Howard 10316* (GH), *10341* (GH), *10452* (GH), *10507* (A); Aripo road near ¾ mile post, *Broadway 5992* (K); Blanchisseuse road N. of Arima, *Broadway 7467* (BM), *Howard 10371* (A, GH); Brazil, *Britton, Britton & Freeman 2139* (GH, K, NY); Caparo, *Broadway 2760* (FM); Cleaver wood west of Arima, *Simmonds 189* (TRIN); Cumaca road, *Simmonds 322* (TRIN); Between La Brea and Irois, *Crueger 2694* (TRIN), *2695* (TRIN), *2696* (S, TRIN); Long Stretch, 22–23-mile post, *Broadway 6942* (BM, FM, GH, K, MO, S); Maravel, collector unknown (TRIN *5953*); Mt. Tucuche, *Baker 14329* (TRIN), *14816* (TRIN), *Williams 11012* (NY–TYPE of *C. quadrifida*, TRIN); Southern Guyapo road, *Broadway 6142* (A, BM, K, S); Toco road near Sangre Grande, *Howard 10367* (GH).

Coccoloba ascendens in the Antilles is a clearly distinct species characterized by being a liana with shiny, coriaceous and heavily veined leaves and having a large fruit with a thick, vascular hypanthium. In the original description, Lindau cites material from Brazil which I have not seen and which is not represented in the material from the Berlin Herbarium. It would be unusual if this species were not found in the Guianas or Brazil; there may even be an older name for the species.

Lindau cited a number of specimens in the original description without indicating a holotype. The specimens in the Berlin Herbarium carry no designation to indicate a type and therefore the collection *Hahn 1005* from Martinique is selected as the type collection, with the lectotype being in the Berlin Herbarium. In 1897 Duss redescribed *Coccoloba ascendens*, including with his description the citation of specimens which Lindau had previously described as *C. dussii*. It is unfortunate that one large collection, *Duss 2180*, selected by Lindau as the type of *C. dussii*, is a mixed collection and was included by Duss in his description. While the specimen of *Duss 2180* in the Berlin Herbarium represents the taxon described by Lindau as *C. dussii*, a great number of the other collections of this number represents *C. ascendens*.

In habit *Coccoloba ascendens*, as I have seen it in the field, is a scrambling shrub or a liana. The plants were generally climbing to the tops of the tallest trees. If these were small, the plants of *C. ascendens* formed a heavy tangle on and through the low shrubs. Leaf variation on a single plant was tremendous. Different types of leaves seem to be produced by the mature wood, the young shoots and the adventitious branches. The greatest variation in leaf size and type was seen in specimens in St. Lucia. I made one collection (*Howard 11336*) where trees had recently been cut along the Castries-Dennery road. The plants on the edge of this clearing had some branches sprawling out into the cleared area while other branches climbed into the undisturbed woods. On one such plant some stems were hollow while others retained the solid pith. Some stems had lanceolate-elliptic leaves, acuminate to acute at the apex and the base, while other branches of the same plant had leaves broadly ovate-oblong, acute at the apex and truncate to cordate at the base. Variation in texture was evident in the thin, young shade leaves in contrast to the larger coriaceous leaves in full exposure to the sun. Similar variation was found on plants in the forest reserve in the center of the island. A plant of a coastal river valley had thick basal stems with leaves to 45 cm. long and 30 cm. wide, while the scrambling branches produced oblong leaves averaging 13 × 9 cm. long and broad.

Coccoloba quadrifida described by Britton is clearly a restricted growth form of *C. ascendens*. Britton reports his plant to be a small tree instead of the usually liana type, but the cited material, as well as subsequent collections from the same area, show clearly the variation that makes *C. quadrifida* the same as *C. ascendens*.

Many of the specimens cited above bear an unpublished specific name referring to the island of Guadeloupe. These are not distinguishable from *C. ascendens* in other parts of its range.

Coccoloba urbaniana was described by Lindau in his monograph of the genus in 1890. He cited specimens from Trinidad (*Crueger 2694, 2696*) and from Puerto Rico (*Sintenis 1527, 1585*); however, the description published fits only the Puerto Rican material. In a subsequent treatment of the West Indian species (Symb. Ant. 1: 225. 1899), Lindau again cites the Puerto Rican specimens but fails to list the Crueger specimens anywhere in the treatment. Britton later redescribed the Puerto Rican material as *C. borinquensis*, stating that Lindau had erroneously included this in *C. urbaniana* of Trinidad. As no type was selected for *C. urbaniana* and the original author chose to limit the species to Puerto Rico, I feel that the species name has no validity in the Trinidad flora. *Coccoloba urbaniana* is best considered as a form of *C. swartzii* (Jour. Arnold Arb. **37**: 328. 1956).

A most striking variation was found in the plants of this species growing in the Aripo Savannah. A number of specimens were found with the staminate and pistillate flowers on different branches of the same plant. Most of the species of *Coccoloba* which I have studied in the field have been completely or functionally dioecious. This was also true of the majority of plants found in the savannah area. However, there were enough monoecious plants seen in this area to suggest the need for careful field study in the South American species of this genus.

One collection seen but not cited above is *Duss 72*, represented by one specimen in the New York Botanical Garden herbarium. The handwritten label reports the plant to be from Antigua. During my visit to Antigua I failed to find a single ecological location which might possibly have supported the species. Since other recent collectors have not reported the species, I suspect that the label of this specimen is in error.

Coccoloba × boxii Sandwith (pro sp.); Howard, Jour. Arnold Arb. **37**: 329. 1956.

Coccolobis boxii Sandwith, Jour. Bot. **78**: 97–98. 1940.

Tree to 8 m. tall; current year's branches cinereous, striate, sulcate, pubescent; ocreae to 1.5 cm. long, densely pubescent, the base persistent, sub-coriaceous, the apex membranaceous-evanescent; leaves cordiform-ovate, 11 × 6.5 cm. long, 27 × 17.5 cm. broad, coriaceous, light, midrib pubescent; lateral veins 8–12, slightly prominent; petiole densely pubescent, 0.7–1.3 cm. long; apex obtuse, the base oblique, auriculate-cordate or rounded to nearly evenly cordate; inflorescence solitary, simple, 17–22 cm. long; rachis 1.5–2 mm. wide, sulcate, densely minutely pubescent, the nodules 1–4-flowered, the bracts broadly triangular-ovate, rounded-obtuse, 1.3 mm. long, 2 mm. wide, conspicuously pubescent, the ocreolae 2 mm. long, membranaceous, flaring, almost bilobed, glabrous at the base; pedicels to 0.75 mm. long, the hypanthium 1.3 mm. long, the perianth lobes ovate-obtuse, 2 mm. long, 1.75 mm. broad, the interior smaller, the filaments (in bud) 0.6 mm. long; ovary ovoid-ellipsoidal 2.3 mm. long, 1.3 mm. in diameter, glabrous; styles shorter than the ovary, about 0.75 mm. long.

Antigua: Pelican Bay, *Box 539* (BM, US), *1497* (BM-HOLOTYPE, US).

The suggested hybrid nature of this species and the possible parents, *C. uvifera* and *C. swartzii* or *C. swartzii* forma *pubescens*, have been discussed in a previous paper.

Coccoloba cruegeri Lindau, Engl. Bot. Jahrb. **13**: 209. 1890.

Coccoloba ernstii Johnston, Proc. Amer. Acad. **40**: 685. 1905.

Tree to 12 m. tall, d.b.h. 30 cm., the wood extremely hard and tough.

the bark gray; young stems glabrous, ash-colored, striate, solid; ocreae 4–5 cm. long, membranaceous and translucent when dry, deeply split, deciduous; leaves deciduous, the petioles 2–3 cm. long, deeply grooved above, glabrous, inserted at the base of the ocrea, the blades ovate-elliptic to suborbicular, 14 × 12 to 22 × 16 cm. long and broad, coriaceous when mature, glabrous, the apex acute to rounded, the base rounded, the margin flat, the midrib prominent above, sharply keeled below, the primary veins 6–8 pairs, slightly prominent above, sharply keeled and prominent below, slightly decurrent on the midrib, straight becoming arcuate and anastomosing near the margin, the secondary veins and nerves reticulate; leaves of adventitious shoots with ocreae to 7 cm. long, on petioles 5 cm. long, blades mostly elliptical to 54 cm. long and 32 cm. broad, with 11 pairs of conspicuous primary veins; inflorescence racemose, laxly flowered, 7 cm. long, the rachis angled when dry, puberulent, the bracts ovate, 0.5 mm. long, the ocreolae membranaceous 0.75 mm. long, the pedicels tenuous, as long as the ocreolae, the hypanthium glabrous, 1 mm. long, the perianth lobes ovate to oblong, 1 mm. long, only staminate flowers known, these borne singly with functional stamens exserted on filaments 1.25 mm. long, the pistil rudimentary; immature fruit (according to Lindau) subglobose, the lobes of the fruiting perianth conspicuous to the base.

DISTRIBUTION: Trinidad and Margarita.

Trinidad: Without specific location, *Crueger 113* [TRIN *778*] (GOET-TYPE, NY, TRIN); Monos Island, *Howard 10415* (GH); Aripo Savannah, *Howard 10505* (GH); Toco Road between Arima and Sangre Grande, *Howard 10365* (GH).

Lindau assigned *Coccoloba cruegeri* to his section Campderia, believing that the perianth lobes surrounding the achene remained free in fruit. The associated characters of this section of black-colored bracts and normally large, conspicuous ocreolae were not described by him and cannot be seen on the type material. The specimens in Berlin and Goettingen do not have fruits, in spite of Lindau's description of them, and the material in the Trinidad Herbarium has only fragments of a flowering inflorescence axis. Therefore it seems unwise to assign *C. cruegeri* to the section Campderia.

Lindau cites specimens for this species as "*Crueger 113, 778*" (Engl. Bot. Jahrb. 13: 210. 1890). Examination of the original material which is preserved in the Trinidad Herbarium shows that Crueger assigned his own collection numbers to some specimens and failed to do so to others. However, nearly all sheets were assigned numbers for the Trinidad Herbarium and in the present case the "113" is Crueger's number while the "778" is the serial number of the collection in the Trinidad Herbarium. The original collection of this material was assigned by Grisebach to *Coccoloba plumieri,* according to the label on the specimen, although this information was never published. The label also indicates that the collection was made in the vicinity of Caroni.

There is a strong similarity between *Coccoloba nigrescens* and *C. cruegeri*, and perhaps future collections of more adequate material will indicate either that they are the same or that material called *C. cruegeri* is in reality a hybrid population. Both species are unique in the Trinidad area in having deciduous leaves. *Coccoloba nigrescens* appears to develop flowers when the leaves are very small, while *C. cruegeri* has nearly mature leaves before any indication of the inflorescence is produced. I found only one plant in flowering condition and on this the flowers were just beginning to open. These were borne singly at the nodules and were staminate.

The several plants seen in the field all possessed multiple trunks but were without indication of injury. One trunk possessed leaves much larger than normal as described above. In both normal and adventitious shoots the leaves were characterized by the remarkably sharply keeled midribs. In this characteristic the plant could be distinguished easily from neighboring plants of *C. nigrescens*. Several of the local residents were familiar with plants assigned to these two species. They recognized these as "grapes" similar to *Coccoloba uvifera* but could not recall having seen fruits on the trees.

Coccoloba ernstii Johnston described from Margarita Island is to be referred here. The type specimen (*Johnston 250*) in the Gray Herbarium indicates that this tree, also, is deciduous and that the young leaves and inflorescences are comparable to the material cited from Monos. Johnston indicated the alliance to *C. cruegeri* in his original description.

Coccoloba diversifolia Jacq. Enum. Pl. 19. 1760, Hist. Stirp. Amer. 114. *pl. 76.* 1763.

Coccoloba cubensis Meisner, DC. Prodr. **14:** 162. 1857.

Coccoloba laurifolia Lindau, Engl. Bot. Jahrb. **13:** 158. 1891, and all recent authors, not Jacquin.

Coccoloba longifolia Schmidt, Rep. Spec. Nov. **24:** 73. 1927, not Fischer ex Lind.

Shrub or tree to 8 m. tall; branches terete, often geniculate by limited growth, glabrous, the nodes rarely slightly swollen; ocreae coriaceous in the persistent lower portion, membranaceous and deciduous above, 3–5 mm. long; leaves of normal shoots with petioles 7–10 mm. long, glabrous, arising from the base of the ocreae; blades ovate, oval, oblong, elliptic, lanceolate or obovate, variable on one branch, 4× 3.5, 7 × 5.5, 8 × 4.5, 12 × 8 cm. long and broad, coriaceous, often shining above, dull beneath, glabrous, the apex rounded, obtuse, acute or acuminate, the base cuneate, rounded or subcordate, the margin entire; midrib and primary veins slightly prominent above, the secondary venation reticulate on both surfaces, the primary veins 3–7 pairs, arcuate, anastomosing before reaching the margin; leaves of adventitious shoots on petioles 1–2.5 cm. long, with blades of varying shapes 17 × 8, 24 × 13, to 32 × 12.5 cm. long and broad; leaves of windswept specimens often much smaller than those of normal shoots with blades 2 × 1.3 to 3 × 2 cm. long and broad; inflorescence terminal 4.5–18 cm. long, the rachis glabrous, the flowers on pedicels 2–4 mm. long, the staminate flowers 2–4 at each locus, the pistillate flowers borne singly at each locus, the bracts ovate, less than 0.5 mm. long, the ocreolae membranaceous, less than 0.5 mm. long, the hypanthium 1 mm. long, the perianth lobes ovate to oblong, 2–3 mm. long, 1–2 mm. broad, the functional stamens 1 mm. long, the sterile stamens rudimentary; fruiting pedicels 3–4.5 mm. long, the fruit globose to obpyriform, 10 × 7, 12 × 8, 13 × 8 mm. long and in diameter, the apex rounded, the perianth lobes imbricate and appressed.

DISTRIBUTION: Florida, the Bahamas, the Greater Antilles and Antigua.

Antigua: Pelican Bay, *Howard 11990* (GH).

Coccoloba dussii Lindau, Notizblatt Berlin **1**: 213. 1896, Symb. Antil. **1**: 226. 1899; Duss, Ann. Inst. Col. Marseille **3**: 167. 1897.

Coccoloba scandens Benth. in obs. Lond. Jour. Bot. **4**: 625. 1845, nomen.
Coccoloba excelsa Smith (?), Kew Bull. **1893**: 272. 1893.

Woody shrub with scrambling branches or a vine; young stems terete, minutely short pilose becoming glabrous, the older stems flattened through bilateral development; ocreae to 1 cm. long, membranaceous, deciduous; petiole inserted below the ocrea, 2.5–4 cm. long, minutely pilose; blades ovate to oblong, 6.5 × 4.5, 12 × 7.5 to 17 × 10.5 cm. long and broad, thin-coriaceous, glabrous, the apex acute to short-acuminate, the base rounded to slightly cordate, the margin entire, the midrib prominent below, slightly keeled above, the secondary veins 7–8 pairs, arcuate, anastomosing near the margin, the ultimate venation reticulate and conspicuous on both surfaces; leaves of adventitious shoots on petioles 3.5 cm. long, the blades broadly ovate to elliptic-ovate, 25 × 16 to 30 × 19 cm. long and broad, the apex rounded to acute, the base broadly cordate; leaves of younger shoots elliptic-lanceolate, 19 × 10 to 24 × 10.5 cm. long and broad, the apex acuminate, the base rounded or acute; inflorescence terminal, 9–15 cm. long, the basal ocrea 1.3–4.3 cm. long, the rachis minutely pilose or puberulent, the bracts less than 1 mm. long, the ocreolae 0.5 mm. long, the flowering pedicels to 3 mm. long, the hypanthium 2 mm. long, the perianth lobes ovate, 2 mm. long, the staminate flowers borne 2 or 3 at a node, the pistillate flowers not known; fruiting pedicels 4–6 mm. long, usually slightly reflexed, slender, the mature fruit short stipitate, spherical, dark blue-purple in color, extremely astringent, the surface of dried fruit rugose, the fruiting perianth tightly adherent to the achene, the achene dull brown, rugose.

LOCAL NAMES: *Raisinier marron*, *Raisin marron* (Guadeloupe).

DISTRIBUTION: Guadeloupe, St. Lucia, St. Vincent, Grenada, Trinidad and Tobago.

Guadeloupe: Ravine Chaude (Lamentin), *Duss 2180* (B–TYPE, C, FM, NY); Between Pointe Noire and Ravine Chaude, *Duss 3711* (B, FM, NY, US); Between Lamentin and Pris d'Eau, *Howard 11852* (A, GH); Grande Savane, Gourbeyre, *Duss 3430* (B, NY); Goyave, Pont Moreaux, *Stehlé 931* (US); Basse Terre near Duclos, Petit Bourg, *A.C. Smith 10347* (A). **St. Lucia:** Without location, *Anderson s.n.* (K). **St. Vincent:** Silver Spoon district above Three Rivers, *Howard 11161* (GH), *11185* (GH), *11189* (GH). **Grenada:** Grand Etang, *Howard 10656*

(GH). **Tobago:** Easterfield, *Broadway 4371* (NY); The Widow, *Broadway 4653* (K, MO). **Trinidad:** Between Arima and Sangre Grande, *Howard 10362* (GH); Blanchisseuse Road, *Broadway 6456* (A); Morne Bleu, *Britton, Freeman & Bailey 2271* (GH).

Similar to many other lianas, *Coccoloba dussii* varies according to the attitude of the stem and its branches. Over fifty feet of liana was pulled from trees or untangled from prostrate growth in several locations to determine the range of leaf variation in single plants. Basal leaves which persisted on the older stems were usually larger than the others on the plant. Leaves on apical portions of the stem were usually longer and narrower than the other leaves, while the smallest leaves occurred on the lateral flowering or fruiting branches. Such flowering branches are represented by most of the herbarium specimens cited. Flowering branches which were twisted around limbs of the supporting trees as an aid in climbing had the smallest leaves and the shortest inflorescences.

The bilateral development of the older stems was conspicuous. Such stems were often 5–6 times as wide as thick. Young stems were cylindrical but slightly fluted, with a conspicuously large pith.

Coccoloba dussii is similar to *C. excelsa* and in sterile condition it is often difficult to distinguish between them. In most South American material of *C. excelsa* the leaves, young stems and inflorescences are conspicuously pubescent. In some South American material the pubescence has been lost, leaving relatively large hair bases with evidence of hairs only along the midrib, on the lower surface of the lamina and in the axils of the lateral veins. Such hair bases have often been mistaken for glands or secretions. Both functionally staminate and pistillate flowers of *C. excelsa* are known and in each the ocreolae surrounding the flowering pedicels are large, membranaceous and more or less persistent, almost equalling the pedicels in length in flowering condition. Only staminate flowers are known for *Coccoloba dussii* and in these the ocreolae are small and less than 1/5 the length of the pedicels. The inflorescence rachis and the ocreolae are only slightly puberulent. I have not observed *C. excelsa* in the field, but on the basis of herbarium material alone the character of the ocreolae in flowering condition is sufficient to distinguish the species. The fruits likewise are similar, as is the growth habit, and the appearance of the leaves in dried condition. In general the leaves of *C. dussii* tend to be more umbonate between the veins and to have thinner and slightly longer petioles. The flowers are commonly reflexed on the inflorescence, although this characteristic may be associated with the growth habit of the plant. Further field study and additional collections may indicate that *C. dussii* should be considered a variety of, or even synonymous with, *C. excelsa*.

Lindau described *Coccoloba dussii* in 1896, citing only one specimen, *Duss 2180*, in the herbarium of Krug and Urban. The type in the Berlin Herbarium consists of one branch and is as Lindau described. Other specimens bearing this collection number are mixtures of *C. dussii* and *C. ascendens*.

In describing *Coccoloba excelsa*, Bentham notes that "In Forsyth's herbarium, I found, under the name of *C. scandens*, an imperfect specimen of a plant gathered by Anderson in Saint Lucia, very much like the above, but with the leaves perfectly smooth, the racemes much longer and the bracts very small. These are the only two species as yet known to be climbers." I have seen the plant from Bentham's herbarium which is now in the collection at the Royal Botanic Garden at Kew. It is a fragment consisting of two leaves and one inflorescence; the latter is staminate, but very few flowers remain. The specimen is better referred to *C. dussii* than to *C. excelsa*. It is to be expected that more thorough exploration of St. Lucia will reveal *C. dussii*, which has not been reported in recent collections from that island. *Coccoloba dussii* is known from Guadeloupe, but has not been found on Martinique or Dominica to the present.

Coccoloba fallax Lindau, Engl. Bot. Jahrb. 13: 172. 1890.

Coccoloba crescentiifolia Griseb. Fl. Br. W. I. 163. 1859, not Cham.

Tree to 10 m. tall (Swabey), d.b.h. 6 cm.; branches thick, strongly striate; ocreae coriaceous, 2–4 cm. long, flaring, strongly bilobed, conspicuously striate, glabrous; petioles arising from the base of the ocreae, 2.5–4.5 cm. long, stout, deeply grooved, striate, glabrous; leaf blades oblong-ovate to oblong-obovate, 14 × 5, 23 × 10, 25 × 11, 36 × 13 cm. long and broad, thick-coriaceous, glabrous, the apex acute to acuminate, the base rounded or narrowed, the ultimate base slightly cordate, the midrib conspicuous above, keeled, sulcate or grooved at both sides, strongly keeled and conspicuous below, the veins 7–10 pairs, ascending arcuate, anastomosing near the margin, slightly impressed above, conspicuous below, the ultimate venation reticulate but inconspicuous; inflorescence lateral, fasciculate, racemose, laxly flowered, the basal ocreae conspicuous, coriaceous 3 cm. long, mostly persisting, commonly strongly keeled or striate, glabrous or puberulent, the rachises 7–23 cm. long, puberulent, the flowers borne singly at each nodule, the bracts ovate, minute to 0.5 mm. long, puberulent, the ocreolae puberulent, scarcely exceeding the bracts, the staminate flowers with pedicels 2–3 mm. long, puberulent, the hypanthium 1 mm. long, the perianth ovate, the lobes 1.5 mm. long, the functional stamens with filaments 2–2.5 mm. long, the pistillate flowers not seen; fruiting pedicels 2–3 mm. long.

LOCAL NAMES: *Black grape* (Trinidad).

DISTRIBUTION: Trinidad and Venezuela.

Trinidad: Without locality, *Crueger 114* (GOET-TYPE), *779* (TRIN); S. W. Reserve, *Swabey* [TRIN 12292] (NY); Cat's Hill Reserve, *Swabey* [TRIN 12543, 12536]; Black River, *Freeman 8102* (NY, TRIN); Windbelt Reserve, *Brooks* [TRIN 12502] (NY). **Chacachacare:** *Britton, Freeman & Watts 2694* (GH, NY, TRIN). **Venezuela:** Cristobal Colon, *Broadway 685* (GH); Cariaquita, *Bond, Gillin & Brown 244* (GH); Fundo la Argentina, *Delgado 209* (A).

Coccoloba fallax is very similar to *C. densifrons* and *C. padiformis*. When more adequate material is available, especially when there is a good series of fruits and more information on the growth habits, these species may be considered to be merely varieties, or even identical.

I was unable to find *Coccoloba fallax* in Trinidad or on Chacachacare. Data on the specimens cited are inadequate for a complete understanding of the form of the plants. No female flowers are known and the few fruits associated with specimens collected by Swabey (TRIN 12536) and Freeman (TRIN 8102) are crushed and in poor condition. The fruits were probably round or spherical with imbricated perianth lobes. The achenes were a pale tan color in the material seen, apparently also spherical and very thin-walled.

Swabey reports that one specimen which he collected grew as a clump tree of 2 to 6 stems. Some of these reached 30 feet in height. Neither these nor other specimens studied appeared to represent adventitious shoot material.

At present *Coccoloba fallax* seems distinct on the basis of the fascicled inflorescence of simple racemes, the conspicuously large ocreae, particularly those of the inflorescence, and the strongly keeled midribs of the leaves.

Coccoloba krugii Lindau, Engl. Bot. Jahrb. **13**: 145. 1890; Symb. Antil. **1**: 222. 1899; Howard, Jour. Arnold Arb. **37**: 337. 1956.

Coccoloba børgesenii Schmidt, Rep. Spec. Nov. **24**: 75. 1927.

Coccoloba børgesenii forma *ovato-lanceolata Schmidt*, Rep. Spec. Nov. **24**: 76. 1927.

Shrub or small tree to 6 m. tall; branches terete, glabrous, slightly geniculate and nodose; ocreae membranaceous, persistent, 3–5 mm. long; leaves of normal shoots with petioles 5–6 mm. long, corky at the base, arising from the base of the ocreae; blades ovate to suborbicular, 2 × 1.8, 4 × 3.5, 5 × 4 cm. long and broad, thin-coriaceous, glabrous or rarely with a few hairs near the attachment of the petiole, the apex obtuse or rounded, the base cordate or rounded, the margin flat or recurved; midrib flat above, slightly prominent below, the primary veins 4–6 pairs, straight bifurcating and anastomosing near the margin, flat on both surfaces, the secondary venation minutely reticulate below, smooth above; leaves of adventitious shoots with petioles 1 cm. long, the blades cordate or elliptic to 7 × 6 cm. long and broad; inflorescence terminal 5–8 cm. long, the rachis glabrous, the staminate flowers 1–3 per node, the pistillate flowers borne singly, the bracts broadly ovate, membranaceous, 1 mm. long; ocreolae membranaceous, flaring to 1 mm. long; pedicels wanting or shorter than the ocreolae, the hypanthium 1 mm. long, the perianth lobes ovate, to 2 mm. long, the filaments of fertile stamens 1.5 mm. long; fruit ovoid or angularly fusiform, strongly triangular in outline, 4–5 mm. long, 3–3.5 mm. in diameter, the perianth lobes appressed, about half the length of the fruit.

DISTRIBUTION: The Bahamas, Hispaniola, Jamaica, Puerto Rico, the Virgin and the Leeward Islands.

Antigua: Goble creek near Gaynors, *Box 1388* (A, GH, US).

Coccoloba latifolia Lam. Encycl. 6: 61. *t. 316, f. 4.* 1804; Lindau, Engl. Bot. Jahrb. 13: 133. 1890.

Small tree to 15 m. tall, d.b.h. to 45 cm.; branches thick, angular and vertically ridged at least when dry, hollow but septate at the nodes, glabrous; ocreae large, conspicuous, coriaceous, tubular or sub-campanulate, 3–7 cm. long, glabrous, acute to strongly bilobed; leaves of flowering branches variable in size, the petioles generally 2–3 cm. long, glabrous or puberulent or occasionally with long pilose hairs; blades generally orbicular to obovate, 13 × 10, 20 × 15 to 28 × 28 cm. long and broad, coriaceous, glabrous or with scattered pilose hairs on the midrib and veins on the lower surface, the apex rounded or emarginate to short acuminate, the base rounded to deeply cordate, the margin flat or strongly recurved, entire, often undulate; midrib and veins impressed above, conspicuous below, the primary veins 9–12 pairs, arcuate and anastomosing near the margin, the secondary venation conspicuous, the blade strongly bullate between the primary veins or between the secondary veins as well as the primary or scarcely bullate and nearly flat; leaves of adventitious shoots larger with petioles to 5 cm. long and blades to 48 × 50 cm. long and broad or larger, similar in other characteristics; inflorescence terminal, panicled to 30 cm. long and broad, with solitary or 2–3-fascicled undivided pseudoracemose branches or rarely the lowest branch paniculate, the rachis puberulent, the staminate flowers 1–3 per node, the pistillate flowers usually borne singly but some apparently 3–4 per node, the bracts minute, to 0.5 mm. long, the ocreolae membranaceous to 0.75 mm. long, the pedicels very thin 1–2 mm. long, the hypanthium tapered at the base, 1–1.6 mm. long, the perianth lobes 1.5 mm. long, the functional stamens with filaments to 2 mm. long; fruit ovoid, 7–10 mm. long, 5–6 mm. in diameter, the base rounded to slightly attenuate, the apex rounded with imbricate perianth lobes, the immature fruits showing 9 conspicuous basal nerves when dry, the mature fruit black, fleshy when fresh, the outer pericarp commonly loose, the achene dark brown shining, smooth.

LOCAL NAMES: *Grape, cuchape, stave wood, big leaf.*

DISTRIBUTION: Trinidad, Tobago, Venezuela, British Guiana, Brazil.

Trinidad: San Fernando, La Retraite, *Crueger 2690* (B, TRIN); Tamana, *Marshall* [TRIN 12313] (NY); St. Joseph, *Dannouse, s.n.* (TRIN); Aripo Savanna, *Britton, Broadway & Hazen 316* (GH, NY), *Howard 10355* (GH); Talparo, *Simmonds* [TRIN 14652]; Arima, *Eggers 1377* (C); Piarco Savanna, *Britton, Britton & Hazen 113* (NY); Chancellor Road, St. Ann's, *Broadway 8989* (TRIN); Caroni, *Eggers 912* (M); cultivated, *Broadway 4332* (TRIN). **Monos Island:** *Howard 10416* (GH).

A well-defined and easily recognized species. The trees are common in savanna areas and probably for these reasons have not been collected and so the species is poorly represented in herbaria. The wood tends to be soft and the branches are relatively brittle and fragile. An equal hazard to the collector is the occurrence of colonies of stinging and biting ants in the hollow pith and in the ocreal sheath.

Coccoloba nigrescens Lindau, Engl. Bot. Jahrb. 13: 192. 1890.

Tree to 10 m. tall; youngest stems pubescent with long strigose hairs, becoming glabrate; ocreae lax, membranaceous to extremely thin and translucent even when fresh, to 3.5 cm. long, divided 2/3 its length, acute at the apex, pubescent with long scattered hairs, deciduous to the base; petioles attached at the base of the ocreae, stout, 5–7 mm. long, densely pubescent on the adaxial surface when young, becoming glabrate; leaf blades obovate-oblong to ovate-oblong, 12 × 7 to 16 × 9 cm. long and broad, thin-coriaceous when mature, glabrous, the apex acute to rounded, rarely short-acuminate, the base cuneate or rounded, the margin slightly recurved, the midrib prominent on both surfaces, not keeled, the primary veins 6–9, mostly straight becoming arcuate and anastomosing near the margin, the lesser nerves inconspicuous; inflorescence terminal or lateral, to 10 cm. long, the peduncle 6 mm. long, strigose pubescent becoming glabrous, the bracts triangular, acute, puberulent, 0.75 mm. long, the ocreolae erect, truncate, not exceeding the bracts; staminate flowers 2 (rarely 1) per nodule, the pedicels shorter than the ocreolae, the hypanthium 0.75 mm. long, the perianth lobes ovate to 0.75 mm. long, the stamens exserted on filaments 1 mm. long; pistil rudimentary, the pistillate flowers not known; old fruiting inflorescence with stout pedicels to 1 mm. long; fruit not known.

DISTRIBUTION: Islands near Trinidad.

Chacachacare Island: *Crueger 116* (B, GOET-TYPE, TRIN), *Howard 10440* (GH). **Monos Island:** *Crueger* [TRIN 3244], *Britton & Hazen 1742* (FM, GH, NY, TRIN), *Broadway 7457* (TRIN), *Howard 10422* (GH).

Coccoloba nigrescens is apparently one of the few species of the genus which loses all of its leaves at certain seasons. However, there is no indication of this characteristic in the shape or texture of the mature leaf. Lindau described the species from specimens collected in May while the leaves and inflorescences of the plant were very young and immature. Subsequently, Britton and Hazen collected the species again on an adjacent island in the month of April and obtained specimens comparable in quality. Lindau commented on the fragility of the leaves which turn black in drying. The Broadway collection cited above was collected in November and consists of mature leaves from a sterile shrub. The collections which I made were obtained in the month of February in the type locality and in the same area where Britton visited. These also possess fully mature leaves. The leaves turn dark on drying and all parts of the plant are glabrous, lacking the hairs apparently characteristic of the younger parts. My companion in the field, a local resident and employee at the leper colony, assured me that this plant does indeed lose its leaves. At present this species is poorly represented and not well known. Further collections are needed, especially to determine whether this species is truly distinct from *C. cruegeri*. At present *C. cruegeri* may be distinguished in the juvenile leaf condition by the lack of the strigose pubescence and in mature leaf form by the longer petioles, larger adventitious shoot leaves and the sharply keeled midrib.

Both of the Crueger specimens which represent the type collection are in very poor condition.

Coccoloba nitida HBK. Nov. Gen. **2**: 176. 1818.

Polygonum arborescens Vell. Flor. Flum. 163. *1825*, **4**: *pl. 43.* 1827.
Coccoloba marginata Hooker, Jour. Bot. **4**: 626. 1845.
Coccoloba guianensis Meisner, Linnaea **21**: 264. 1848.
Coccoloba martii Meisner, Fl. Bras. **5**: 37. 1855.
Coccoloba martii Meisner var. *major* Meisner, Fl. Bras. **5**: 38. 1855.
Coccoloba nitida HBK. var. *rotundata* Meisner, Fl. Bras. **5**: 88. 1855.
Coccoloba nitida HBK. var. *cordata* Meisner, Fl. Bras. **5**: 38. 1855.
Coccoloba trinitatis Lindau, Engl. Bot. Jahrb. **13**: 182. 1890.

Plants of variable habits most commonly tree-like at the base with scrambling, liana-like branches, the nodes extremely long and the leaves much reduced at the ends of these or liana-like from the base, rarely shrub-like; branchlets terete, smooth or striate, minutely puberulent, the lenticels elliptical, conspicuous, whitish; ocreae obliquely truncate, 1–1.5 cm. long on normal as well as scrambling shoots, ferrugineous puberulent when young becoming glabrate, the base coriaceous and persistent usually tightly investing the stem; petioles inserted at the base of the ocreae, usually 1.5–2 cm. long, minutely puberulent, canaliculate above, striate; leaf blades of flowering branches ovate, elliptic, oval-oblong or obovate-oblong, 10 × 5, 13 × 6 to 20 × 8 cm. long and broad, coriaceous, shining or dull, usually drying darker above than below, glabrous on both surfaces, the apex acute, rarely acuminate or almost rounded, the base rounded to cordate, the margin flat rarely slightly recurved, the midrib and veins slightly impressed above, conspicuous below, the primary veins 8–10 pairs, arcuate, anastomosing near the margin, the ultimate venation finely reticulate; leaves of conspicuously scrambling shoots either much smaller or even larger (to 24 × 10 cm.) than those of normal flowering branches, generally of shinier texture; leaves of adventitious shoots on petioles 1.2–3.5 cm. long, with blades generally oblong or elliptic-oblong, 17 × 10 to 21 × 12 cm. long and broad, the apex usually rounded, the blade often strikingly umbonate between the primary veins; inflorescence generally terminal but often lateral, a solitary raceme, 7, 10, 22 to 36 cm. long, occasionally fascicled with one or two small racemes at the base or with 1 or 2 basal racemes developing from the main axis; rachis puberulent; bracts ovate 0.5–1 mm. long, the ocreolae strongly bilobed, membranaceous, puberulent, 1.5–2 mm. long, the staminate flowers 2 or 3 at each node, on pedicels shorter than the ocreolae, the hypanthium conical 1–1.5 mm. long, the perianth lobes ovate, 1–1.5 mm. long, the stamens 1.5–2 mm. long, the pistil abortive; pistillate flowers borne singly on pedicels about equalling the ocreolae, the stamens rudimentary and shorter than the perianth lobes, the pistil exserted, the fruiting pedicels 2–2.5 mm. long; fruit ovoid (usually 12 mm. long, 9 mm. diameter), the perianth lobes slightly coronate, the hypanthium in fruit smooth to strongly striate when dry, the achene dark brown, smooth.

LOCAL NAMES: *Black grape* (Trinidad), *masari* (British Guiana), *pipoca* (Brazil).

DISTRIBUTION: Trinidad, the Guianas, Brazil.

Trinidad: Arima, *Howard 10359* (GH), *10368* (GH), *10506* (GH); Aripo Savannah, *Crueger 2693* (B-TYPE of *C. trinitatis*, TRIN), *Howard 10507* (GH), *Britton, Britton & Hazen 272* (GH, NY), *Baker s.n.* (HT *15122*), *Broadway* (TRIN 10480); Caroni, *Crueger 671* (TRIN); Long Stretch, *Simmonds 329* (TRIN 14255), *s.n.* (TRIN 15378); Santa Cruz, *Dannouse s.n.* (NY, TRIN); Valencia, *Broadway 5584* (A, BM, MO, S), *6652* (A, B), *8988* (TRIN), *Britton, Britton & Hazen 1023* (GH, NY); *Britton & Britton 2103* (GH, NY); without locality, *Fendler 1010* (BM). **British Guiana:** Amakura River, *De La Cruz 3552* (GH); Assakatta, *De La Cruz 4270* (GH); Barima River, *De La Cruz 3363* (GH); Bartica River, *De La Cruz 1962* (GH); Kaieteur Plateau, *Maguire & Fanshawe 23316* (A); Kuyuwini River, *Smith 3030* (A); Mazaruni Station, *For. Dept. Brit. Guiana 4269* (NY); Upper Rupununi River, *De La Cruz 1442* (GH). **Dutch Guiana:** without location, *Samuels 419* (GH), *Wullschlagel 882* (B). **French Guiana:** Acaronany, *Sagot 887* (NY); Paramaribo, *Regel 492* (NY); without location, *Broadway 307* (GH), *Leblond s.n.* (B), *Jelski* (B), *Perrottet 84* (NY), *Poiteau* (B). **Brazil:** Maranhão, Island of São Luiz, *Froes 11698* (A), *11716* (A); Minas Geraës, river San Francisco near Salgado, *Martius* (M-TYPE of *C. martii*); Bahia, Joazeiro, *Martius* (M-TYPE of *C. nitida*).

In the field there is considerable variation among plants of this species. I was fortunate to have one full week in the Arima area of Trinidad, where attention was given to the growth habits and the variation seen in plants then referred to *Coccoloba trinitatis* Lindau. The three collections made at that time (*Howard 10359, 10368 and 10506*), comprise the equivalent of 47 herbarium sheets. However, each number was made from only one plant and each number was collected on a separate wooded island in the Aripo Savannah. By carefully following the branches of each tree I was able to determine that a tenuous "liana" of one part of the forest canopy was actually the same individual as the "different" plants of the forest floor which were, in reality, either flowering branches or adventitious shoots.

As a result of this experience in the field, it seems clear to me that the specimens Lindau saw and referred to *Coccoloba nitida*, *C. guianensis*, *C. marginata* and *C. trinitatis* could all have come from one plant. They obviously did not come from one plant, but nevertheless I conclude that they represent only one species. Many of the morphological differences by which Lindau distinguished species can be found on a single plant in the field. Moreover, he failed to understand the sexual differences between staminate and pistillate plants. Meisner, Lindau's predecessor, treated as varieties the different leaf sizes on a series of specimens. These varieties "major" and "minor" are easily found on one branch in the living plant.

Coccoloba nitida will be recognized in future collections as a liana, for the flowering branches are usually short lateral shoots on a scrambling branch system. The flowers are a clearer white than most of the *Coccoloba* species I have seen in the field and the staminate inflorescence in full flower is conspicuous. The long inflorescence, the membranaceous, bilobed ocreolae and the ovate fruits aid in the determination of this species.

Coccoloba novogranatensis Lindau, Engl. Bot. Jahrb. 13: 192. 1890.

Coccoloba caribaea Urban, Symb. Antil. 5: 337. 1907.

Shrub 2 m. to tree 27 m., trunk commonly muscular, the bark red; branchlets terete, glabrous, the nodes slightly swollen; ocreae cylindrical, the upper portion membranaceous and deciduous, the lower portion coriaceous and persistent; leaves of normal shoots with petioles 8–11 mm. long, puberulent when young, with age glabrous except in the groove, attached above the base of the ocreae; blades ovate to ovate-elliptic, 6 × 4, 9 × 5, 10.5 × 5.5 cm. long and broad, thin-coriaceous, glabrous above, glabrate below except for long hairs along the midrib at the base of the blade, the apex attenuate, the base narrowly cordate, the margin entire; midrib and primary veins inconspicuous above, prominent below, the primary veins 5 or 6 pairs, the ultimate venation finely reticulate; leaves of adventitious shoots generally similar but occasionally obovate and narrowed at the base, ovate-lanceolate or lanceolate-elliptic, the blades 11 × 7 to 18 × 15 cm. long and broad, the basal lobes of leaves on adventitious shoots often overlapping; inflorescence terminal on short lateral shoots, 3–9 cm. long, the basal ocreae 5–10 mm. long, bilobed at the apex, the rachis glabrous, the flowers commonly borne singly at each nodule (occasionally 2 in staminate plants), the bracts oblong; 2 mm. long, 0.5–0.75 mm. broad, the ocreolae 3 mm. long, bilobed at the apex, membranaceous and persistent, the pedicels 2.5–4 mm. long, the hypanthium 0.75 mm. long, the perianth lobes ovate, 1.5 mm. long and broad, the functional stamens 2.5 mm. long, the functional pistil 2 mm. long; fruit generally spherical with coronate perianth lobes, occasionally narrowed at the base, 1 cm. long, 5–9 mm. in diameter, the achene brown, shining.

DISTRIBUTION: St. Vincent, Grenada, Trinidad, Tobago, Margarita, Colombia, Venezuela and Panama.

St. Vincent: *H.H. & G.W. Smith 1790* (B, NY). **Grenadines:** Bequia, *Howard 11231* (GH), *11241* (GH); Cannuoan, *Howard 11091* (GH); Carriacou, *Howard 10815* (GH), *10818* (GH), *10890* (GH); Large Island, *Howard 10965* (GH); Mayero, *Broadway 5748* (TRIN), *Howard 11038* (GH); Mustique, *Howard 11223* (GH); Petit Martinique, *Howard 10935* (GH); Petit St. Vincent, *Howard 10896* (GH); Tobago Cays, *Howard 11024* (GH); Union, *Howard 10988* (GH). **Grenada:** St. Georges, *Broadway 1760* (B, FM, GH, NY), *1795* (FM, GH, NY), *Howard 10692* (GH); Grand Anse, *Broadway 2503* (FM, MO), *3361* (B, M); Sauteurs, *Howard 10705* (GH). **Trinidad:** Caledonia Island, *Hart 5834* (TRIN). **Tobago:** The Lodge, *Broadway 4019* (B, FM), *Howard 10453* (GH), *10454* (GH), *10458* (GH). **Carrera Island:** *Broadway s.n.* (NY). **Margarita:** *Johnston 274* (GH).

In the original description of *Coccoloba novogranatensis*, Lindau cited a Karsten collection from Sabanilla, Colombia, and a Triana specimen without specific locality. In the Berlin Herbarium there are two sheets representing this species, but in contrast to his usual practice, Lindau did not indicate by abbreviation, or otherwise, his choice of a type. The Triana specimen is a fragment of a leaf in a packet with a pencil sketch of a fruit on the packet. The Berlin sheet attributed to Karsten consists of two flowering fragments of different ages. It would appear that the Karsten specimen in Berlin could be considered the holotype; however, when botanists from the Field Museum photographed this specimen, temporary annotations were placed on the "Karsten" sheet to indicate that one of the two flowering fragments was a Karsten collection and the other a Triana collection. The labels have since been removed. Thus I have been unable to verify whether this sheet is truly a mixed collection. Both flowering fragments apparently represent the same species, but I am unable to state positively which is the type. It is likely that additional Karsten material from Colombia exists in other herbaria and that a lectotype should be selected at a future date.

I have seen in the herbarium of the Muséum National d'Histoire Naturelle in Paris two full sheets of *Triana 978*, a number cited by Lindau. The collection was made between Anapoima and Apulo, Province of Bogota in Colombia. Each of the two sheets has a branch with young flowers and a second branch in fruiting condition. No fruits remain with the specimens.

I have not seen additional material collected by Karsten. Lindau indicated that his specimens of this species came from Berlin, Leningrad and Vienna. The first two collections are intact and I have seen all the material. The Vienna collection of this genus was destroyed during World War II. While it is possible that Karsten material exists in some other herbarium, it seems practical at this time to designate *Triana 978* as the type collection and one of the two sheets in the Paris herbarium is selected as the lectotype.

In the herbarium material from the Muséum d'Histoire Naturelle in Paris there are three additional sheets to be referred to *Coccoloba novogranatensis*. All were collected by Pleé. Two sheets, one with a printed and one with a script label, were collected at Maracaibo (Venezuela). The third carries a printed label "Martinique." I cannot distinguish the specimens as distinct and different collections and since *C. novogranatensis* has not as yet been collected in Martinique, I suspect that this sheet too should bear a Maracaibo label.

Urban did not indicate a holotype in his publication of *Coccoloba caribaea*, but the specimen *Broadway 1760* in the Berlin Herbarium is indicated as the type in Urban's handwriting. This collection is in flower and is comparable in all characteristics to the fragments on which Lindau based *C. novogranatensis*. There have been no recent collections assigned to *C. novogranatensis*; in fact, the name has been overlooked in recent years. A number of recently described species from Colombia and Peru and from Central America will be assigned in synonymy to *C. novogranatensis* in a later paper.

A large number of *Coccoloba novogranatensis* populations were studied in the Lesser Antilles and a considerable morphological variation was recognized as being of an ecological nature. The size, color, texture and attitude of the leaves on the shoots seemed to depend upon whether the populations are growing in full sunlight, in shade, in an area subject to salt spray or in moist situations. A similar set of variations has also been recognized in *C. venosa* and collections of these two species from the Lesser Antilles have been confused by various authors. For example, the plants on Mt. Royal in Cannuoan in the Grenadines which John Beard refers to *C. venosa* are more properly referred to this species. *Coccoloba venosa* and *C. novogranatensis* may be readily distinguished by referring to the point of attachment of the petiole to the ocrea.

Coccoloba pubescens L. Syst. ed. 10. 1007. 1759; Hooker, Bot. Mag. *t. 3166*. 1832; Fawcett & Rendle, Jour. Bot. **51**: 123. 1913; Howard, Jour. Arnold Arb. **38**: *227*. 1957.

Scortea arbor americana, amplissimis foliis, aversaparte nervis extantibus hirsutie ferruginea refertis; Pluk. Phytographia *t. 222, f. 8*. 1691.

Coccoloba grandifolia Jacq. Enum. 19. 1760.

Coccoloba rubescens L. Sp. Pl. ed. 2. 523. 1762.

Coccolobis pubescens Sandwith, Jour. Bot. **78:** 98. 1940.

Coccolobis antiguensis Sandwith, Jour. Bot. **78:** 98. 1940.

Mature tree to 13 m. tall, d.b.h. 5 cm., much branched above a well-defined trunk; branches terete, swollen at the nodes, the lenticels not conspicuous, tomentose to pilose; ocreae to 1 cm. long, generally completely deciduous, pubescent; leaves of completely mature plants vary considerably in size and shape, the petioles 3–6 mm. long, inserted below the ocreae, densely short-pubescent, the blades broadly orbicular to orbicular-ovate, 4 × 6, 7.5 × 10 cm. long and broad grading into size of leaves of adventitious shoots, rugose or bullate, the apex rounded, the base cordate, the basal lobes rounded and only rarely approximate, sparsely pubescent above to glabrate, densely to sparsely pubescent below or glabrate, the margin undulate, the venation of 5 pairs of primary veins, arcuate to the margin, strongly anastomosing, slightly impressed above, conspicuous and reticulate below; adventitious shoots generally strict and sparsely branched, to 10 m. tall; branches stout, terete, slightly swollen at nodes, strongly grooved or striate; ocreae 2 cm. long, membranaceous and evanescent above, coriaceous and persistent below, the petioles stout 1–2 cm. long, densely tawny pubescent; blades large, generally orbicular except for the terminal leaf, frequently broader than long, 30 × 40, 50 × 80 cm. long and broad, coriaceous, rugose or bullate when mature, thin and plane when young, the apex rounded, the base rounded to cordate, the basal lobes commonly encircling the stem, the terminal leaflet commonly rhombic, longer than broad when mature, densely tomentose, the veins slightly impressed above, all venation conspicuous and reticulate below; midrib and secondary veins persistent pubescent above, the others sparsely pubescent when young, becoming glabrate above, the veins and leaf surface pubescent or becoming glabrate below, the margin irregular, commonly undulate; inflorescence terminal, often stout, the basal ocreae to 7 mm. long, membranaceous, the peduncle to 1.5 cm. long, the rachis minutely and often densely puberulent, 10–18 cm. long on mature shoots, to 45 cm. long on adventitious shoots, the bracts broadly ovate, about 1 mm. long, puberulent, the ocreolae membranaceous spreading, 1 mm. long, minutely puberulent or glabrate; staminate flowers 2–4 at each locus, the pistillate flowers 1–3 at each locus, the pedicels 2–3 mm. long, the hypanthium 0.6–1 mm. long, the perianth lobes broadly orbicular, 1.5 mm. long, 2 mm. wide, puberulent, the fertile stamens 2.5 mm. long, the sterile stamens rudimentary 0.5–1 mm. long, the fertile pistil glabrous or rarely slightly puberulent, on the ovary, the sterile pistils glabrous, rudimentary, 0.5–1.5 mm. long; fruit globose to ovoid, 5–6 mm. long and 4.5 mm. in diameter, the fruiting perianth imbricate at the apex, not coronate, the fruiting hypanthium with conspicuous vascular bundles; achene subglobose, dark brown, shining, slightly triradiate at the apex, the fruiting pedicels puberulent, 3–4 mm. long.

DISTRIBUTION: Dominican Republic, Puerto Rico, Virgin Islands and the Lesser Antilles south to St. Lucia and Barbados.

Barbuda: *Ponthieu s.n.* (FM). **Antigua:** Carrs Gut, *Box 301* (US), *1496* (A, US, ISOTYPES of *C. antiguensis*); Macarthy Hills, *Box 1495* (BM, US); Wallings Area, *J. Beard 283* (A, MO), *Howard 11984* (GH); Blubber Valley, *Howard 11863* (GH), without location, *Wullschlaegel 486* (M). **Montserrat:** Cudjoe Head, *Shafer 457* (FM, NY, US); Harris' Lookout, *Howard 11873* (GH). **Nevis:** Ward's Mountain, *Howard 11933* (GH). **Guadeloupe:** Pigeon, *Duss 3379* (US); Désirade, *Stehlé 195* (GH, NY); Deshaies, *Stehlé 2018* (US); Jarry, *Questel 602* (US); Vieux Fort, *Howard 11847* (GH), *11849* (GH); without location, *Duss 1743* (NY), *2193* (FM, GH, MO, NY). **Dominica:** Calibishie, *W.H. & B.T. Hodge 3142* (GH); Pointe Ronde to Milton Estate, *W.H. & B.T. Hodge 2668* (GH); Pointe Baptiste near Calibishie, *W.H. & B.T. Hodge 3499* (GH). **Martinique:** Presqu'ile de la Caravelle, *Egler 39–252* (NY), *Duss 1743* (NY), *Howard 11728* (GH), *11729* (NY). **St. Lucia:** Between Le Toc and Cul de Sac Bay, *Howard 11371* (GH); Vieux Fort, *Howard 11475* (GH). **Barbados:** Turner's Hall Woods, *Eggers 7158* (A).

The growth forms of *Coccoloba pubescens* have been discussed in earlier papers (Jour. Arnold Arb. **38**: 229–231. 1957, **39**: 37–39, 44–46. 1958). Immature forms with wand-like branches and very large leaves are the most common habit found in the Lesser Antilles. Beard illustrates such growth forms in his publication "Vegetation of the Windward and Leeward Islands" (Oxford Forestry Memoir **21**: *f. 32.* 1949). A few isolated mature plants with the smaller leaf type were seen and collected on St. Lucia (*Howard 11475*), Guadeloupe (*Howard 11849*) and Martinique (*Howard 11729*). The variation in the texture, size and pubescence of the leaves within the populations studied in the field will include that described by Sandwith for his species *C. antiguensis.* I have previously placed that species in the synonymy of *C. pubescens* (Jour. Arnold Arb. **38**: 231. 1957).

Coccoloba striata Benth. Hooker Lond. Jour. Bot. **4**: 626. 1845.

Coccoloba guianensis Griseb. Fl. Brit. W. I. 163. 1859, not Meisner.
Coccoloba grisebachiana Lindau, Engl. Bot. Jahrb. **13**: 195. 1890.
Coccoloba pittieri R. Knuth ex Pittier, Man. Pl. Usuales Venez. 355. 1926.

Tree with scrambling branches; branches hollow, striate, glabrous; ocreae membranaceous above, coriaceous and persistent below, strongly ribbed; petioles attached above the base, strongly grooved above, 1.5–2 cm. long, glabrous; blades ovate to ovate-elliptic, 9 × 5.5 to 14 × 8 cm. long and broad, chartaceous, usually turning dark on drying, the apex shortly and obtusely acuminate, the base rounded to cordate or slightly cordate-auriculate, the midrib and primary veins almost immersed above and only slightly prominent below, the primary nerves 6–8 pairs, arcuate and anastomosing near the margin, the ultimate venation densely reticulate; leaves of scrambling shoots broadly ovate to 23 cm. long and 18 cm. broad, on petioles 3 cm. long; inflorescence to 27 cm. long, the rachis thin and glabrous or slightly puberulent, the flowering nodules widely separated in the pistillate plants and less conspicuously so in the staminate plants, the peduncle about 1 cm. long, the bracts ovate to triangular generally 1 mm. long, the ocreolae flaring, scarcely as long as the bracts, the pedicels equalling the ocreolae in the staminate flower; staminate flowers generally 2–4 per nodule, the hypanthium 0.75 mm. long, the perianth lobes ovate to oblong, 0.5 mm. long, the functional stamens with filaments 1 mm. long; pistillate flowers not seen; fruiting pedicels 2–2.5 mm. long, the ripe achenes red, ovoid, about 9 mm. long and 6 mm. in diameter, the apex acuminate, the lobes inconspicuous, the fruit slightly stalked at the base, obscurely 3-angled.

British Guiana: Without specific location, *Richard Schomburgk 1265* (B). **Trinidad:** Mount Tocuche, *Crueger* (TRIN 776-ISOTYPE of *C. grisebachiana*), *Baker* (TRIN 14804), *Freeman* (TRIN 9045), *Britton, Hazen and Mendelson 1262* (GH, NY). **Venezuela:** Carababo, Guaremales, *Pittier 8880* (A, GH, ISOTYPES of *C. pittieri*); Carruao, *Pittier 11847* (A).

This species is distinctive among the other species of *Coccoloba* reported from Trinidad on the basis of the hollow scrambling branches, the attachment of the petioles above the distinctive base of the ocrea and by the widely separated flowering nodules on the inflorescence rachis of the pistillate plants. The extremely fine reticulate pattern of the ultimate venation of the leaves is also characteristic, although this expression is not always seen in the herbarium collections.

One sheet of *Pittier 8880* in the Gray Herbarium collections cited above probably represents an adventitious shoot. A short piece of the stem 9 cm. long contains one node. The stem is hollow and the ocrea extends 5.5 cm. above the apex of the petiole scar and 1.5 cm. from this point down the stem. The ocrea is coriaceous, appressed and deeply bifid. The leaf on the same herbarium sheet is not attached but is oblong in shape and 40 cm. long and 17 cm. broad. The margin is obviously undulate when fresh. Unless this is a mixed collection, which does not seem likely, the dissimilarity of the leaves of fertile and adventitious shoots is as large in this species as in other species of *Coccoloba.*

The material cited above from Trinidad is all from pistillate plants in fruiting condition or with old inflorescence axes. The types of *Coccoloba striata* and *C. pittieri* are staminate plants. There is no question in my mind that these are all conspecific, although I have not seen this species in the field.

Coccoloba paraensis Meisner, based on Spruce and Martius' material from Para and Amazonas, and *C. glaziovi* Lindau, based on a Glaziou specimen collected from Rio de Janeiro, probably represent the same species and should be assigned to synonymy here. Regrettably, I have insufficient material either to include or exclude these species with certainty at the present time.

Coccoloba swartzii Meisner, DC. Prodr. **14**: 159. 1856; Lindau, Engl. Bot. Jahrb. **13**: 157. 1890; Howard, Jour. Arnold Arb. **30**: 420. 1949, **37**: 317–339. 1956.

Coccoloba swartzii var. (?) *portoricensis* Meisner, DC. Prodr. **14**: 160. 1856.
Coccoloba barbadensis Lindau, Engl. Bot. Jahrb. **13**: 148. 1890; Duss, Ann. Inst. Col. Marseille **3**: 166. 1897, not Jacquin.
Coccoloba diversifolia Lindau, Symb. Antil. **1**: 223. 1899; Griseb. Fl. Brit. W.I. 163. 1859, and most recent authors, not Jacquin.

Trees 8 to 20 m. tall; branches terete, the youngest puberulent, becoming glabrate, the nodes slightly tumid; ocreae 10–12 mm. long, the basal portion 3–5 mm. long, coriaceous, persistent, the upper portion membranaceous and deciduous, puberulent to glabrate; leaves of normal shoots with petioles 10–18 mm. long, puberulent to glabrate, the blades ovate to elliptic, 2.2 × 1.3, 7 × 5, 11 × 9, 15 × 7.5 cm. long and broad, coriaceous, usually turning black on drying, glabrous, having pit-like depressions on the upper surface and small glands on the lower surface, the apex acute, often rounded, the base narrowed, rounded or slightly cordate and usually oblique, the margin entire; midrib and veins inconspicuous or flat above, prominent below, the primary veins 6 or 7 pairs, arcuate, anastomosing, the secondary venation conspicuous, reticulate; leaves of adventitious shoots with petioles 1.5–2.5 cm. long, the blades generally ovate to lanceolate 23 × 8.5, 45 × 18.5, to 70 × 25 cm. long and broad, the apex acute to acuminate, the base rounded; inflorescence terminal 10–15 cm. long, the rachis glabrous or with glandular exudate, rarely papillose; staminate flowers in clusters of 3–5 flowers at each node, tightly surrounded by membranaceous ocreolae which form a truncate cylinder after the flowers have fallen, the pistillate flowers borne singly at each node, the bracts ovate 0.5 mm. long, the ocreolae 1.1.5 mm. long, membranaceous, the pedicels shorter than the ocreolae; hypanthium 0.5 mm. long, the perianth lobes 1–1.5 mm. long, the fertile stamens 1–1.5 mm. long, the sterile stamens rudimentary, 0.5 mm. long; fruit ovoid 8–10 mm. long, 6 mm. diameter, the perianth lobes 1–1.5 mm. long and coronate in fruit; achene dark brown.

DISTRIBUTION: Jamaica, the Bahamas, Dominican Republic, Puerto Rico, St. Croix, St. Jan, Virgin Gorda, St. Thomas, Saba, St. Kitts, Montserrat, Nevis, Antigua, Guadeloupe, Dominica, Martinique, St. Lucia and Barbados.

Antigua: Pearl Hill, *Box 975* (US). **St. Kitts:** Mt. Misery, *R.A. & E.S. Howard 11938* (GH). **Nevis:** *R.A. Howard 11921* (GH). **Montserrat:** Central Hills, *R.A. & E.S. Howard 11868* (GH), *11866* (GH), *11871* (GH), *11872* (GH); Gage's Upper Soufriere, *R.A. & E.S. Howard 11882* (GH); Gardu Gut, *Shafer 323* (F, NY, US), *615* (F, NY, US). **Guadeloupe:** Bois de Gombeyre, *Duss 3251* (F, GH, NY, US); Bouillante to Pointe Noire, *R.A. & E.S. Howard 11843* (GH). **Dominica:** Antilles near Marigot, *R.A. & E.S. Howard 11754* (GH); Salybia, *W.H. Hodge 3404* (GH); South Chiltren Estate, *W.H. & B.T. Hodge 1583* (GH). **Martinique:** Casa Pilote, *Hahn 1187* (F, GH, US), *R.A. & E.S. Howard 11712* (GH); Diamant, *Duss 37, 248* (NY); Mt. Pelee, *Duss s.n.* (NY); Montagnes des Trois Flotz, *Hahn 629* (F, GH); Presqu'ile de la Caravalle, *R.A. & E.S. Howard 11727* (GH), *Egler 39–230* (NY); Trois Islets, *R.A. & E.S. Howard 11731* (GH). **St. Lucia:** Castries-Dennery Road, *R.A. & E.S. Howard 11335* (GH), *11329* (GH), *11355* (GH); Gros Piton, *R.A. & E.S. Howard 11506* (GH); Le Toc to Cul de Sac Bay, *R.A. & E.S. Howard 11377* (GH); Vieux Fort, *R.A. & E.S. Howard 11404* (GH). **Barbados:** Turners Hall Wood, *Eggers 7161* (US).

Coccoloba swartzii forma **pubescens** Howard, Jour. Arnold Arb. 30: 420. 1949.

Similar to the species, but the young shoots, petioles, the lower end of the upper leaf surface, especially the midrib, the ocrea and the inflorescence rachis, at least at the base, puberulent to pilose pubescent.

Antigua: Blubber Valley, *Box 1411* (US-HOLOTYPE), *R.A. & E.S. Howard 11860* (GH), *11985* (GH), *11986* (GH); Carr's Ghaut, *R.A. & E.S. Howard 11994* (GH); Orange Valley, *Box 1184* (GH, US); Pelican Bay area, *R.A. & E.S. Howard 11990* (GH); Sugar Loaf Mt., *Box 1543, 1544* (US), *A.C. Smith 10489* (A). **Barbuda:** Codrington Village, *Fairchild 3830* (A, US); Martello Tower, *J.D. Beard 372* (A, MO); without location, *Box 602* (US). **Guadeloupe:** *De Ponthieu 86* (FM).

Coccoloba uvifera L. Syst. Nat. ed. 10. 1007. 1759.

Polygonum uvifera L. Sp. Pl. 365. 1753.
Guaiabara uvifera House, Amer. Midl. Nat. **8**: 64. 1922.

Tree of strand areas, 2–17 m. tall, branches terete, stout, papillose to pilose, the nodes not tumid; ocreae rigid, coriaceous at the base, membranaceous at the apex, 3–8 mm. long, papillose to pilose; leaves of normal shoots with petioles stout, 7–10 mm. long, papillose to pilose, the blades orbicular to reniform, 6 × 8, 11 × 13, 13 × 18 cm. long and broad, thick and fleshy when fresh, coriaceous when dry, glabrous and minutely punctate on both surfaces, the apex rounded truncate or emarginate, the base rounded to broadly cordate one lobe often extending around the petiole; midrib and primary veins prominent on both surfaces, frequently brightly colored when fresh, the primary veins 3–5 pairs, usually straight, bifurcate and weakly anastomosing near the margin, commonly barbate in the axils of the basal veins, the secondary venation minutely reticulate or obscure; leaves of adventitious shoots usually variable in size and shape, commonly obovate; inflorescence stout, 15–30 cm. long, the rachis puberulent; staminate flowers in clusters of 1–7, the pistillate flowers solitary at each locus, the bracts ovate, 1–1.5 mm. long, 2 mm. broad, puberulent, the ocreolae membranaceous, 1 mm. long, puberulent, the flowering pedicels 1–2 mm. long, the perianth yellow-white or greenish, the hypanthium 2–3 mm. long, the perianth lobes 4 mm. long, 3–4 mm. wide, the fertile stamens to 4 mm. long; fruiting pedicels 3–4 mm. long; fruit obpyriform, 1.2–2 cm. long, 8–10 mm. diameter, narrowed at the base, rounded-truncate at the apex, the perianth lobes appressed against the apex of the achene, the perianth rose-purple when mature, the achene black.

DISTRIBUTION: Throughout tropical America along the coasts.

Antigua: Carr's Ghaut, *R.A. & E.S. Howard 11992* (GH); without location, *Box 1434* (A, US). **St. Barts:** *Euphrasen s.n.* (S), *Forsström s.n.* (S), *Questel* 82 (NY). **Montserrat.** Harris' Lookout, *Howard 11874* (GH). **St. Kitts:** *Britton & Cowell 247* (NY), *Sargent s.n.* (A). **Guadeloupe:** St. Francois, *Howard 11787* (GH); without location *Duss 2183* (US). **Dominica:** Carib Reserve, *W.H. & B.T. Hodge 3316* (GH); Cabrites, *Howard 11750* (GH); Hatton Garden, *W.H. & B.T. Hodge 2957* (GH); Pointe Ronde, *W.H. & B.T. Hodge 2686* (GH); Scot's Head, *W.H. & B.T. Hodge 1605* (GH). **Martinique:** Casa Pilota, *Howard 11720* (GH); Presqu'ile de la Caravalle, *Howard 11726* (GH); Salinas Pie Beach, *Egler 39–19* (NY); without location *Belanger s.n.* (B), *Duss 1742* (US), *Sieber 103* (MO, US). **St. Vincent:** Kingshill, *Howard 11125* (GH). **Grenadines:** Bequia, *Dalton for H.H. Smith B–128* (GH); Mayero, *Howard 11041* (GH), *11042* (GH); Petit St. Vincent, *Howard 10912* (GH); Kick 'em Jenny, *Howard 10782* (GH). **Grenada:** Grande Anse, *Broadway s.n.* (FM, GH), *J.S. Beard 203* (A). **Barbados:** Christ Church, *Dash 129* (FM); St. Philip, *Bovell 129* (US); without location, *Curran.* (FM, MO), *Eggers 7347* (A). **Trinidad:** Galera Point, *Broadway s.n.* (A); Monos Island, *Williams* (TRIN). **Tobago:** Buccoo Bay, *Elmore V–4* (FM); Crown Lands, Palo Saco, *Russell* (TRIN *13071*); Farm Road, *Williams* (TRIN *11143*); Lower Scarborough, *Broadway 3617* (FM, S); Mt. St. Georges, *Howard 10480* (GH); Speyside, *Turley* (TRIN 15244).

Coccoloba venosa L. Syst. Nat. ed. 10, 1007. 1759; Fawcett & Rendle, Jour. Bot. **51**: 123. 1913.

Uvifera arbor americana, fructu aromatico punctatus, Pluk. Alm. 394. *t. 237, fig. 4.* 1696, as to leaf only.
Coccoloba punctata L. Sp. Pl. ed. 2, 523. 1762.
Coccoloba nivea Jacq. Hist. Stirp. Amer. 115, *pl. 78.* 1763; Enum. Pl. 19. 1762.
Coccoloba excoriata Duss, Ann. Inst. Col. Marseille **3**: 168. 1897, not L.
Guaiabara venosa House, Am. Midl. Nat. **8**: 64. 1922 as *Guaibara.*

Trees to 15 m. tall; branches terete, glabrous, the nodes not tumid; ocreae membranaceous, deeply cleft, acuminate on one side, or truncate, to 2 cm. long; glabrous or with flattened glands; leaves of normal shoots with petioles 5–10 mm. long, glabrous, the blades oblong-lanceolate to elliptic, 8 × 4, 10 × 4.5, 16.5 × 6.5, 21 × 9, 27 × 10.5 cm. long and broad, membranaceous, glabrous except for clusters of hairs in the axils of the veins, sparsely glandular below, the apex short-acuminate, the base narrowed and slightly cordate or cuneate or obtuse; midrib and primary veins slightly prominent on both surfaces, the primary veins 8–13 pairs, straight or arcuate, bifurcate and anastomosing at the margins; leaves of the adventitious shoots about the same size, the internodes much elongate and the ocreae to 4 cm. long; inflorescence terminal or terminal on short lateral branches, the rachis puberulent, angular; staminate flowers in clusters of 2–5, the pistillate flowers solitary, the bracts lanceolate-ovate, to 1.5 mm. long, black, puberulent to pilose or commonly with a fringe of hairs at the apex; ocreolae membranaceous, enlarging with the expanding bud, each flower with an ocreola, to 2 mm. long, the flowering pedicels 1–2 mm. long, glabrous; hypanthium less than 0.5 mm. long, the perianth lobes broadly ovate, 1.5–2 mm. long and broad, slightly unequal, the fertile stamens to 1 mm. long; fruiting pedicels 1.5–2.5 mm. long, the perianth lobes fleshy, white or pink, enclosing the black achene, the hypanthium scarcely evident in the fruit, the fruit 3–4 mm. long and broad, the fruit broadly ovoid.

DISTRIBUTION: Cuba (introduced), Hispaniola, Puerto Rico, Jamaica (?), Virgin Islands, Lesser Antilles and Trinidad.

Antigua: Galley Bay, *Box 1081* (US); Morris, *J.S. Beard 351* (A, MO); Wallings, *Howard 11989* (GH), without location, *Fairchild s.n.* (US). **St. Martin:** *Forsström s.n.* (S), *Boldingh 2993B* (NY). **St. Barts:** *Forsström s.n.* (NY, S), *Le Gallo 2371* (A). **Montserrat:** Harris' Lookout, *Howard 11875* (GH). **Tortola:** *Schafer 1125* (US). **Guadeloupe:** Bouillante to Pointe Noire, *Howard 11842* (A); Gourbeyre, *Duss 3250* (FM, NY, US); Riviere, *Stehlé, Quentin & Bena 5313* (US); Les Saintes, *Questel 1763* (US). **Dominica:** Roseau to Canefield, *Hodge 443* (GH, NY, US). **Martinique:** Carbet, *Duss 1744* (NY); Casa Pilota, *Hahn 967* (G, US), *1182* (S), *Howard 11714* (GH). **St. Lucia:** Soufriere, *Howard 11580* (GH). **Grenadines:** Kick 'em Jenny, *Howard 10792* (GH); Isle of Ronde, *Howard 10713* (GH), *10717* (GH). **Grenada:** *Broadway s.n.* (MO, NY, US). **Barbados:** Dodd's Botanical Station, *Waby 131* (FM); Turners Hall Woods, *Gooding 594* (NY), *Dash 262* (NY). **Trinidad:** Castara, *Sandwith 1831* (NY); Cat's Hill Reserve, *Swabey 12535* (TRIN); Galera Point, *Broadway 2788* (BR, FM, GH, MO, NY, TRIN); Guanapo, *Dannouse s.n.* (TRIN); Quinam Reserve, *Williams 12015* (NY, TRIN); Southwest Reserve, *Marshall 12404* (TRIN), *Swabey 12271* (TRIN); Southern Watershed Reserve, *Russell 12261* (TRIN); Toco, *Freeman & Williams 11768* (NY, TRIN). **Tobago:** Mason Hall, *Broadway 4160* (A, FM, GH, MO, NY, S, TRIN), *Howard 10470* (GH); Point opposite Melville Island, *Freeman & Williams 11422* (TRIN). **Little Tobago:** *Swabey 12959* (TRIN).

THE GENERA OF THE NYMPHAEACEAE AND CERATOPHYLLACEAE IN THE SOUTHEASTERN UNITED STATES

CARROLL E. WOOD, JR.

THE TREATMENTS of the ranalian families Nymphaeaceae and Ceratophyllaceae presented here continue a series of studies toward a biologically oriented generic flora of the southeastern United States made possible by the interest and support of George R. Cooley and a grant from the National Science Foundation. The first paper in this series of generic treatments (The genera of the woody Ranales in the southeastern United States. Jour. Arnold Arb. **39**: 296–346. 1958) includes a general explanation of the aims and scheme of this work. As noted there, the area covered in these studies is bounded by and includes North Carolina and Tennessee, Arkansas and Louisiana. The pattern of the descriptions, notes and references is the same as outlined and followed in the introductory paper. It may be called to attention again, however, that the descriptions are based upon the species which occur within this area, items in brackets being supplementary and not applying to our plants. The abbreviations of journals follow those of Schwarten and Rickett (Abbreviations of titles of serials cited by botanists. Bull. Torrey Bot. Club **76**: 277–300. 1958). References which have not been checked are marked by an asterisk.

The illustration of *Nelumbo* by Dorothy H. Marsh is from living materials obtained through the enthusiastic assistance of Richard A. Eaton and Kenneth A. Wilson.

NYMPHAEACEAE (WATER-LILY FAMILY)

Aquatic perennial [or annual] rhizomatous herbs, with alternate cordate to peltate floating or emersed leaves with involute vernation, and solitary, axillary, perfect, at least partially cyclic flowers. Plants usually with air-spaces, latex, vascular bundles without cambium or vessels, the leaf-tissues (especially) often with sclereids. Sepals 3–6[–12], green to petaloid, free or slightly united, hypogynous [in ours]. Petals 3-many, showy and colored, to stamen-like, free [in ours], hypogynous, or, with the stamens, inserted on the surface of the ovary, sometimes transitional to stamens. Stamens 3–200, extrorse or introrse; pollen more or less "monocotyledonoid," (monocolpate or derived types) or (in *Nelumbo*) 3-colpate. Gynoecium of [1]2–many carpels, free or united, superior to inferior. Ovules anatropous, many–2–1, pendulous from the top, the walls, or the abaxial suture of the carpels. Fruit a many-seeded berry, a nut, or 1–3 seeded, small and indehiscent. Seeds operculate (except *Nelumbo*), with or without an aril; embryo with thick and fleshy cotyledons, small and with abundant perisperm and little endosperm or (in *Nelumbo*) large and lacking both. (Including Cabombaceae, Nelumbonaceae.)

A family of eight well-marked genera (five of which occur in our area), of very wide distribution in quiet fresh waters. The genera are linked together by the aquatic rhizomatous habit, the usually long-petioled simple leaves (with a strong tendency towards peltation), the solitary, long-peduncled flowers with at least partially cyclic arrangement of parts, the anatropous, pendulous parietal ovules, the presence of air spaces, the latex-producing habit, and the monocotyledonoid vascular bundles. In respect to other characteristics (e.g., pollen morphology, embryology, operculum and other features of seeds, seedlings, anatomy, floral structure, etc.) the relationships are reticulate. Although a large body of literature exists, many of these latter items have been investigated only partially and it is difficult to draw complete comparisons throughout the family. Various divergences occur between the genera, especially in respect to the structure of flower and fruit, these generally being associated with special mechanisms which function in connection with pollination and with the protection, dispersal, and survival of seeds. The structural features of all these plants need further study and interpretation in connection with their biology.

The treatment of Caspary, who regarded the family as composed of three well-marked subfamilies, is followed here. Some authors, however, split the group into three or even five families (in as many as three orders). These latter treatments seem unjustified, particularly in respect to the Cabomboideae (*Cabomba* and *Brasenia*) and to *Euryale*, *Victoria* and *Barclaya*, all of which clearly seem to be linked to *Nuphar* and *Nymphaea*. *Nelumbo*, the single genus of the Nelumboideae, is perhaps the most divergent member of the family, but even this genus may be regarded merely as being specialized in regard to leaves, dispersal mechanism, embryo and pollen. (See also *Brasenia* and *Nelumbo* below.)

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Key to the Genera of Nymphaeaceae

A. Carpels united, either along their sides or along the outer margins by adnation to a cup-like "receptacle;" stigmas radiate; ovules numerous in each locule; stamens numerous, introrse; fruit an irregularly dehiscent berry, ripening in the water; leaves with a basal sinus. Subfam. NYMPHAEOIDEAE.

B. Perianth wide-spreading, of 4 sepals and 12–32 showy white, pink, blue or yellow petals; carpels sunken in a cup-shaped fleshy receptacle or hypanthium on the outer surface of which petals and stamens are inserted; carpels prolonged upward into slender incurved projections (carpellary styles); seeds arillate. . . . . 1. *Nymphaea.*

B. Perianth subglobose, of 6 concave yellow (green- or red-tinged) sepals and numerous scale-like or stamen-like "petals" inserted with the numerous stamens on the receptacle beneath the ovary; carpels completely united, the stigmas radiate and sessile on a disc; seeds not arillate. . . . . 2. *Nuphar.*

A. Carpels free (although in *Nelumbo* embedded in the receptacle); ovules solitary or 1–3 in each carpel; stamens hypogynous, few to many (3–36) and extrorse to slightly introrse, or very numerous and extrorse; fruits leathery or hard, indehiscent; leaves (at least the floating or emersed ones) peltate, lacking a basal sinus.

C. Perianth of 6–8 segments, the flowers small; receptacle small, with 4–18 free, superior carpels; fruit small, 1–3 seeded; leaves all floating or submersed; plants more or less coated with mucilage. Subfam. CABOMBOIDEAE.

D. Plants with dissected, opposite submersed leaves and small, peltate floating leaves; perianth petaloid, white or purple; stamens 3–6. . . . . 3. *Cabomba.*

D. Plants with only undivided, alternate, peltate floating leaves; sepals persistent, the petals dull purple; stamens 18–36; plants heavily coated with mucilage. . . . . 4. *Brasenia.*

C. Perianth of numerous segments, the flowers large and showy; receptacle large, top-shaped, with the many uniovulate carpels sunken separately in cavities in the upper side, only the stigmas protruding; receptacle enlarging greatly in fruit, the carpels maturing into nuts; stamens very numerous, extrorse, hypogynous; all leaves floating or emergent on strong petioles, centrally peltate, large, glaucous; plants lacking mucilage. Subfam. NELUMBONOIDEAE. . . . . 5. *Nelumbo.*

Subfam. NYMPHAEOIDEAE Casp.

1. **Nymphaea** L. Sp. Pl. 1: 510. 1753, partim, emend. J. E. Smith in Sibth. & Smith, Fl. Graec. Prodr. 1: 360. 1808–9, nom. cons.

Perennial rhizomatous aquatic herbs with floating ovate to orbicular leaves, cleft at the base, the submerged stipulate petiole inserted at the base of the deep sinus; aerial leaves exceptional; submersed leaves often present, filmy and delicate. Flowers solitary, showy, white (to pink), blue or yellow, borne either at the surface of the water or raised above it. Sepals 4, nearly free, one completely outside the others; petals 12–ca. 32, in whorls of 4, 8, 8 (in subg. BRACHYCERAS), or 4, 8, with the arrangement of petals within these not clear (in subg. NYMPHAEA), in this last the petals often transitional to stamens. Stamens numerous, 50–150, introrse, with or without an appendaged connective. Gynoecium of 7–25 carpels, apocarpous or syncarpous, in a circle abutting and adnate to a central prolongation of the floral axis and sunk in the cup-shaped fleshy receptacle (or hypanthium?), upon the outer surface of which petals and stamens are inserted, and produced above it as "carpellary styles;" upper surfaces of carpels stigmatic to form a broad, concave radiate stigma. Ovules numerous, anatropous, pendulous from the sides of the ovary locules. Fruit an irregularly dehiscent spongy berry, ripening under water; seeds 1–many per carpel, hard, operculate, embedded in mucilage and each surrounded by a bell-shaped floating aril, embryo small, with 2 equal fleshy hemispherical cotyledons, embedded in a thin layer of endosperm and abundant perisperm. (*Castalia* Salisb., nom, rejic.) TYPE SPECIES: *N. alba* L. (From the Greek and Latin, *Nymphaea*, a water-lily, from *Nympha*, goddess of waters, meadows and forests.) — WATER-LILIES, POND-LILIES, WATER-NYMPHS.

A genus of about 35 species of very wide occurrence (lacking in New Zealand and the Pacific slope of North America) in quiet, fresh (rarely brackish) waters. Represented with us by three species in two of the five subgenera.

Subgenus BRACHYCERAS Casp., characterized by carpels free at the sides, thick, fleshy carpellary styles, and appendaged stamens, and including about 12 species of the tropics and subtropics, occurs in our area as *N. elegans* Hook., a pale-violet-flowered species of southern Florida, the West Indies and Mexico. The sepals and 4 outer petals persist, becoming turgid in fruit.

Subgenus NYMPHAEA (Subg. *Castalia* DC.) characterized by carpels united at the sides, ligulate carpellary styles, obscurely veined sepals, and outer stamens with petaloid filaments, includes about 7 species, all of the northern hemisphere. In our area the subgenus occurs as the yellow-flowered *N. mexicana* Zuccarini (*N. flava* Leitner), $2n = 56$, of Florida, southern Louisiana, Texas, and Mexico, one of the most restricted in range, and the white-flowered *N. odorata* Ait., a quite variable species. This latter occurs both as the typical form and the much larger var. *gigantea* Tricker (*Castalia lekophylla* Small). Some authors also recognize var. *stenopetala* Fern. and var. *minor* Sims. In view of this diversity and the two chromosome levels recorded for this species ($2n = 56, 84$), further critical studies of *N. odorata* are needed. A perhaps parallel case is the complex *N. alba* L., of Europe, in which 84, 105, 112, and 160 chromosomes have been reported.

Flowers of all species are proterogynous. Some are self-fertile, others self-sterile. Our species are all day-flowering; at the latitude of Philadelphia Conard records the flowers of *N. mexicana* as open for each of 2 days from 10–11 A.M. to 3–4 P.M.; those of *N. odorata* open for 3 or 4 days from 6–7 A.M. to 12–1 P.M.; and those of *N. elegans* open from 7–8 A.M. to 12–1 P.M. When receptive, the stigmatic cup is filled with a sweetish, watery liquid. No nectar is secreted (although some species are very fragrant); insects visit the flowers for the abundant pollen.

Numerous hybridizations (particularly within subg. BRACHYCERAS and subg. LOTOS) since about 1850 have produced many showy horticultural plants. Crosses between members of subg. NYMPHAEA have resulted in hardy forms (all sterile) with white, yellow, pink, orange or red flowers. Natural hybrids occur within this subgenus where two or more species grow in the same pond. All attempts to cross species of different subgenera have failed; within a subgenus interspecific hybrids may be either sterile or fertile. Recorded chromosome numbers range from 28 to 224. The chromosomes of plants used in hybridization work apparently have not been determined. One of the smallest-flowered species (*N. tetragona* Georgi) and one of the largest-flowered (*N. gigantea* Hook.) are both high polyploids ($2n = 120$ and 224, respectively)!

Nymphaea mexicana spreads rapidly by runners and produces on geotropic shoots hibernating bodies or "brood bodies" which consist of a cluster of fleshy roots more or less resembling a "hand" of bananas. Rich in starch, these brood bodies are an important duck food. *Nymphoides aquatica* (Walt.) Kuntze (Gentianaceae) produces similar clusters of fleshy roots at the base of the inflorescence; the two are often confused.

The nomenclatural confusion centering around the application of the name *Nymphaea* to this genus or to that now known as *Nuphar* J. E. Smith has resulted in the conservation of both of these names in the sense in which they are used here.

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2. **Nuphar** J. E. Smith in Sibth. & Smith, Fl. Graec. Prodr. **1:** 361. 1808–1809, nom. cons.

Perennial aquatic herbs with stout, creeping rootstocks, emersed, floating or submersed narrowly lanceolate to orbicular entire leaves with a deep sinus at the base; submersed leaves thin and delicate. Sepals usually 6[5–12], the 3 outer greenish to yellowish, the inner yellow, tinged with red or green. "Petals" numerous, linear to oblong, thick, stamen-like or scale-like, bearing a nectary on the outer surface and inserted with the very numerous introrse stamens on the receptacle under the ovary. Gynoecium of 5–23[–30] carpels, resembling that of *Papaver*, with a stigmatic disc, each carpel with a stigmatic ray; ovary multilocular, with numerous ovules on the inner walls. Fruit an ovoid to columnar berry, dehiscing irregularly by the swelling of a gelatinous covering of the seeds; seeds usually ovoid, yellow to brown, opening by a small operculum, lacking an aril. Embryo with 2 fleshy cotyledons. Pollen monocolpate, oblate-sphaeroidal, spiny. $2n = 34$. (*Nymphaea* L. partim, emend. Salisb. and *Nymphozanthus* L. C. Rich., nom. rejic.) TYPE SPECIES: *N. luteum* (L.) Sibth. & Smith. (The name from Greek *nouphar*, the flowers of a medicinal plant mentioned by Dioscorides, perhaps *N. luteum.*) — SPATTERDOCK, COW-LILY, YELLOW POND-LILY.

Perhaps 19 species in North America, two in Europe and several poorly known in eastern Asia; probably about 14 in our area, but some of these not well understood. The group is taxonomically difficult, especially from herbarium materials, in which the features of the plants are not well retained. Ecological and ontogenetic variations add to the difficulty. Entire populations need study; specimens should be preserved in liquid and carefully pressed flowers and adequate notes made in the field. Taxonomic characters used in the group include habit; shape and pubescence of leaf-blades; cross-sectional shape of petioles; presence or absence of submersed leaves and their shape; number of sepals and color, shape and size of "petals;" shape of pistil; lobing, rays and color of stigmatic disc; shape and coloration of fruit; and color, size and indument of seeds. Special efforts should be made to press open flowers carefully and to record variation in numbers of stigmatic rays; at least some discs should be pressed separately and longitudinal sections of pistils and fruits are valuable.

All of the chromosome counts made thus far indicate a genus with a uniform chromosome number of $2n = 34$. Largely sterile hybrids are known between the European *N. pumilum* and *N. luteum*, between *N. advena* and *N. sagittifolium*, and between *N. variegatum* and *N. microphyllum* (of the northern U. S. and Canada). (This last also exists in a fertile form, *N.* × *rubrodiscum* Morong.) Where *N. advena* and *N. variegatum* overlap in range (e.g., southern Michigan) intermediate plants are known, but these have not been studied in detail. The existence of hybrids of this kind has led to the treatment of the European and American representatives of the genus as a single variable species with 9 subspecies. Most entities appear to be definite units which maintain themselves both ecologically and geographically, however.

The flowers are proterogynous and are visited by pollen-collecting insects (sweat bees, flies and beetles) which work over the introrse anthers exposed by the recurving of the filaments as anthesis proceeds. The fruit ripens generally below the surface of the water, splitting irregularly, the carpels tending to separate and float as decay of the berry occurs.

As in *Nymphaea*, long known for the occurrence of sclereids in blades and petioles, bizarre stellate sclereids occur at the intersections of vertical diaphragms in the petioles. Both genera have been the subject of numerous anatomical and physiological investigations, a great many of which have dealt with the European *Nuphar luteum* and *Nymphaea alba*.

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Subfam. CABOMBOIDEAE Casp.

3. **Cabomba** Aubl. Hist. Pl. Guiane Franç. 1: 321. *t. 124.* 1775.

Strictly aquatic herbs with opposite submersed leaves and sometimes a few alternate floating leaves. Roots adventitious from the nodes. Submersed leaves petiolate, the blade divided into 5–7 parts at the summit of the petiole, each part divided dichotomously and trichotomously several times into many long, narrow segments. Floating leaves (when present) peltate, small, narrow and tapered to both ends, or narrow and forked [or resembling miniature leaves of *Brasenia*]. Flowers borne singly on long axillary peduncles, the perianth white or purple [or yellow], sepals 3 and petals 3, slightly united near the base. Petals clawed, the blade often auriculate. Stamens 3–6, extrorse, the pollen 1-sulcate. Carpels [1]2–4, free, elongate, with small terminal stigmas; ovules usually 3, one on the adaxial, one on the abaxial suture and one on the wall near either. Fruit indehiscent; seeds 3, pendulous, operculate, covered with elongated processes; embryo as in *Nymphaea*, small. TYPE SPECIES: *C. aquatica* Aubl. (The name presumably a barbaric one.) — FANWORT, WATER-SHIELD.

Seven species of warm and temperate regions of the New World. Two species, *C. caroliniana* Gray ($2n = 24$) and *C. pulcherrima* (Harper) Fassett, in our area. *Cabomba caroliniana*, with yellow-based white petals rounded at the summit, ranges from south-central Texas to southern Florida, northward to Kentucky, southern Michigan and along the Atlantic coast to New York, Connecticut, and southeastern Massachusetts. Often used as an aquarium plant, this species appears to be adventive north of Virginia. *Cabomba pulcherrima,* with purple, emarginate perianth segments, occurs at low altitudes from southwestern South Carolina to southwestern Georgia and adjacent Florida. The terminal divisions of the leaves of both species have spathulate tips.

As an aquarium plant *Cabomba* is most likely to be confused with *Limnophila* (*Ambulia*) *heterophylla* Benth. (Scrophulariaceae), which has sessile ternate leaves with the segments pinnately divided.

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4. **Brasenia** Schreb. Gen. Pl. ed. 8. 1: 372. 1789.

Aquatic herbs with floating, alternate, long-petioled, elliptic, centrally peltate leaves and small, solitary, axillary dull-purplish flowers. Rhizome small, bearing leaves and axillary runners which creep on the surface of mud, root at the nodes, and produce leafy branches and other runners.

Submersed leaves present, at least in seedlings. Submersed parts of plant heavily covered with a mucilaginous jelly. Sepals 3–4, colored within, persistent. Petals 3–4, linear, sessile. Stamens 18–36, the filaments filiform, and anthers slightly introrse; pollen 1-sulcate. Carpels 4–18, free, oblong-ovate, the ovules 2 in each, anatropous, pendulous from the abaxial suture. Fruit clavate, indehiscent, with 1 or 2 small, dull, grayish white, operculate seeds. TYPE SPECIES: *B. Schreberi* Gmel. (Origin of name not explained by Schreber.) — WATER-SHIELD, WATER-TARGET, PURPLE BONNET, PURPLE WEN-DOCK.

A single species widely but sporadically distributed in ponds and slow streams in the West Indies, Mexico and Central America, Florida to Texas, north to Prince Edward Island, southern Quebec, southern Ontario, and Minnesota; also Idaho, California to British Columbia and Alaska; eastern Asia, Australia and Africa.

This curious plant with centrally peltate leaves is clearly linked to *Cabomba* through leaves, floral structures, and pollen morphology. Both plants are sometimes treated as a separate family, the Cabombaceae. Seeds, seedling ontogeny, pollen morphology and embryology, as well as structural features, do not bear out such a segregation, however. It may be noted that in *Brasenia* the mode of seed germination and the early seedling stages are essentially the same as in *Nymphaea* and *Nuphar*. The first leaf is awl-like, the second narrowly oblong with the petiole at the margin at the lower end. Subsequent leaves are eccentrically peltate, then centrally peltate, a total of 6–9 submersed leaves being produced before the first characteristic floating leaves.

The submersed parts of the plant are notable for the extremely heavy covering of mucilaginous jelly, the secretion of numerous ephemeral glandular hairs (found also, but to a lesser degree, in the other genera, with the exception of *Nelumbo*). Specimens should be prepared with waxed paper, for the leaves become quite brittle in drying and adhere firmly to newsprint.

Dianthesis has been reported in *Brasenia* in Japan by Tokura (cf. H. L. Mason, Fl. Marshes Calif. 491. 1957). The proterogynous flowers are raised above the water and are open for the first time from about 6 to 9 A.M., are then drawn into the water to reappear the following morning when the pollen is shed, and finally are withdrawn again. (Cf. dianthesis in *Persea* [Lauraceae]).

In the southern part of our range the plant is evergreen, but at least in the northern United States it produces in autumn winter buds which absciss from the parent plant and overwinter at the bottom of the pond. These reddish, translucent bodies consist of the thickened stem-tip with dwarf leaves with thickened petioles and the characteristic gelatinous covering. Dispersal is effected not only by the winter buds but by the fruiting peduncles which become detached and float.

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Subfam. NELUMBONOIDEAE Casp.

5. **Nelumbo** Adans. Fam. Pl. **2**: 76. 1763.

Aquatic herbs with fibrous roots borne at the nodes of slender horizontal vegetative rhizomes and thickened storage rhizomes, and with large, dimorphic (floating and emersed) peltate leaves and large yellow or pink flowers borne on stout peduncles well above water. Perianth of ca. 14–26 petaloid tepals, the outer 2–5 persistent (and thus calyx-like), the inner caducous in 2–4 days. Stamens ca. 200, with a conspicuous fleshy terminal appendage, extrorse, spirally inserted; pollen tricolpate. Carpels usually 12–28 (9–39), borne singly in cavities in the pithy obconical receptacle, basally attached, flask-shaped, the ovary oblong-cylindric, completely immersed, the style short, neck-like, the stigma circular, centrally depressed; ovule solitary in each carpel, anatropous, pendulous from the top of the locule. Carpels becoming in fruit acorn-like very hard-walled nuts in the greatly enlarged receptacle. Embryo with only a rudimentary primary root, filling the fruit with two large fleshy cotyledons which inclose in a delicate stipule-like sheath a green plumule with two peltate involutely folded leaves and two rudimentary leaves. Seedling floating upon germination; all roots adventitious. $2n = 16$. (*Nelumbium* Juss.) TYPE SPECIES: *N. nucifera Gaertn.* (Name derived from the Ceylonese name for *N. nucifera*.) — YELLOW LOTUS, YELLOW NELUMBO, GREAT YELLOW LILY, POND-NUTS, WATER-NUT, WATER-CHINQUAPIN, WONKAPIN, YONKAPIN, YOCKERNUT, DUCK ACORNS, RATTLE-BOX, ALLIGATOR BUTTONS.

Two species, *N. lutea* (Willd.) Pers. (West Indies, Central America, Florida to Texas, and locally northward to southern New England, New York, southern Ontario, Minnesota and Iowa) and *N. nucifera* Gaertn. (China to Australia, India and Persia and introduced and established locally through cultivation in the United States). The former species has sulfur-yellow to white flowers and nearly spherical fruits, the latter pink to white flowers and somewhat larger ellipsoidal fruits.

Nelumbo lutea is one of our showiest and most interesting native plants. The greatly enlarged top-shaped receptacle with numerous separate carpels is a unique dispersal mechanism. The petals fall after 2–4 days leaving the

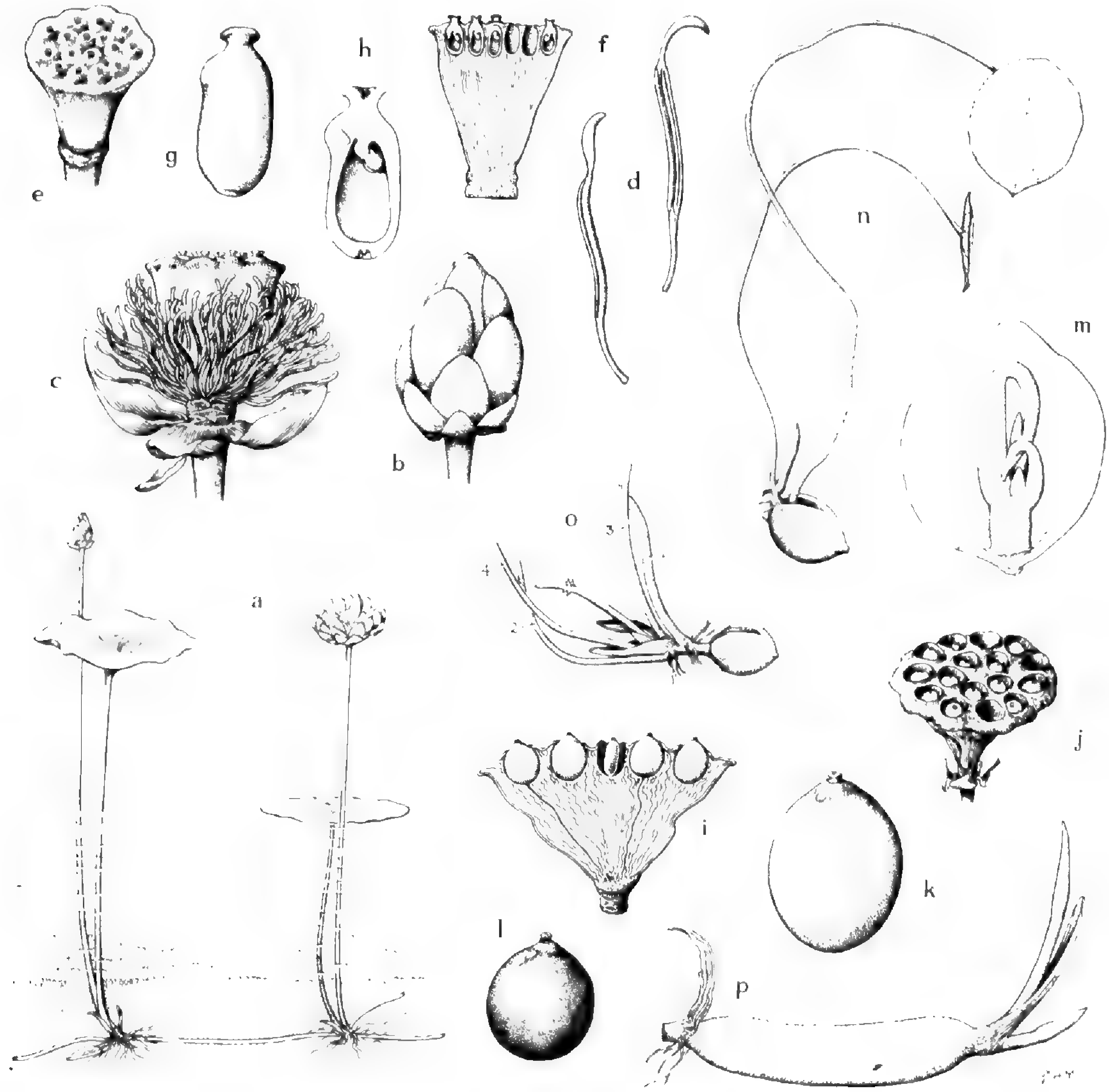

FIG. 1. **Nelumbo.** a–p, *N. lutea*: a, habit, × 1/20; b, flower-bud, × ¼; c, flower with petals removed, sepals persistent, × ½; d, stamens — note extrorse dehiscence, appendages, × 1; e, receptacle at anthesis, the stigmas of carpels protruding, × ½; f, receptacle and carpels, vertical section, × ½; g, carpel at anthesis, × 2; h, carpel, vertical section, with pendulous anatropous ovule, × 2; i, receptacle with nearly mature green fruit, vertical section, × ¼; j, dry receptacle with mature fruit, × ¼; k, green fruit at maximum size, × 1; l, mature fruit, the ovary wall sclerified, × 1; m, embryo from mature but green fruit, one cotyledon removed — note absence of hypocotyl and radicle, × 2; n, seedling with two leaves — note eccentric peltation, involute vernation, adventitious roots, × ½; o, seedling with four leaves (only bases of petioles numbered in sequence shown), the fruit coat removed — note distribution of roots, beginning of rhizome, × ½; p, tuber (a single swollen internode) with terminal bud and leaf-bud to right, × ¼; f, i, semi-diagrammatic.

outermost 4–5 tepals which persist into fruit. Within a few days the peduncle bends just below the receptacle, tilting it first to about 45 degrees and later to an almost horizontal position. As the fruits near maturity the receptacle is returned to an upright position, but later is bent downward through 180 degrees. The dry receptacle breaks off, falls into the water and floats with the cavities downward. The individual fruits shrink greatly (½–⅔ their volume) in ripening and the ovary wall becomes very hard and impermeable. Germination of fully ripened fruit may thus be greatly delayed. (*Nelumbo* seeds are the longest lived of any known; roughly 1000-year-old seeds of *N. nucifera* from peat beds in the Pulantien basin of southern Manchuria have germinated consistently.) The fruits strongly resemble those of the chinquapin, *Castanea pumila*, in appearance and the very edible cotyledons (the green plumule is bitter) taste much like those of the same plant.

The plant grows best in organic soil in water up to 6(8) feet deep and spreads as much as 50 feet radially each year by slender runners with internodes up to 5 feet long, the longest of any plant in our flora. It may thus under favorable conditions cover acres crowding out other aquatic vegetation and becoming a pest. The roots are entirely adventitious in 6 groups at the nodes, where lateral branching also occurs. In autumn one or two nodes at the growing tip develop into enlarged banana-like tubers 8–28 cm. long, the overwintering structures from which growth proceeds the following spring. The tubers of both species are highly edible: *N. lutea* was planted by the American Indians for both seeds and tubers and *N. nucifera* is widely cultivated in Asia for the same items.

Although a unique plant, *Nelumbo* appears to be related to the other Nymphaeaceae, differing from them primarily in the seed-dispersal mechanism, the more fully developed embryo (an enlarged and somewhat more specialized version of that of *Nymphaea* and *Nuphar*), the elimination of all submersed leaves, the more completely peltate leaves, and the tricolpate pollen. It is notable that in the leaves there are usually about 25 main veins, all but one of which branch dichotomously, this last being simple. Seedling leaves are apiculate at the end of the simple vein and are eccentrically peltate in the opposite direction, indications of the derived and specialized nature of the centrally peltate leaves which have proceeded to an evolutionary level beyond *Brasenia* (q.v.). Leaf vernation is involute as in the other genera. *Nelumbo* is placed by some in a separate family (Nelumbonaceae Dumort., 1829; Nelumbiaceae Lindl., 1836), or even in a separate order, but it seems better for the present to retain the genus in the Nymphaeaceae in the status accorded it by Caspary.

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CERATOPHYLLACEAE (HORNWORT FAMILY)

The family includes only a single small genus, *Ceratophyllum* L., of nearly cosmopolitan distribution, the plants growing entirely submerged in quiet, fresh waters. The group is easily recognized by the rather brittle and rough, whorled, dichotomously dissected leaves, the minute imperfect flowers, each solitary in the axil of one leaf of a whorl, the equally solitary branching, and the complete lack of roots.

Ceratophyllum was first placed near the Nymphaeaceae in 1837 by Asa Gray, largely on the basis of comparisons drawn with *Nelumbo* [itself highly specialized but mostly along other lines], the chief points being the simple, one-seeded ovaries, the pendulous orthotropous, exalbuminous seeds, the large and fleshy cotyledons, and the unusually developed plumule. Unfortunately, the most strongly emphasized evidence, the ovule, is not orthotropous in *Nelumbo, Brasenia* and *Cabomba,* but anatropous. However, Strasburger and others have maintained the same position for the Ceratophyllaceae, citing the convex receptacle, the numerous extrorse stamens, the superior ovary with the single pendulous parietal ovule, and the details of embryogeny (which seem to agree well with Nymphaeaceae). It may be noted that the stamens of *Ceratophyllum* seem to be spirally (not cyclicly) arranged, that the orthotropous ovule has but a single integument (instead of the two usual in Ranales) and that the pollen has lost all features which might be used as an indication of the relationships of the genus

1. **Ceratophyllum L.** Sp. Pl. 2: 922. 1753; Gen. Pl. ed. 5. 428. 1754.

Aquatic herbs with whorled dissected leaves; monoecious, with minute, sessile, axillary flowers lacking a perianth but with an 8–12-cleft involucre in place of a calyx. Plants entirely submerged, branching, a single branch produced at a node. Roots lacking (even in the embryo) but leafy branches sometimes modified as "rhizoids." Leaves 6–10 at a node, rather rigid, 1–4-dichotomously dissected, with two rows of minute teeth along the upper side of the ultimate segments, tipped by two bristles, usually with a purplish hair of tannin-filled cells between. Flowers usually solitary in the axil of one leaf of a whorl. Staminate flowers with an involucre of 8–12 segments, slightly united at the base, each tipped with a purplish hair, with a convex receptacle and 10–20 extrorse, 4-locular stamens with large, sessile, often 2-cuspidate anthers; pollen large, nearly smooth, thin-walled, acolpate. Pistillate flower of a solitary pistil with involucre, the style filiform, oblique, the stigma a lateral pocket, the ovary ovate, 1-locular, with a single orthotropous 1-integumented suspended ovule; embryo sac development normal (Polygonum type). Fruit an achene tipped by the indurated persistent style [or its base] and often with additional basal or marginal spines. Seeds filling the fruit, nucellar tissue forming the only seed coat, with a large embryo with 2 ovate cotyledons, a well-developed plumule of several nodes with simple or forked leaves, and lacking a hypocotyl and radicle; endosperm scant or lacking. TYPE SPECIES: *C. demersum* L. (The name from Greek, *keras*, a horn, and *phyllon*, leaf, in reference to the stiff, divided leaves.) — HORNWORT, COONTAIL.

Six or more species, three of which occur in our area: *C. demersum* L., of very wide distribution, from Canada to Argentina and also in Europe, Asia, Africa, and perhaps Australia; *C. echinatum* Gray, distributed from Quebec to Michigan and south to Florida and eastern Mexico; and *C. floridanum* Fassett, known only from the Florida Keys.

The genus is almost completely adapted to an aquatic life. The plants lack cuticle, stomata and roots (even in the embryo, the anchoring function being taken over by leafy branches which grow into the mud); both xylem and phloem are reduced, mechanical cells are lacking, and about a third of the plant is occupied by air spaces. The greatly reduced flowers are borne abundantly and pollination is entirely subaquatic. Fruits develop only if water temperatures are maintained above 80°F (cf. Guppy), a phenomenon which may account for the scarcity of fruiting collections in herbaria. The plants may vegetate indefinitely, however, even under ice in winter; vegetative reproduction occurs by fragmentation.

Species of *Ceratophyllum* are highly variable and are difficult taxonomically. The principal taxonomic characters used are those of fruits and leaves, the fruits being unarmed, or with either long or short spines at the base and the apex or along the margin, the leaves varying in the amount of forking, width of segments, degree of tapering at base, coarseness and distribution of the teeth. The female flowers are so reduced as to be useless in classification, but stamens need further examination, particularly in connection with their terminal cusps and hairs. Chromosome numbers reported from European plants include 24 in *C. demersum* and 40 and 72 in *C. submersum* L. These, combined with the wide range of morphological characteristics, suggest that much more needs to be done toward an understanding of the biosystematics of the genus.

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STUDIES IN ARTOCARPUS AND ALLIED GENERA, III. A REVISION OF ARTOCARPUS SUBGENUS ARTOCARPUS

FRANCES M. JARRETT

Artocarpus J. R. & G. Forster, Char. Gen. 101. *t. 51, 51a.* 1776, nomen conservandum; Linn. f. Suppl. Pl. 61, 411. 1781; Lamarck, Encycl. Méth. **3**: 207. 1789; Willd. Sp. Pl. ed. 4. **4**: 188. 1805; Persoon, Syn. Pl. **2**: 531. 1807; Blume, Bijdr. 479. 1825; Roxb. Fl. Ind. **3**: 521. 1832; Blanco, Fl. Filip. 666. 1837, "*Arctocarpus*"; Trécul, Ann. Sci. Nat. Bot. III. **8**: 109. 1847; Miq. Fl. Ind. Bat. **1(2)**: 284. 1859, Suppl. 417. 1861, Ann. Mus. Lugd.-Bat. **3**: 211. 1867; King in Hook. f. Fl. Brit. Ind. **5**: 539. 1888; King, Ann. Bot. Gard. Calcutta **2**: 1. 1889; Becc. For. Borneo, 625. 1902; Renner, Bot. Jahrb. **39**: 363. 1907; Elmer, Leafl. Philip. Bot. **2**: 609. 1909; Gagnep. Bull. Soc. Bot. Fr. **73**: 86. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 731. 1928; Corner, Wayside Trees of Malaya, 649. 1940; Jarrett, Jour. Arnold Arb. **40**: 8, 11. *fig. 1, f–k, fig. 3, d–f.* 1959. TYPE SPECIES: *Artocarpus communis* J. R. & G. Forster.

Saccus or *Soccus* Rumph. Herb. Amb. **1**: 104–115. *t. 30–34.* 1741.

Sitodium [Banks & Solander ex] Parkinson, Jour. Voy. Endeavour, 45. 1773, nomen subnudum.

Rademachia Thunb. Vet. Akad. Handl. Stockholm **37**: 251. 1776; Houttuyn, Nat. Hist. II. Pl. **11**: 446. 1779. TYPE SPECIES: *Rademachia incisa* Thunb. (= *Artocarpus communis* J. R. & G. Forster).

Sitodium [Banks & Solander ex] Thunb. Philos. Trans. Roy. Soc. London **69**: 465. 1779, nomen illegitimum.

Sitodium Banks [& Solander] ex Gaertn. Fruct. **1**: 344. *t. 71, 72.* 1788, nomen illegitimum.

Polyphema Lour. Fl. Cochinch. 546. 1790. TYPE SPECIES: *Polyphema jaca* Lour. (= *Artocarpus heterophyllus* Lamarck).

Saccus O. Kuntze, Rev. Gen. 633. 1891, nomen illegitimum.

Small to large trees. *Leaves* spirally arranged (subg. *Artocarpus*) or alternate and distichous (subg. *Pseudojaca*), simple and entire to pinnatifid, or pinnate (*A. anisophyllus*), penninerved (basally trinerved in *A. altissimus*), thinly to thickly coriaceous, glabrous to pubescent or hispid; epidermal gland-hairs superficial to deeply immersed, heads globose to flattened and peltate, 1–16-celled; spongy mesophyll long-armed and usually very loose (subg. *Artocarpus*), with ellipsoid to globose resin-cells (except in *A. integer* and *A. heterophyllus*), or compact, lacking resin-cells (subg. *Pseudojaca*); juvenile leaves entire to pinnatifid, or pinnate (*A. tamaran*), or with the lamina reduced to a sinuous wing along the midrib. *Stipules* paired, large, intrapetiolar, amplexicaul, scars annulate (subg. *Artocarpus*) or small, non-amplexicaul, scars lateral or intrapetiolar (subg. *Pseudojaca*).

Inflorescences unisexual, capitate, head cylindric to clavate, obovoid, ellipsoid or globose, lobed (in syncarp) or not, pedunculate (rarely subsessile), solitary or paired in leaf-axils, rarely borne on short shoots on older wood (subg. *Pseudojaca*) or rami- or cauliflorous (*A. integer, A. heterophyllus*); numerous flowers compactly covering surface, the perianths enclosing a single ovary or stamen, mixed with abundant stalked, peltate, varying to clavate or spathulate interfloral bracts, these often caducous from syncarp, or in some species entirely lacking, or in one (*A. styracifolius*) enlarging to form flexuous processes on syncarp; involucre absent (top of peduncle forming an annulus in *A. heterophyllus*). *At anthesis*: *male head* with perianths tubular and bilobed or perforate above, to 2–4-partite, stamens short- to long-exserted, anther-cells globose to oblong; *female head* with perianths tubular, thin-walled below and enclosing ovary, thick-walled above with a narrow lumen containing the style, partially or completely (in some species of subg. *Pseudojaca*) fused with one another to form syncarp; partial fusion occurring only between distal thick-walled region of perianths to form an external wall, with proximal thin-walled region remaining free; perianths completely fused above to form a smooth or areolate surface with the styles exserted through perforations, or the apices free, forming cylindric, conical, umbonate or truncate, rigid or flexuous processes on surface, all with styles exserted from their tips, or some processes sterile (in some species of subg. *Artocarpus*), solid, elongate and projecting beyond the rest (some of these species also with sterile, solid, elongate flowers in the male head); ovary unilocular, the style apical to lateral, simple or bifid (branches sometimes very unequal), the ovule subapical to lateral. *Mature syncarp* formed by the enlargement of the entire female head, with one to many flowers forming fruit; proximal portions of fruiting perianths, if free, either becoming fleshy or not, the remaining perianths elongated and ribbon-like; mature ovary thin-walled to fleshy or horny, or developing an indurated endocarp freed by decay of rest of wall, the style apical to sub-basal, the seed large, attached subapically to sub-basally, testa membranous to pergamaceous, endosperm none, the embryo straight, orientation longitudinal or oblique, cotyledons equal or not, appressed faces at an angle of 0–90° to median plane of ovary, radicle and plumule small to minute, apical or lateral; germination hypogeal.

DISTRIBUTION: Ceylon, India, Pakistan, Burma, Siam, Indochina, southern China, Malaysia, Solomon Islands; two species (*A. communis*, *A. heterophyllus*) cultivated throughout the tropics.

HISTORY OF THE GENUS AND NOMENCLATURE OF BREADFRUIT, CHEMPEDAK AND JACK

The genus *Artocarpus* is represented by indigenous species in an area extending from India and Ceylon to southern China, and through Malaysia to the Solomon Islands, while two species — the Breadfruit and the Jack — are now cultivated throughout the tropics. That it was, nevertheless, unknown to Linnaeus is somewhat surprising in view of the distinctiveness and economic importance of some of the species and the excellent descriptions which they had received from earlier authors.

The Jack was probably briefly mentioned by Theophrastus in about 300 B.C. as occurring in India and it figured more extensively in many later travellers' tales. The Breadfruit was first mentioned at the end of the sixteenth century by voyagers in the Pacific, where it was already widespread and of great importance to the Polynesians; it was recorded as far west as Java in 1642 and had become circumtropical in cultivation at least by the close of the eighteenth century.

Pre-Linnaean botanical descriptions. Among early botanical writers, Rheede described in 1682 both the Jack, which was already cultivated through most of tropical Asia and Malaysia, and a species of the Western Ghats, *Artocarpus hirsutus*, under the vernacular names *Tsjaka-maram* and *Ansjeli* (Hort. Ind. Malab. **3**: 17, 25. *t. 26–28, 32*). At about the same time Rumphius prepared very full descriptions of the Jack and the Chempedak (then, as now, almost restricted to and less commonly cultivated in Malaysia) as *Saccus arboreus major* and *S. a. minor*; of the seedless and seeded forms of the Breadfruit and an allied wild species of the Moluccas as *Soccus* [sic] *lanosus*, *S. granosus* and *S. silvestris*, respectively; and, finally, of another Malaysian species, *Artocarpus fretissii*, as *Metrosideros spuria* (Herb. Amb. **1**: 104–115. *t. 30–34.* 1741, **3**: 26. *t. 13.* 1743). These are the most important pre-Linnaean botanical references to members of the genus, but several species from the Philippines were listed under their vernacular names, with brief descriptions, by J. G. Kamel (in Ray, Hist. Pl. 3, App. 51, 52. 1704). No attempt was made to identify Rumphius' plants by Linnaeus in 1754 (Herb. Amb. [resp. O. Stickman]), except for *Metrosideros spuria*, which he wrongly equated with *Ochna jabotapita* L. Nor did Burman provide any further identifications in his indices to the "Herbarium Amboinense" published in 1755 and 1769.

In 1891 Kuntze held that the generic name *Saccus* had been validly published by Rumphius and, accordingly, he made many new combinations under it. These are illegitimate, however, and are omitted from the synonymy of the various species.

Post-Linnaean botanical descriptions. Once the genus had become known to post-Linnaean botanists, it was described, within about twenty years, under four different generic names, *Sitodium* (1773, 1779 and 1788), *Artocarpus* (1776), *Rademachia* (1776) and *Polyphema* (1790), but the name *Artocarpus* has been in continuous and undisputed use until doubt recently arose as to its priority, resulting in its conservation over *Sitodium* (1773). A review of the facts concerning these various publications follows, in which an attempt is made to determine their status and hence to establish whether the conservation of *Artocarpus* was necessary. This review is extended to cover the nomenclature of the Breadfruit, Chempedak and Jack — the only species in which any serious problems have arisen — since this will involve the addition of only two items to the material literature and will avoid later repetition, as well as provide a detailed picture of the early botanical history of the genus. Except for the earliest description of *Sitodium* and Houttuyn's publication of *Rademachia* the discussion will be largely based on the two papers published by Corner in 1939, although all the references have been carefully re-examined. For each name the Rumphian and post-Linnaean synonyms cited will be given and the factors taken into consideration in deciding its status will be clearly stated.

SITODIUM, ARTOCARPUS AND RADEMACHIA. The Breadfruit was the first species of the genus of which a description was published under a Linnaean binomial. This was done, under the name *Sitodium-altile* [sic], by Stanfield Parkinson in 1773 in his edition of "A Journal of a Voyage to the South Seas, in His Majesty's Ship, The Endeavour," which was written by his brother Sydney, who accompanied Sir Joseph Banks and Dr. Solander as an artist on Cook's first voyage around the world (1768–1771) but died on the way home from Batavia. In this was included a series of notes on plants seen in Tahiti, to most of which were appended, without acknowledgement, hyphenated "Latin names" corresponding to the binomials in Solander's manuscript "Primitiae Florae Insularum Oceani Pacifici, . . ." now in the British Museum (Natural History), London. This journal had been generally overlooked until Fosberg drew attention to it in 1939 (Am. Jour. Bot. **26**: 229–231) and stated that Parkinson's description would necessitate the conservation of *Artocarpus* over *Sitodium*, which was finally achieved on these grounds in 1955 (Taxon **4**: 162. 1955). In anticipation of this action the new combination *Artocarpus altilis* (Parkinson) Fosberg was published by him in 1941 (Jour. Wash. Acad. Sci. **31**: 95) as the correct name for the Breadfruit.

However, Sydney Parkinson's notes are totally unscientific and mostly very brief; he was apparently quite unaware of the significance of his action in using those of the binomials that were new, as was his brother in publishing them, and few of them have any claim at all to valid publication. The account of the Breadfruit happens to be rather longer than the others but is merely a general description of which the "botanical" part is given below.

> E ooroo *Sitodium-altile.*
>
> . . . This tree grows to between thirty and forty feet high, has large palmated leaves, of a deep grass-green on the upper-side, but paler on the under; and bears male and female flowers, which come out single at the bottom or joint of each leaf. The male flower fades and drops off; the female, or cluster of females,

> swell and yield the fruit, which often weighs three or four pounds, and is as big as a person's head when full grown. It is of a green colour; the rind is divided into a number of polygonal sections; the general shape a little longer than round, and white on the inside, with a pretty large core. The fruit, as well as the whole plant, is full of a white clammy juice, which issues plentifully from any part that is cut: . . .

In order for this description to be validly published it would have to be adequate as a "generico-specific" description, as was pointed out by Dandy and Exell *in litt.*, cited by Merrill (The Botany of Cook's Voyages. Chron. Bot. **14**: 330. 1954) in the course of a detailed discussion of Parkinson's journal. Merrill's view that the description is not valid seems fully justified, the more so if the circumstances of publication are taken into consideration. This question must, however, always remain a matter of opinion and, since it has now been settled, for any who feel that they must recognize the validity of Parkinson's description, by conservation, its chief importance is in determining the specific epithet to be applied to the Breadfruit. The source of the generic name *Sitodium* is nowhere directly indicated in the literature of the eighteenth century, but it is now generally recognized that the authors should be cited as [Banks & Solander ex] (or [Solander ex]) Parkinson, etc.

A botanical description of the Breadfruit was published in 1776 under the name *Artocarpus communis*, with *Soccus* [*lanosus* and *granosus*] in synonymy, by J. R. & G. Forster, who were the botanists on Cook's second voyage around the world (1772–1775) (the generic name being derived from the Greek *artos*, bread, and *karpos*, fruit). In the same year another description of the Breadfruit, together with one of the Chempedak, was published under the generic name *Rademachia*, with the specific epithets *incisa* (synonyms: *Soccus lanosus*, *S. granosus* and *S. silvestris*) and *integra* (synonyms: *Saccus arboreus major* and *S. a. minor*), respectively, by C. P. Thunberg in a paper dated Batavia, d.15 Junii 1775. The name was given in honour of Herr Radermacher, then "Baillou" of Batavia, from whom Thunberg received much assistance, especially later, when he returned from Japan. It has not been possible to determine which of these two names was published first. The preface to the Forsters' "Characteres Generum Plantarum" was dated November 1775, and there is no reason to doubt that the title-page is correct in giving the date as 1776, but no more precise evidence is available. Thunberg's description was published in the July–September issue of the Kongl. Vetenskaps Acadamiens Handlingar for 1776, but Merrill (l.c., 359) stated that Hultén had been unable to find any record of the date of publication in Stockholm. Although it seems likely that *Artocarpus* was actually published before *Rademachia*, unless this can be established, the first person to choose between the two names must be followed. It has always been assumed that this choice was made by Linnaeus *filius* in 1781 in his "Supplementum Plantarum" when he used the name *Artocarpus*, combining both generic descriptions, though without giving *Rademachia* as a synonym. He recognized two species, *A. incisus* and *A. integrifolia* [sic], basing his descriptions on those of Thunberg and citing his names, and the same Rumphian names, but not *A. communis*, in synonymy.

It has, however, been overlooked that in 1779 Houttuyn had republished, in an account entitled "Beschryving van den Oostindischen Broodboom" which he included in his "Natuurlyke Historie," Thunberg's description of *Rademachia* (from a manuscript in Thunberg's hand sent to him by Radermacher) and had chosen his name to replace that of the Forsters on the grounds that the description was more complete, in that the formation of seeds was mentioned, whereas the description of *Artocarpus* was based solely on the seedless form of the Breadfruit. Houttuyn cited "*Artocarpus*" in synonymy under *Rademachia incisa*, in addition to the Rumphian names, and this would certainly have necessitated the conservation of *Artocarpus* over *Rademachia*, but for the fact that he did not know of the earlier publication of Thunberg's name in Sweden and hence was, giving his state of knowledge and intentions priority over the fortuitous circumstances, acting in contravention of present-day rules of nomenclature. Houttuyn's specific descriptions were based, in part at least, on material sent to him by Radermacher and, from his account of *Rademachia integra*, it seems that he had received the foliage of the Chempedak, but the fruit of the Jack. He also described very briefly a third species, *R. rotunda* (*Artocarpus rotunda* (Houtt.) Panzer, Pflanzensyst. **10**: 380. 1783; in a translated and amplified version of Houttuyn's paper), which it has not been possible to identify, although Merrill (Jour. Arnold Arb. **19**: 331. 1938) reduced *Artocarpus rigidus* to synonymy under Panzer's name. *Rademachia rotunda* will therefore be discussed further under that species. (Merrill did not comment on Houttuyn's reduction of *Artocarpus*.)

THE BREADFRUIT. In determining the correct name for the Breadfruit, if the specific epithet *altilis* is rejected as invalidly published and Houttuyn's action is ruled illegitimate, it remains to consider whether the choice made by Linnaeus *filius* in forming the name *Artocarpus incisus* for this plant is legitimate. The use of the name *Artocarpus communis* in its place was first formally recommended by Richter in 1894 (Bot. Centralbl. **60**: 169) on the grounds of its priority, and he was followed by various authors, including Merrill. The question was next fully discussed by Corner in 1939 (Gard. Bull. Singapore **10**: 280) who concluded that, as the Rules then stood, Linnaeus *filius* was perfectly free, in making the choice between two simultaneously published names, to take the generic name from one genus and the specific epithet from the other (although he had chosen *incisus* over *communis* only by implication, this is all that is now required). According to Article 57 of the International Code of Botanical Nomenclature, 1956, this is still true; there is nothing to indicate that the choice of generic name determines the specific epithet, where both are simultaneously published. Therefore, if the generic names and specific epithets are considered *independently*, the argument is valid and it is only after much deliberation that the decision has been made to reject it in the interests of stability of nomenclature and in order to follow the general principles of the Rules.

In the present example, Article 57 is in conflict with Principles III and IV, especially the latter: "Each taxonomic group can bear only one correct name [which for a species is a binary combination; see Art. 23], the earliest that is in accordance with the Rules, ..." *Artocarpus* became the correct generic name through the choice made by Linnaeus *filius*; thus the earliest *combination* based on the Breadfruit that is in accordance with the Rules is *Artocarpus communis* (1776). The name *Artocarpus incisus* (1781) is also legitimate at present (apparently it is not in conflict with Article 11), but, if any change were considered necessary in Article 57 in order to deal with this unusual problem, the Article would undoubtedly be brought into line with the Principles.

St. John (Pacific Sci. **2**: 109. 1948), in the only other detailed consideration of the nomenclature of the Breadfruit, concluded that the name *Artocarpus incisus* should be used, following both Article 57 (then no. 56) and established custom. However, there has been uncertainty as to the correct name of the Breadfruit for over fifty years. *Artocarpus communis* has been gaining gradually in acceptance over *A. incisus* and is now perhaps more widely used. With the addition of *Artocarpus altilis* as a third possibility, the situation has become more confused during the last two decades. It is evident that "established custom" cannot provide a stable solution to the problem. Moreover, in view of the long-standing uncertainty, any argument based on custom has lost much of its force in this particular instance, although the general desirability of following custom, where there is genuine doubt as to the consequences of the Rules, is not questioned. It is regretted that the name *Artocarpus incisus* was used in the first paper of this series.

THE CHEMPEDAK. Turning now to the second species described by Thunberg and Linnaeus *filius*, this was until recently erroneously identified as the Jack, to which the name *Artocarpus integrifolia* was universally applied from the beginning of the nineteenth century until it was partially replaced in the literature by the legitimate combination *A. integer.* This was made by Merrill in 1917 (as *A. integra*, Interpr. Rumph. Herb. Amb. 190), to replace Linnaeus *filius*' superfluous name, and was used by him in his consideration of Rumphian names in the same sense, i.e., as the correct name for *Saccus arboreus major.*

In 1939, however, Corner demonstrated conclusively, in a paper on the distinguishing characters and nomenclature of the Jack and the Chempedak (Gard. Bull. Singapore **10**: 56–81. *t. 1, 2*), that Thunberg's description had been based solely on the Chempedak. Although the latter had cited both *Saccus arboreus major* and *S. a. minor* as synonyms, and had given the Malay name of the tree as *Tjampeda*, but that of the fruit as *Nanca* (the Malay name for the Jack) and thus had, apparently, attributed the fruit of the Jack to the foliage of the Chempedak (as is also indicated by the material received by Houttuyn), only the vegetative parts were included in his description (with a note in Swedish that the roots, stems, branches and flowers were as in the preceding species [*Rademachia incisa*]). From the shape and colour of the leaf and the indumentum of rigid, patent hairs on the lower surface, twigs and peduncles, Corner showed that the description could refer only to the Chempedak (the Jack being glabrous), so that, in spite of the confusion in the Malayan and Rumphian names, the application of Thunberg's name is unambiguous. The distribution was given by Thunberg as Java, around Batavia, and (from Rumphius) Amboina and other places. Corner stated that Professor Svedelius had examined the type specimen at Uppsala and had found that it consisted of material of the Chempedak agreeing with Thunberg's description and including male inflorescences without the annulus at the base of the head that is found only in the Jack. Mixed with it was material of the Jack (see photographs in Corner, l.c.) which, from the note on the back of the sheet, "e Ceylona Thunberg," had probably been collected in Ceylon, where the Chempedak does not occur (presumably on Thunberg's visit there in 1777–78 on the way back from Batavia). Professor Svedelius thought that by an error the two plants of different origin had been put on the same sheet when Thunberg's collections were mounted some years later. This was confirmed by the discovery, in the course of the present revision, of a sheet in the Rijksherbarium, Leiden, bearing only the Chempedak and labelled by Thunberg "RADEMACHIA integra Thunb.," which was presumably part of the material sent to Houttuyn.

THE JACK. Thunberg showed that he had completely failed to perceive any difference between the Jack and the Chempedak in a paper published in 1779 with the title "Sitodium *incisum et macrocarpon, ususque fructuum qui exinde nascuntur, descripta a* Carolo Petro Thunberg, *M.D.*," in which he altered the generic name *Rademachia* (now spelling it more correctly as *Radermachia*) to *Sitodium* without giving either his reasons or any source for the name, although he had presumably obtained it from Banks, who communicated the paper to the Royal Society of London. The generic description (with *Soccus, Saccus, Radermachia,* and *Artocarpus* as synonyms) had only minor changes in wording and *Rademachia incisa* and *R. integra* were cited (in addition to the previous Rumphian names) under the two species, respectively, in synonymy. Therefore, although they are validly published here, the generic name *Sitodium* and the specific epithet *macrocarpon* must be rejected as nomenclaturally superfluous and thus illegitimate. Under *Sitodium macrocarpon*, Thunberg added to his previous Latin description of the Chempedak an account of the juvenile leaves and the fruit of the Jack (with a popular account of its uses in Ceylon, including recipes!). His paper renders illegitimate as a later homonyn Gaertner's independent publication in 1788 of the generic name *Sitodium*, attributed by him to Banks. This was based on another description of the fruit of the Jack under the name *Sitodium cauliflorum*, but, as stated by Corner, the latter must also be regarded as a superfluous name for the Chempedak, since the author's intention, as indicated by the indirect citation of *Artocarpus integrifolia* ("*Artocarpus foliis integris.* LINN. [ed. Murray,] *syst. veg. 838.*" [1784]) together with *Soccus arboreus* [sic] in synonymy, was to replace the earlier name, and this intention must be given priority over the description and plates. Gaertner was the only author previous to Corner (l.c.) to describe and draw the female perianths (called by him "baccae partiales") as free below, though fused above.

Lamarck, in 1789, was the first post-Linnaean author to make a distinction between the Jack and the Chempedak, when he described in his "Encyclopédie Méthodique" three new species based on the Jack: *Artocarpus heterophyllus* (as *A. heterophylla*), with *Saccus arboreus major* as a synonym; *A. jaca*, which he recognized as close to the former, with Rheede's *Tsjaka-maram* among its synonyms; and *A. philippensis*. Under *Artocarpus jaca* he recognized a variety "*β. Eadem ramulis petiolis foliisque subhirsutis*," giving *Saccus arboreus minor, Artocarpus integrifolia* and *Rademachia integra* as synonyms. Unfortunately Lamarck's "illegitimate" action, while making this perfectly correct distinction, in thus subordinating the variety based on the earlier names and descriptions applicable to the Chempedak (of which he had seen no specimens) under his new species must, following Corner, make *Artocarpus jaca* yet another superfluous name for the Chempedak. The latter therefore, since no previous effective choice had been made between the two other simultaneously published names (for both of which Lamarck had mentioned the characteristic annulus at the base of the inflorescence head), took *A. heterophyllus* as the more appropriate, so that this becomes the correct name for the Jack. Examination in 1955 of the type material of the three species in the herbaria of Lamarck and de Jussieu (the latter including that of Commerson) at the Muséum National d'Histoire Naturelle, Paris, has confirmed that it consists solely of specimens of the Jack and that the species were based on somewhat marked differences in the leaves. Lamarck also included *Artocarpus incisus* (synonyms: *Soccus lanosus, S. granosus, Rademachia incisa,* "*Artocarpus* Forst.") in his account of the genus and described a fourth new species, *A. hirsutus* (as *A. hirsuta*), which he based entirely on Rheede's *Ansjeli.*

In spite of this distinction between the Chempedak and the Jack, the transference of the name *Artocarpus integrifolia* (with *Rademachia integra*) from the former to the latter was effectively achieved by Willdenow in 1805 in his edition of the "Species Plantarum" (the next work in which the genus was treated at all fully). He then "corrected" Lamarck's nomenclature, changing the name of his second species based on the Jack from *Artocarpus jaca* to *A. integrifolia.* He cited *A. jaca*, together with *Rademachia integra* and *Tsjaca-maram*, in synonymy, and recognized two varieties, "β. ramulis petiolis, foliisque subtus hirsutis" with *Saccus arboreus minor* as the only synonym, and "γ. foliis indivisis trilobisve" with *Artocarpus heterophylla* and *Saccus arboreus major* as synonyms.

Polyphema. The description by Loureiro in 1790 of a new genus *Polyphema* to take the place of Linnaeus *filius' Artocarpus integrifolia* was due to a complete misunderstanding of the latter's generic description, which led Loureiro to suppose that it could only correspond to the first species, *Artocarpus incisus*, not seen by him, and to make several distinctions between it and the plants he was studying which he felt justified their segregation as a new genus. Under this he described the Jack as *Polyphema jaca,* with *Saccus arboreus major* as a synonym, and the Chempedak as *P. champeden*, with *Saccus arboreus minor* as a synonym, and thus correctly separated the elements confused in *A. integrifolia* (though only in the synonymy). His description of the Jack appears to be entirely original (the type is in the British Museum (Natural History), London), but that of the Chempedak is largely based on Rumphius' account and it is doubtful whether he had ever seen a specimen. The plant is not found in Indochina in spite of his statement that it occurs in high woods there, and he may have been referring to a native species which he also used in making the description; the precise derivation of his account will be discussed further under *Artocarpus integer.*

Willdenow did not mention Loureiro's generic name, but in 1807 Sprengel made it the basis of an illegitimate name for the Chempedak, *Artocarpus polyphema*, under which this plant has been most widely known in the literature, although it was corrected to *A. champeden* in 1812 (by Stokes, Bot. Mat. Med. **4**: 330; but universally ascribed to Sprengel, Syst. Veg. **3**: 804. 1826).

HISTORY OF THE GENUS FROM 1807. A few other species were described in *Artocarpus*, but the first major contribution to the taxonomy of the genus was made by Trécul in 1847 in his paper on the Moraceae: Artocarpoideae and Conocephaloideae entitled "Mémoire sur la Famille des Artocarpées." He based his account mainly on the material then in the Muséum National d'Histoire Naturelle in Paris, and distinguished fifteen species, of which seven were new. In view of his limited material his work was very accurate and it is the only complete revision of the genus previously undertaken. He divided *Artocarpus* into two subgenera, *Jaca* (= subg. *Artocarpus*) ["*Perigonium* masculum diphyllum, foliolis plus minusve inter se cohaerentibus; *stipulae* duae oppositae, amplexicaules, altera marginibus alteram tegens; *folia* alterna"] and *Pseudojaca* ["*Perigonium* masculum tetra- rarissime triphyllum; *stipulae* 2 minimae, axillares vel sublaterales, non oppositae, nec amplexicaules; *folia* disticha"]. These subdivisions have been found to be well marked, although, as was pointed out by King (1889), the distinction based on the male perianth is not valid, since this is more variable within subgenus *Pseudojaca* than Trécul realized, even within the species studied by him. His use of the term opposite with respect to the stipules was a source of confusion to King, as shown by Renner (1907), since he restricted it to stipules having their midlines 180° apart.

In the years 1861 and 1867, Miquel published altogether 16 new species and combinations in *Artocarpus* (in addition to four that had appeared earlier), but many of the descriptions were based on poor material and it has only been possible to identify them by studying the types. More than one species was described under several different names and, although Miquel recognized Trécul's subgenera, he included in subg. *Artocarpus* a species of *Sloetia* (Moroideae) and in subg. *Pseudojaca* one species (*A. limpato*) later transferred to *Prainea* and three which have been reduced to *Parartocarpus venenosus* (Zoll. et Mor.) Becc. (itself originally described as a species of *Artocarpus* in 1845).

The next important paper on the genus was King's monograph of 1889, "The species of *Artocarpus* indigenous to British India," in which he described seventeen species (seven of them and two varieties as new) known to him as native in India, Ceylon, Burma and Malaya. They were usually correctly defined (except for the two varieties), but, owing to his inability to study the types of Miquel and other authors, several of King's names must be replaced by earlier ones. He rejected Trécul's subgenera and arranged the species in two groups, in the first of which [the distal portions of] the "anthocarps"[1] were only partially united with each other so that the syncarp was spiny or tuberculate, while in the second they were completely united and the surface of the syncarp was smooth. Except for two new species included at the beginning of his first group (*Artocarpus forbesii* and *A. bracteata*) the subdivision does, however, correspond to Trécul's subgenera; this distinction between them happens to be fairly satisfactory in the species which King was considering, although, as was pointed out in the introductory paper, it does not hold for the entire genus. These two species should have been referred to *Parartocarpus* (in which the leaves are spirally arranged with non-amplexicaul stipules and the inflorescences are involucrate) and they represent the two other species which will be recognized in the genus. King did not mention *Parartocarpus*, and, although the description had been published in 1875, it may not have been available to him. The syncarps of these two species closely resemble those of some species of *Artocarpus* and King mistook the solid spinous process on the surface (the nature of which was discussed in the introductory paper) for tubular, perforate perianth apices. He did not consider leaf arrangement (explicitly at least), although his two groups differed in this respect also, and he rejected Trécul's perianth and stipular characters. The rejection of the stipular character was due to a double confusion: as already noted, King failed to comprehend Trécul's peculiar use of the term opposite; it has further been found in this study that he assigned a sterile specimen of *Artocarpus rigidus* to his *A. bracteata*, which caused him to describe the shoot as annulate, as it was in all the other species of his first group except *A. forbesii*, so that the stipular character would not give a "natural" classification, whereas the syncarp character apparently would. He considered that whether or not the stipules were amplexicaul depended merely on their size, and evidently attached no special significance to the occurrence of a basal involucre, which he observed only in *A. bracteata*.

In 1902 Beccari described nine new species and one new variety of *Artocarpus* from Borneo and New Guinea in an appendix to his "Nelle Foreste

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[1] I.e., the female perianths; this term can, strictly, be applied only to those perianths enclosing mature seeds. It has not been used, since it would merely complicate the specific descriptions.

di Borneo," in which he also considered the characters in which *Prainea* and *Parartocarpus* differ from *Artocarpus*, though without fully clarifying them (see under *Prainea* above and *Parartocarpus* to follow), and removed King's two wrongly assigned species to *Parartocarpus*.

Finally, Renner, in a paper entitled "Beiträge zur Anatomie und Systematik der Artocarpeen und Conocephaleen, insbesondere der Gattung *Ficus*" published in 1907, discussed the systematy of the genera being studied, chiefly on the basis of their leaf anatomy, and, reinstating Trécul's subgenera, concluded that they, together with *Prainea*, should be treated as sections under *Artocarpus*. Renner's action in uniting *Prainea* with *Artocarpus* has been fully discussed in the introductory paper to this series and has been rejected, since the differences in leaf anatomy (and leaf arrangement) between the two subgenera (here maintained at this rank) could well have arisen by divergence from a common ancestor with the somewhat intermediate *Prainea*, whereas the unique syncarpium of *Artocarpus* indicates a close taxonomic relationship between the subgenera and contrasts markedly with the free female perianths of *Prainea*. Later authors have ignored both Renner's reduction of *Prainea* and Trécul's subgenera. Renner listed the anatomical characters for each of the species of *Artocarpus* available to him, citing the specimen(s) he had examined, but suggested no further taxonomic innovations, although his arrangement of the species follows a fairly "natural" order. The examination of leaf anatomy has been repeated for each of the species here recognized and details of the microscopic epidermal gland-hairs and of the hypodermis, if present, are given for each of the species in subg. *Artocarpus*, since their characters are of value in establishing the series.

Two purely taxonomic treatments should perhaps be mentioned, namely, Elmer's "Synopsis of *Artocarpus*" treating 16 species of the Philippines (1909), and Gagnepain's account of the genus in the "Flore Générale de l'Indochine" (1928) for which he described eight new species in 1926, several of which must be reduced.

There should also be added here a note on a paper which has only recently come to my notice, on the structure of the jackfruit, by D. D. Sundararaj and K. Ramanujam, "Studies on the floral morphology of Jack, *Artocarpus heterophyllus* Lamk. (Syn.: *A. integrifolius*, L.f.)," S. Indian Hort. **1**: 56–61. *figs. 1–12*. 1953. These authors have described and illustrated the structure of the jackfruit at anthesis and maturity, and have emphasized, as was done in the introductory paper to this series, that the perianths are free below but fused above, in this species leaving the apices free, so that they have recognized three regions in each perianth. They have also pointed out again that, as had been made clear by Corner (Gard. Bull. Singapore 10: 56–81. 1939), the true fruits are enclosed by the free fleshy lower portions of the fruiting perianths. They describe the syncarp as a false fruit. However, they do not seem to have examined any very young female heads, in which the perianths would presumably be entirely free (as in *A. rigidus*, described in the introductory paper). They also state positively, but without bringing forward any evidence, that the annulus represents the involucral bract of the inflorescence, whereas Corner had noted (l.c., 62, 76) that he had been unable to discover its morphological nature, although it was probably comparable to the bracts in *Parartocarpus*. This may well be the origin of the irregular row of bracts and the slight swelling of the top of the peduncle seen in some other species of *Artocarpus* but it is possible that the annulus represents a secondary enlargement of the latter.

GENDER OF ARTOCARPUS. Although the International Code of Botanical Nomenclature now states that *Artocarpus* must be treated as a masculine noun, since the Greek masculine noun *karpos* has been further altered to the masculine form in Latinization (Recommendation 75A), the genus has been considered as feminine by almost all previous authors except Linnaeus *filius* (1781), Renner (1907) and Corner (1939, 1940). The original specific epithet in *Artocarpus* — *communis* — was ambiguous in this respect, while Linnaeus *filius* treated his first species as masculine — *A. incisus* — but the second as feminine — *A. integrifolia*. Renner pointed out that this error probably arose in type-setting, since both the other species on the same page had feminine terminations, and he supposed that it had been perpetuated through the custom in Latin of treating all names of trees as feminine. In this revision only the original form in which a given name was published is indicated, if different from that now accepted (in addition to significant typographical errors).

CLASSIFICATION OF THE GENUS

The two subgenera of *Artocarpus*, established by Trécul in 1847, are here recognized on grounds which have already been fully discussed in the introductory paper in which they were also keyed out with the genera (p. 26, above). The characters distinguishing them, of which the vegetative are of more practical importance than the reproductive, may be summarized as follows: in subg. *Artocarpus* the leaves are spirally arranged with large, amplexicaul stipules leaving annulate scars and they have a long-armed, usually very loose spongy mesophyll with ellipsoid to globose resin-cells, and epidermal gland-hairs with a 4–16-celled head, whereas in subg. *Pseudojaca* the leaves are alternate and distichous with small non-amplexicaul stipules leaving lateral or partially intrapetiolar scars, the mesophyll is compact, and the heads of the gland-hairs are usually unicellular. The syncarp in subg. *Pseudojaca* is globose or somewhat lobed with a fleshy, smooth or papillate surface, while in subg. *Artocarpus* both shape and surface are variable, though the syncarp usually bears distinct indurated or fleshy processes, or, where it is smooth or nearly so, it is ellipsoid to cylindric.

While the species in this genus are, on the whole, distinct and readily separable, this is not always the case with the subdivisions between the level of the subgenus and the species. There is also a marked contrast in the range of variation exhibited within the two subgenera and this is reflected in the classification here suggested for the species within them. In subgenus *Artocarpus* there is a wide range of variation — within the fairly strict limits imposed by the structure — in the syncarps (especially in the shape, length, consistency and indumentum of the processes) and the species can be recognized on the differences in these alone, although they are supported by more or less marked differences in the male inflorescences (in shape, size and surface, and in peduncle indumentum and length) and in the shoot (in indumentum and leaf size and shape). The pattern of variation warrants the creation of two sections with two and four series, respectively, the basis for which will be discussed below.

In subgenus *Pseudojaca*, on the other hand, while two sections will also be created, one is for an anomalous species, *Artocarpus altissimus*, and the other presents little variation between the species. The inflorescences are so reduced that the entire male and female heads provide the unit of variation in establishing the species. The heads of different species vary in size and shape, in the length and indumentum of the peduncle, and, in the female head, in the appearance of the surface at anthesis and maturity, its indumentum, the degree of exsertion of the styles, and whether or not the interfloral bracts persist or lobing develops. There are also vegetative differences between the species — in shape, size, prominence of venation, petiole length and indumentum of the leaf — but, while most species can, with practice, be identified when sterile, the differences are often not readily definable. As might be expected where there are limited possibilities for variation, parallel evolution has occurred, especially in the vegetative characters, and the species may only be definable by using a combination of characters. The only discontinuous "morphological" variation occurring in this section is in the shape of the interfloral bracts, which is used to separate three species as one series of limited geographical distribution, leaving the remainder as a large group which is probably best treated as a single series. Although subsidiary groups can be recognized within the latter, the definitions necessary for these are somewhat complex, and there are also several species showing reticulate relationships, and a few of which the alliances are doubtful.

In the keys to both subgenera proportions have been used — length to breadth of inflorescence head in subg. *Artocarpus*, and length of head to length of peduncle in subg. *Pseudojaca*. These recognize and utilize characteristic differences between species groups in the shape of the head or in the relative length of head and peduncle. These differences hold, with a few exceptions, for both male and female inflorescences, thus making possible the construction of a "natural" key which can be used (at this dichotomy at least) at any stage in the development of the inflorescence, since the relationships remain fairly constant throughout its growth. The use of these ratios also allows for the considerable variation in size, rather than shape, which may occur in the inflorescences, depending largely on the part of the plant on which they are borne. There are some species, especially in subg. *Pseudojaca*, where these relationships do not always hold, but they are relatively few in number and have been allowed for as far as possible.

ECOLOGICAL AND BIOLOGICAL NOTES

The species of *Artocarpus,* except for a few belonging to subg. *Pseudojaca,* are large trees of the high forest and are mainly restricted to evergreen forest in the tropical everwet zone or in areas with a relatively mild monsoon climate. They are usually found below an altitude of 3000 ft., though several species may occur up to 5000 ft. One species, *Artocarpus communis,* is abundant in swamp forest in New Guinea, and others are recorded from swampy areas or from the banks of streams. The majority of the species in everwet forest are themselves evergreen, although they may, especially in subg. *Pseudojaca,* show marked flushes of new growth, but *Artocarpus dadah* is deciduous. Of the species restricted to regions with monsoon climate some, including *A. lakoocha,* are deciduous, but others, such as *A. gomezianus,* are evergreen. The latter (as ssp. *gomezianus*) is the only entity within the genus to show a marked climatic discontinuity — between Lower Burma and Siam, and central and eastern Java. *Artocarpus lakoocha,* which is the most wide-ranging species on the continent of Asia, is also the most tolerant of cool temperatures and low rainfall, although it is damaged by frost.

In considering biological aspects of the variation in growth habit and in the syncarp in this genus several more or less parallel trends may be distinguished. The first tendency is shown in the arrangement of the leaves, which in subg. *Artocarpus* are borne spirally on usually ascending twigs, whereas the ultimate shoots in subg. *Pseudojaca,* with their alternate and distichous leaves form more or less applanate sprays of foliage. Associated with the latter habit is a general reduction in massiveness, but within each subgenus there are also tendencies to reduction in the size of parts, culminating in subg. *Artocarpus* in *A. kemando,* and in subg. *Pseudojaca* in *A. styracifolius.*

There is in subgenus *Artocarpus* considerable variation in the form of the adult leaves, which are pinnate in *A. anisophyllus* (though unusual in not disarticulating when they fall) and pinnatifid in *A. communis* and its allies, all these species having very stout twigs. In the saplings of several species the leaves are very large and highly dissected (twice or thrice pinnatifid and to six feet in length in *A. elasticus*). Members of this subgenus were mentioned by Corner in his exposition of the "Durian Theory" (Ann. Bot. II. **13**: 367–414. 1949) as showing in their sapling and adult stages the transition from a "pachycaul" habit, with a sparingly branched trunk and large, compound leaves, to the modern "leptocaul" tree, with slender twigs and horizontal sprays of simple leaves. They were also noted as exhibiting the principle of "axial conformity" or correspondence between the massiveness of the axis and the size and complexity of its appendages, which may be extended through *A. anisophyllus* and *A. communis* to the most slenderly constructed species of both subgenera. Except in two cauliflorous species of subg. *Artocarpus* (*A. integer* and *A. heterophyllus*) there is a general correspondence throughout the genus between the size of the twigs and leaves and that of the syncarps, which are borne with the male inflorescences among the foliage (although before they mature the subtending leaves may have fallen). A different trend was pointed out by Corner in *A. heterophyllus*, in which the twigs were slender with simple leaves, tending to form an applanate spray (cf. subg. *Pseudojaca*), while the enormous syncarp was borne on the trunk or large branches, a necessary development if the massive fruit was to be retained.

The syncarps within the genus also vary between two types of organization, namely, those in which each seed is surrounded by a pulpy perianth and the rest of the syncarp is more or less fibrous or indurated, and those in which the entire syncarp is soft and fleshy but the fruiting perianths are not markedly hypertrophied. The first type is best developed in the armoured syncarps of the first section of subgenus *Artocarpus* (which includes *A. rigidus*), and the second is found in the small, nearly smooth syncarps of *A. kemando* and its allies, and of subg. *Pseudojaca*. The remaining species in subg. *Artocarpus* have small to fairly large, moderately fleshy syncarps, usually with well developed firm, or fleshy and often flexuous processes on the surface. They lack (so far as evidence is available) conspicuously enlarged fruiting perianths, except in the very large syncarps of the two cauliflorous species. However, the perianths in *A. elasticus* and *A. sericicarpus* are apparently somewhat pulpy. In the species with an armoured syncarp and also in a number of species in subg. *Pseudojaca* the seeds are enclosed in more or less well differentiated horny endocarps which may become free by the decay of the rest of the pericarp, while in other species of subg. *Artocarpus* the entire pericarp is indurated. This protection is lacking in the cauliflorous species, but in *A. heterophyllus* there is a horny outer testa.

In spite of the varying nature of the attractive element in the syncarp of *Artocarpus* the mode of dispersal is much the same throughout the genus, which is primarily adapted for distribution by arboreal mammals, although the smaller fruits of subg. *Pseudojaca*, many of which are yellow, red or purple, may also be eaten by birds. (Troup (Silvicult. Ind. Trees 3: 884. 1921) records that the fruit of *A. lakoocha* is eaten by parrots and minahs, and also by monkeys.) The larger fruits in the genus, according to Ridley (The Dispersal of Plants. 1930), are bitten to pieces on the tree by monkeys, squirrels and civet-cats. He describes how the orange syncarps of *Artocarpus rigidus* (for which the English name is the Monkey Jack) are eaten in Malaya by a macaque monkey, which readily tears apart the spiny covering to reach the edible sweet orange pulp surrounding the seeds, and how as much fruit may be thrown away as is eaten. It is presumably by means of this wastage of portions of the fruit, which are let fall by the animals eating them, that the seeds are more widely dispersed, but they will, in any case, germinate in syncarps which fall to the ground from the tree. Ridley suggests that the enormous syncarps borne on the trunk in *A. integer* (and presumably also in *A. heterophyllus*) are eaten by forest ungulates, such as wild cattle, pigs and elephants, which can easily reach them. It should be noted that the seeds in this genus have no period of dormancy, but germinate immediately, and that they are unable to withstand dessication.

The mode of pollination in *Artocarpus* is variable. Corner (Wayside Trees, 650. 1940) recorded that male heads in *A. heterophyllus*, *A. integer* and *A. dadah* had a sweet scent of honey and burnt sugar, attracting small flies and beetles, which were the pollinating agents, but that *A. rigidus*, *A. communis* and *A. elasticus* were apparently wind-pollinated, since the male heads had no scent, but gave off clouds of pollen when they were moved. Van der Pijl (Ann. Bogor. **1**:79–82. 1953) studied pollination in *Artocarpus heterophyllus* and found that the anthers emerged over a period of some days and produced a sticky pollen. The flies bred on the decaying flower-heads which had fallen from the tree and thus established a brief symbiotic relationship with the plant during the period of anthesis.

Subgenus **Artocarpus**

Artocarpus subgenus *Jaca* Trécul, Ann. Sci. Nat. Bot. III. **8**: 110. 1847.
Artocarpus section *Jaca* Renner, Bot. Jahrb. **39**: 363. 1907.

Leaves spirally arranged, simple and entire to pinnatifid, or pinnate (*A. anisophyllus*); gland-hairs superficial to deeply sunken, heads 4–16-celled; spongy mesophyll long-armed and usually very loose, with ellipsoid to globose resin-cells (except in *A. integer* and *A. heterophyllus*). *Stipules* large, intra-petiolar, amplexicaul, scars annulate. *Inflorescences* with or without sterile, solid, elongate perianths. *Male head*, perianths tubular, shallowly (rarely deeply) 2(–3)-lobed above, or perforate. *Syncarp* globose or subglobose, covered by indurated processes, or ellipsoid to cylindric, varying subglobose, covered by firm or flexuous processes or less commonly areolate.

This subgenus is divided into two sections, *Duricarpus* and *Artocarpus*, based on the shape of the inflorescence heads and the presence or size of the interfloral bracts, on various characters of the syncarps, and, less certainly, on the mode of germination; but there are also three anomalous species which will be discussed below. The first section is a fairly homogeneous group of seven species, characterized primarily by the syncarp which has the surface armoured (whence its name) by the indurated free apices of the perianths. The free proximal region of those perianths that form seeds becomes fleshy, and encloses an ovary having a terminal style and developing a more or less clearly differentiated horny endocarp (becoming free by the decay of the rest of the pericarp in *A. anisophyllus* and *A. lanceifolius*). The embryo is symmetrical with a minute apical radicle and the appressed faces of the cotyledons at an angle of 30–90° to the median plane. The syncarp is globose or nearly so, and the male head varies from globose to cylindric or clavate, but is never more than three and one half (rarely four) times as long as broad. In both there are conspicuous peltate interfloral bracts, but these are mostly lost from the syncarp at or before anthesis, although a few frequently persist. The mode of germination is known in several species and the first pair of leaves subsequent to the cotyledons is consistently opposite, though later leaves are spirally arranged. For comparison with the series of the next section, it may be noted that a hypodermis is present in the leaves of only two species and that it consists of cells which are elongate in surface view, while the gland-hairs have a globose, 4–16-celled head. On the basis of the leaf characters, together with a difference in the shape of the male heads, two species are separated as series *Laevifolii*, leaving the rest in series *Asperifolii*.

The second section, *Artocarpus*, is larger and more heterogeneous, but the species are united and are distinguished from sect. *Duricarpus* by their more or less elongate inflorescences, the absence or small size of the interfloral bracts and the fleshy syncarp with the fruiting perianths becoming markedly fleshy in only two species, and the mature ovaries with a lateral or sub-basal style and no clearly differentiated endocarp (so far as the internal structure is known; exceptions presented by the anomalous species will be noted below). The contrast in the shape of the inflorescences is more marked in the male head which is usually at least four times as long as broad (though as little as one and one half times in *A. heterophyllus*). The syncarp is, however, usually ellipsoid to cylindric and only rarely subglobose, and the surface is either covered by firm, or more or less fleshy and often flexuous processes of varying shape or, less commonly, merely areolate. Interfloral bracts are frequently entirely lacking and, when present, they are scattered and inconspicuous, with small heads to 0.2 mm. across. The position of the style, though variable, is always at least one third of the way down the ventral face of the ovary at maturity, and the radicle is likewise ventral, so that the long axis of the embryo is oblique. The appressed faces of the cotyledons lie either in the median plane of the ovary, in which case the embryo is usually symmetrical, or they are also more or less oblique, with the uppermost cotyledon frequently reduced in size. Details of germination are known for only four species (*A. communis*, *A. integer*, *A. heterophyllus* and *A. elasticus*) but the first leaves appear to be always spirally arranged, except, perhaps, in *A. communis*, and to be preceded by scale leaves.

The classification of the species within section *Artocarpus* has presented some problems, in addition to those originating in the three species that have been separated as anomalous. It has been concluded that four series should be recognized and these are based, as in sect. *Duricarpus*, primarily on characters of the leaves, namely the shape of the gland-hairs, and the presence or absence of a hypodermis and of resin-cells. However, with one exception, each is further distinguished by characters that are unique to it. Series *Rugosi*, with seven species, is readily distinguished by the anatomical characters of the leaves, which have a continuous hypodermis of isodiametric cells and gland-hairs with a depressed-globose, 4-celled head, and by the variously ridged surface of the male head, from which it receives its name.

In the other species of the section the surface of the male inflorescence is smooth (except occasionally in *A. integer*) and an irregular hypodermis is found only in some specimens of *A. blancoi*. Series *Incisifolii*, with six species, is also well distinguished by the flattened, peltate, 8(–16)-celled heads of the gland-hairs, the frequently pinnatifid adult leaves, the inflated hairs usually covering the syncarp processes and male perianth lobes, and the relatively large size of the anthers, which range from 0.3–1.5 mm. in length (in no other species of the subgenus do they exceed 0.5 mm.). The remaining series, *Cauliflori* and *Angusticarpi*, each with two species, have entire adult leaves with gland-hairs having a depressed-globose, 6–10-celled head and consistently slender twigs, as compared with series *Incisifolii*. Series *Cauliflori* is distinguished from series *Angusticarpi* (and all other species of the subgenus) by the very large syncarps borne on the branches and trunk, with markedly hypertrophied fleshy fruiting perianths, the absence of resin-cells from the leaves, and possibly also by the germination of the seed, in the course of which the two cotyledons separate to allow the emergence of the plumule. Although the cauliflorous syncarp of these species gives them a very distinctive appearance, the characters just listed do not appear to be of sufficient importance to justify separating this series from the rest in the section. Series *Angusticarpi* thus remains as an unspecialized, though generally reduced, group which does not show clear alliances with any other series. The appearance of the leaves is quite distinct from that of series *Cauliflori*, as may be seen from the key to the subgenus. The value of the syncarp in classifying this section, although considerable in distinguishing the species, is limited at the level of the series, since there has been parallel evolution in the development of sterile perianths forming elongate, solid processes on the surface in one or more species of all series except *Cauliflori*; in series *Incisifolii* and *Angusticarpi* there may also be similar perianths in the male inflorescence. While the embryos may well provide characters distinguishing the series — those of series *Incisifolii* have relatively well developed cotyledonary stalks and radicles and the entire pericarp wall is indurated — they are very variable from species to species and evidence is unfortunately insufficient to determine their taxonomic value. Details are given for each species in the section when available.

The validity of these groups is supported by their geographical distribution. Section *Duricarpus* and series *Rugosi* are both centred in western Malaysia (Malaya, Sumatra, Borneo, Java) and the former occurs northward to Sikkim and Indochina, and is perhaps represented by indigenous species in the Philippines, while the latter has one species reaching southern Tenasserim and Palawan, and another extending through the Philippines, to Celebes and the Moluccas. Series *Incisifolii*, on the other hand, has species in the Philippines, the Moluccas and New Guinea (and perhaps Melanesia if *Artocarpus communis* is indigenous there). The most widespread groups are series *Cauliflori* and *Angusticarpi*. The first has one species (*A. integer*) extending from western New Guinea to Malaya and reaching peninsular Burma and Siam, although it is absent from the Philippines, and another (*A. heterophyllus*) perhaps indigenous in peninsular India. The second has one species in Malaya and Sumatra, and one with a distribution similar to that of *A. integer* but extending to the Nicobar Islands instead of north of the Malayan border.

On the basis, primarily, of the shape of the inflorescence heads, three species, which are otherwise anomalous in that each is, in various characters, intermediate between the sections, are placed at the end of sect. *Artocarpus.* Owing to this intermediacy and the fact that the structure of the mature syncarp is known in only one of them, they are not assigned to any of the series here established. Although a separate series should, perhaps, be created for each one of them, this is deferred, pending a more complete knowledge of the syncarps.

Of these species, *Artocarpus hirsutus*, from peninsular India, has an exceptionally long and slender male inflorescence indicating an affinity with sect. *Artocarpus*, but a subglobose to shortly cylindric syncarp covered by indurated, narrowly cylindric processes, which is somewhat similar to the syncarps of sect. *Duricarpus.* From the account given in Troup (Silvicult. Indian Trees **3**: 876. *fig. 323.* 1921) it is evident that the mode of germination is also the same as that found in sect. *Duricarpus.* The characters of the perianth and ovary do not, however, appear to be in agreement. The internal structure of the mature syncarp is not known, but the submature fruiting perianths are thin and the ovary is membranous with a subapical style. In view of these differences, together with the shape of the male head and the complete absence of bracts from the inflorescences (although this last character may have arisen by parallel evolution), this species is assigned to sect. *Artocarpus.* The induration of the syncarp processes is assumed to be of less taxonomic importance, although it provides, together with the hispid twigs and the appearance of the leaves (the gland-hairs have a depressed-globose, c. 6-celled head), a superficial resemblance to *A. rigidus.*

The two other species, *Artocarpus nobilis* and *A. sepicanus*, are remarkable in that, although one comes from Ceylon and the other from New Guinea, they share the characters of narrowly cylindric inflorescences (cf. sect. *Artocarpus*) and well developed, peltate interfloral bracts (cf. sect. *Duricarpus*) which are persistent and conspicuous on the syncarps. In other respects, however, the appearance of the syncarps is very different: in *A. nobilis* the surface is covered by short, umbonate, indurated processes, while in *A. sepicanus* the syncarp is fleshy, with a pubescent, apparently completely smooth surface (cf. species of subg. *Pseudojaca*) and the styles are exserted through perforations in this. The internal structure is known only in *A. nobilis*, in which the fruiting perianths are thin, the ovary is pergamentaceous with a subapical style, and the symmetrical embryo lies obliquely in the median plane of the ovary with the relatively large radicle ventral (cf. series *Incisifolii*), although in its germination, as in *A. hirsutus*, the first pair of leaves is opposite. *A. nobilis* also shows an alliance with series *Incisifolii* in the shape of the gland-hairs, which have a peltate, flattened, 8-celled head, but in *A. sepicanus* the gland-hairs, which are unusual in being deciduous at a very early stage, have a globose, 6–8-celled head.

These three species and, more especially, the curious resemblances between *A. nobilis* and *A. sepicanus* are a reminder of the long evolutionary history that can be assumed for this genus. It would appear that they are "relicts", and the persistence of a few such species that do not readily fit into a classification intended to reflect the affinities of the groups dominant today is scarcely surprising.

The series recognized within section *Artocarpus* are not, however, necessarily closely allied and it is not suggested that any one of them is directly ancestral to the others. Section *Duricarpus* may represent either an offshoot from sect. *Artocarpus* or an independent line of evolution within the genus. The anomalous species, as has already been implied, are probably the remnants of a wider variation exhibited by the genus in the past, and this may also be true of series *Cauliflori.*

KEY TO THE SPECIES OF ARTOCARPUS SUBGENUS ARTOCARPUS

1. Male head globose to clavate or short-cylindric, length/breadth = 1–3.5(–4), the surface largely covered by the peltate heads of numerous bracts; syncarp subglobose, length/breadth = 1–1.5, the surface covered by indurated processes; adult leaves pinnate or entire (rarely trilobed above the middle), the latter usually with fewer than 20 intercostals.[2]
  2. Syncarp processes narrowly cylindric, 5–8 × 1 mm., hispid, peduncle 4.5–6.5 cm. (male head narrowly cylindric, 7–16 × 0.5–0.7 cm.). Southern India. .... 25. *A. hirsutus.*
  2. Syncarp not as above. Sect. DURICARPUS.
    3. Twigs and leaves glabrous; male head ellipsoid to short-cylindric; syncarp processes glabrous or pubescent. Series LAEVIFOLII.
      4. Leaves pinnate; syncarp processes elongate, narrowly cylindric, 6–8 × 1–1.5 mm., glabrous. Malaya, Sumatra, Borneo. .... 1. *A. anisophyllus.*
      4. Leaves simple; syncarp processes short, broadly cylindric, truncate, c. 3.5 × 3 mm., and surface hence tesselate, or slightly tapering, obtuse, c. 1.5 × 1.5 mm., and somewhat separated, appressed-pubescent. Malaya, Sumatra, Borneo. .... 2. *A. lanceifolius.*
    3. Twigs and leaves (at least on the main veins beneath) hispid or hispid-pubescent; male head globose to obovoid or clavate; syncarp processes hispid. Series ASPERIFOLII.
      5. Syncarp processes broadly cylindric, 1.5–3.5 mm. long.
        6. Leaves smooth above, hispid-pubescent on the main veins only beneath; male peduncle 1–5 × 0.3 cm.; syncarp processes hispid from patent, usually slightly crisped hairs. Indochina, British North Borneo. .... 3. *A. melinoxylus.*
        6. Leaves scabrid above, hispid-pubescent throughout beneath; male peduncle 6–7.5 × c. 0.15 cm.; syncarp processes hispid from appressed hairs. Northeastern India, Burma, Andaman and Nicobar Is. .... 4. *A. chaplasha.*

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[2] The intercostal veins should be counted along the distal side of a lateral vein near the middle of the leaf.

5. Syncarp processes elongate, 5–13 mm. long, narrowly cylindric with clavate tips, or tapering.

    7. Leaves hispid-pubescent above; male head 4–9 × 2.5–3.5 cm., peduncle 2.5–7 cm.; syncarp processes narrowly cylindric with clavate tips, 8–13 × 1 mm. Borneo, Philippines. . . . . 5. *A. odoratissimus.*

    7. Leaves becoming smooth or scabrid above; male head to 3 × 2 cm., peduncle to 3 cm.; syncarp processes tapering, 5–9 × 1–1.5 mm.

        8. Twigs and peduncles patent-hispid; male peduncle 1.2–3 cm. Malaya. . . . . 6. *A. hispidus.*

        8. Twigs and peduncles appressed-hispid; male peduncle 0.2–0.6 cm. Indochina, southern Burma and Siam, Malaya, Sumatra, Borneo, Java. . . . . 7. *A. rigidus.*

1. Male head cylindric, varying ellipsoid or clavate, length/breadth = (1.5–) 4–20, bracts usually very few or entirely lacking; syncarp ellipsoid to cylindric, varying to subglobose, length/breadth = 1–4, the surface covered by more or less fleshy, firm or flexuous processes (indurated in *A. nobilis* and *A. hirsutus*), varying to areolate or smooth; adult leaves pinnatifid to entire, the latter frequently with more than 20 intercostals. Sect. ARTOCARPUS.

    9. Inflorescences narrowly cylindric, the surface entirely or partly covered by the peltate heads of numerous bracts, persistent in both sexes.

        10. Twigs 10–12 mm. thick; leaves frequently distinctly and regularly crenate between the lateral veins; male head 7–13 × c. 1.5 cm.; syncarp to 20 × 10 cm., processes short-cylindric, obtuse, 1 × 1–1.5 cm., indurated. Ceylon. . . . . 26. *A. nobilis.*

        10. Twigs 3–5 mm. thick; leaves not as above; male head to c. 3 × 0.5 cm.; syncarp to c. 4.5 × 1.5 cm., fleshy, surface (?) smooth, pubescent. New Guinea. . . . . 27. *A. sepicanus.*

    9. Inflorescences not as above.

        11. Twigs appressed-hispid; male head narrowly cylindric, 7–16 × 0.5–0.7 cm.; syncarp to c. 5 × 4 cm., processes narrowly cylindric, 5–8 × 1 mm., rigid, hispid. Southern India. 25. *A. hirsutus.*

        11. Male head not as above, *or* twigs subglabrous; syncarp not as above.

            12. Male head with the surface smooth; twigs glabrous, *or* villous from greyish, varying pale rufous hairs, *or* pilose or pungent from patent rufous hairs.

                13. Twigs (4–)6–22 mm. thick, villous, varying glabrous or with patent acicular hairs; adult leaves entire or pinnatifid; male head 1–30 × 0.7–3(–5.5) cm.; syncarp processes rough from the apices of deflexed, inflated hairs (except in *A. communis* and sometimes *A. horridus*), styles bifid or simple. Series INCISIFOLII.

                    14. Adult leaves entire or pinnatifid, with up to 5(–9) pairs lateral lobes; inflorescences with all the flowers fertile; anthers 0.3–0.8 mm. long.

                        15. Adult leaves becoming entire; syncarp less than 10 cm. across, the processes (and the perianth lobes in the male head) rough from the apices of deflexed, inflated hairs *and/or* the twigs with rigid, patent, acicular hairs.

            16. Twigs villous to glabrous; syncarp processes never glabrous.
                17. Male head 10–21 × 1.3–2 cm., anthers 0.7 mm. long; syncarp processes 8–15 × 1.5 mm.; inflorescences usually with scattered bracts. Mindoro, Luzon. .... 8. *A. blancoi.*
                17. Male head 1–17 × c. 0.7 cm., anthers 0.3–0.5 mm. long; syncarp processes 2.5–4 × 2.5–3 mm.; inflorescences without bracts. Philippines. ... 9. *A. treculianus.*
            16. Twigs with rigid, patent, acicular hairs, c. 2 mm. long; syncarp processes c. 3 × 1.5–3 mm., varying glabrous. Moluccas. .... 10. *A. horridus.*
        15. Adult leaves generally pinnatifid; syncarp more than 10 cm. across, the processes or facets (and the perianth lobes in the male head) with slender, patent hairs or glabrous (neither inflated nor acicular hairs present). .... 11. *A. communis.*
    14. Adult leaves deeply pinnatifid, with 7–20 pairs of lateral lobes; inflorescences often with solid, sterile, elongate flowers; anthers 1.2–1.5 mm. long.
        18. Lobes of leaf 12–20 pairs; male head with a few solid, cylindric perianths projecting to 0.5 mm. from the surface; syncarp processes all 3 × 2 mm., perforate, styles simple. Luzon. .... 12. *A. pinnatisectus.*
        18. Lobes of leaf 7–10 pairs; male head with numerous solid, cylindric perianths with clavate tips projecting to c. 2 mm. from the surface; syncarp processes of two lengths, 15 × 1 mm., solid, and 5 × 1 mm., perforate, styles bifid. Samar, Mindanao.[3] .... 13. *A. multifidus.*
13. Twigs 2–6 mm. thick, glabrous or pilose from patent, rufous hairs; adult leaves entire; male head 2–7.5 × 0.5–1.2 (–3) cm.; syncarp processes puberulent or minutely hispid, styles simple.
    19. Cauliflorous or ramiflorous; leaves with the lateral veins curved, 6–10 pairs; syncarp 15–100 × 10–50 cm., fruiting perianths markedly fleshy. Series CAULIFLORI.
        20. Twigs and peduncles usually pilose from patent, rufous hairs, c. 3 mm. long; base of leaf abrupt, intercostals to c. 10; inflorescences without a basal annulus. .... 14. *A. integer.*
        20. Twigs and peduncles glabrous; base of leaf decurrent, intercostals c. 10–14; inflorescences with a

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[3] The distribution of series *Incisifolii* within the Philippines is given as a rough guide only; the less common species will probably be found to occur more widely.

basal annulus formed by the enlargement of the top of the peduncle into a narrow flange. .... 15. *A. heterophyllus.*

19. Not cauliflorous or ramiflorous; leaves with the lateral veins straight; syncarps 6.5–8.5 × 2–3.5 cm., fruiting perianths not fleshy. Series ANGUSTICARPI.

21. Leaves elliptic, lateral veins 11–16 pairs; male head without elongate solid perianths; syncarp with processes all perforate, conical and up to 1.5 mm. long, or the apices depressed and the surface hence areolate. Malaya, Sumatra. ...... 16. *A. lowii.*

21. Leaves ovate to ovate-elliptic, lateral veins 6–12 pairs; male head with filiform solid perianths projecting to 1 mm. from the surface; syncarp with processes mostly perforate, conical, to 1.5 mm. long, but a few solid, attenuate, to 4 mm. long. Nicobar Is., Malaya, Sumatra, Borneo, Celebes, Moluccas, New Guinea. ...... 17. *A. teysmannii.*

12. Male head with the surface variously rugose; twigs hispid, hispid-pubescent or villous, the hairs usually rufous. Series RUGOSI.

22. Shoots large to massive: twigs 5–20 mm. thick; male head 6–20 × 1–2.5 cm., the peduncle 3.5–10 cm.; syncarp 8–12 × 5–5.5 cm., usually with solid, flexuous processes, the peduncle 5.5–18 cm.

23. Leaves with 11–16 pairs lateral veins; male head with the surface rugose-sulcate, not pilose; flexuous syncarp processes with short, patent, or long, appressed hairs.

24. Twigs hispid, varying subglabrous; leaves thickly coriaceous; male head rugose-sulcate, perianths without crisped hairs; flexuous syncarp processes to 18 × 1.5 mm., shortly hispid, or none.

25. Leaves smooth above, or nearly so; male head 6.5–10.5 × 1 cm.; syncarp with all processes c. 3 × 2 mm., or a few slightly elongate. Malaya, Sumatra. ...... 18. *A. scortechinii.*

25. Leaves scabrid above; male head 6–15 × 1.5–2.5 cm.; syncarp with flexuous processes 10–18 × 1–1.5 mm., shortly hispid. Peninsular Burma and Siam, Malaya, Sumatra, Borneo, Java, Lesser Sunda Is., Palawan. .... 19. *A. elasticus.*

24. Twigs (often sparsely) villous; leaves coriaceous; male heads rugose or sub-tuberculate, perianths with crisped hairs; flexuous syncarp processes 20–35 × 0.5–1 mm., subappressed-pubescent, hairs to 2 mm. long. Borneo, Philippines, Celebes, Moluccas. .... 20. *A. sericicarpus.*

23. Leaves with 15–23 pairs lateral veins; male head with the surface tuberculate from obtuse processes, c. 3 ×

2 mm., the apices pilose, hairs rufous, to 2 mm. long; flexuous syncarp processes to 10 × 0.5 mm., scabrid from recurved hairs. Borneo. . . . . 21. *A. tamaran.*

22. Shoots smaller: twigs 2–3 mm. thick; male head 2–5.5 × 0.3–0.6 cm., the peduncle 0.5–2 cm.; syncarp 4–4.5 × 2–2.5 cm., without sterile processes, the peduncle 0.5–4 cm.
  26. Leaves subappressed-pubescent throughout beneath; male peduncle c. 2 cm.; syncarp with acute conical processes. Sumatra. . . . . 22. *A. sumatranus.*
  26. Leaves usually appressed-pubescent on main veins only beneath; male peduncle to 1.3 cm.; syncarp with low, obtuse or truncate processes, or nearly smooth, the surface areolate.
    27. Leaves elliptic-oblong varying elliptic, acute to acuminate, glabrous above; peduncles patent-pubescent, in male 0.7–1.3 cm., in female 1.5–4 cm.; syncarp pubescent, with low, obtuse processes, or nearly smooth, the surface areolate. Malaya, Sumatra, Borneo. . . . . 23. *A. kemando.*
    27. Leaves obovate-elliptic varying elliptic, shortly and obtusely acuminate to retuse, young leaves appressed-puberulent above; peduncles velutinous, in male c. 0.5 mm., in female 0.3–0.8 cm.; syncarp velutinous, tesselate from very low, truncate, processes. Malaya, Sumatra. . . . . . . 24. *A. maingayi.*

Artificial keys for the identification of specimens bearing either male or female inflorescences are provided at the end of the treatment of this subgenus, and the second of these is illustrated.

Section **Duricarpus** Jarrett, sect. nov.

Folia adulta pinnata (*A. anisophyllus*) vel simplicia, integra, juvenilia pinnatifida; hypodermis absens, vel imperfectum, cellis elongatis compositum. *Inflorescentiae* bracteis interfloralibus peltatis, syncarpio subdeciduis. *Capitula mascula* subglobosa, obovoidea, clavata, ellipsoidea vel breviter cylindrica. *Syncarpia* globosa, vel subglobosa, processibus induratis obtecta; ovaria stylis terminalibus; semina testis pergamentaceis, rubris, pericarpiis induratis, perianthiis carnosisque inclusa; embryum in longitudinem positum, cotyledonibus aequalibus, radicula supera.

TYPE SPECIES: *Artocarpus rigidus* Blume.

Although the distinctive feature of this section is the syncarp, there is considerable variation in its appearance due to the differing shapes of the indurated processes (free perianth apices) covering it, which may be either narrowly cylindric (*A. anisophyllus* and *A. odoratissimus,* with clavate tips in the latter), or tapering so that the syncarp is echinate (*A. hispidus*, *A. rigidus*), or short and obtuse or truncate so that the surface is more or less clearly tessellated (*A. lanceifolius*, *A. melinoxylus*, *A. chaplasha*). Other characters, however, suggest that these resemblances do not necessarily indicate the closest relationships of the species. *Artocarpus anisophyllus* stands out by reason of its pinnate leaves, but in the presence of a hypodermis, the deeply sunken gland-hairs, and the glabrous shoot, a close affinity is shown with *A. lanceifolius*, which is confirmed by the ellipsoid to cylindric male inflorescences, and the strongly differentiated endocarp. *Artocarpus odoratissimus*, *A. hispidus* and *A. rigidus* are likewise united by their obovoid, subglobose or clavate male inflorescences, the elongate, hispid syncarp processes, and the hispid shoots. Between them may be placed *A. melinoxylus* and *A. chaplasha,* which resemble the latter group in the characters of the shoot and the male inflorescence, but *A. lanceifolius* in the surface of the syncarp. These are the only two species in the section of which the distinctness is in any doubt, and the characters separating them are listed under *A. melinoxylus*. As noted above, two series are distinguished on the basis of leaf anatomy, indumentum of the shoot and shape of the male head, of which the first, series *Laevifolii*, includes *Artocarpus anisophyllus* and *A. lanceifolius,* while the rest of the species are placed in series *Asperifolii*.

Series **Laevifolii** Jarrett, ser. nov.

Ramuli et folia subglabri; folia hypoderme imperfecto, cellis elongatis composito, glandulis profunde immersis, capitibus globosis, 4–6-cellis; inflorescentiae masculae breviter ellipsoideae vel subcylindricae.

TYPE SPECIES: *Artocarpus anisophyllus* Miq.

1. **Artocarpus anisophyllus** Miq. Fl. Ind. Bat. Suppl. 422. 1861, "*anisophylla*;" Renner, Bot. Jahrb. **39**: 366. 1907; Merr. Pl. Elmer. Born. 45. 1929; Corner, Wayside Trees, 652. *t. 191, 192*. 1940. Holotype, Sumatra, *Teysmann HB 3698* (U); isotypes (BO, K, L).

Artocarpus klidang Boerl. Handl. Fl. Ned. Ind. **3**: 333, 371. 1900, in clavis.
Artocarpus superba Becc. For. Borneo, 625. 1902; Merr. Philip. Jour. Sci. **18**: 51. 1921, Enum. Philip. Pl. **2**: 43. 1923; Ridley, Fl. Malay Penin. **3**: 356. 1924. Holotype, Sarawak, *Beccari PB 2997* (FI); isotypes (FI, K).

Evergreen trees, height to 45 m. *Twigs* 10–20 mm. thick, rugose, appressed-puberulent and minutely punctate; annulate stipular scars c. 1.5 mm. broad, prominent; lenticels scattered. *Stipules* 4–17 cm. long, broadly ovate-lanceolate, acute, exterior rugose, subappressed-pubescent, hairs yellow to brown. *Leaves* imparipinnate; rachis 40–80 cm. (fide Elmer in Merrill, 1929, to 150 cm.) long, base to 7 mm. in diameter, terete, finely rugose; pinnae 5–12 on each side, usually in subopposite pairs with longer and shorter pairs alternating and the latter raised above the rachis, terminal pinna often bifid; juvenile leaves with distal pinnae decurrent on rachis and the pinnae pinnatifid; pinnae 3.5–40 × 2–13 cm., oblong to oblong- or ovate-lanceolate, with an acumen to 2 cm. long, the base rounded, varying cuneate, often inequilateral, glabrous, the margin entire or shallowly and distantly crenate; main veins prominent beneath, intercostals slightly so;

lateral veins 7–20 pairs, straight; intercostals parallel only towards margin; dark green, drying red-brown to pale greenish or yellowish brown; hypodermis of one cell-layer present, interrupted over the areolae, cells elongate in surface view; gland-hairs immersed, heads globose, 4–6-celled; petiolules to 40 mm. long.

Inflorescences, male and female heads usually paired in the same leaf-axil. *At anthesis*: *male head* 30–75 × 15–20 mm., ellipsoid-oblong, smooth, covered by flowers and bracts; perianths tubular, 1.8 mm. long, shortly bilobed above, minutely pubescent; stamen 2.0–2.3 mm. long, filament slender, cylindric, anther-cells subglobose, 0.2 mm. long; bracts slenderly stalked, heads infundibuliform, to 0.6 mm. across, pubescent; peduncle 50–65 × 4 mm., surface as in the twigs; *female head* with pubescent peltate bracts being shed and simple styles exserted to c. 1 mm. *Syncarp* to 11 × 8 cm. (fide Elmer, l.c., to 20 cm. in length), subglobose, brown, drying pale brown, covered by closely set, cylindric, rigid, shallowly fluted, obtuse, minutely punctate processes, 6–8 × 1–1.5 mm.; wall c. 6 mm. thick; fruiting perianths numerous, proximal free region orange, pulpy, "seeds" (endocarps) ellipsoid, 17 × 10 mm.; core c. 20 mm. across; peduncle 60–130 × 10 mm., surface as in the twigs.

VERNACULAR NAMES: *Bakil,* Sumatra, Borneo; *Mentawa* or *Mentaba,* Banka, Borneo; *Puan* or *Pupuan,* Borneo.

DISTRIBUTION: in evergreen forest to 4000 ft., Malaya, Sumatra, Banka, Billiton, Lingga, Borneo.

Malaya. MALACCA: *Maingay 1483* (K, ♂, ♀). SINGAPORE: Garden Jungle, *Ridley 4113* (CAL, SING, ♂), *6429* (BM, CAL, K, SING, ♀), *6678* (BM, CAL, K, SING, ♂, ♀); MacRitchie Reservoir, s. side, *Sinclair SFN 40658* (K, ♀); Seleter Reservoir, s. side, *Sinclair SFN 39249* (L, SING). (Fide Corner, 1940, frequent in lowland forest.)

Sumatra. INDRAGIRI: Kwala Belilas, *bb 27580* (A, BO, L); Muara Serangge, *bb 29991* (A, BO, L). BENKULEN: Lebong, Bosch Pengadang, *Olivier 29* (BO, L). PALEMBANG: Banjuasin, Bajunglintjir, *NIFS E 1028* (BO, ♀), *1163* (BO, L, U, ♀); Batu-radja, *Teysmann HB 3698* (BO, K, L, U); Lematang Ilir, Gunong Megang, *NIFS E 952* (BO, K, L, SING, U, ♀), *959* (BO, L, P, U, ♂, ♀), *1029* (BO, U, ♀); Lematang Ilir, Semangus, *bb 31984* (A, BO, SING), *32042* (BO, K); Lematang Ulu, *Grashoff 277* (BO); Muara Dua, *Grashoff 454* (BO, L); Rawas, *Grashoff 1052* (BO, L). LAMPONGS: Semangka, Kuta-Agung, *Gusdorf 289* (BO, L). BANKA: Lobok Besar, *Kostermans & Anta 1230* (A, L); Muntok, Batu-balai, *Teysmann 7245* (BO, C, K, L); Sungei Liat, *Teysmann 7247* (BO, C, K, L). BILLITON: *Rossum 48* (BO, L, ♂, ♀), *Teysmann s.n.*, (BO); Tandjungpandang, *Teysmann s.n.* (BO); Tandjungpandang, Bantan, *bb 8677*, (BO, L). LINGGA: *Teysmann 7282* (BO, L, P).

Borneo. SARAWAK. *Beccari PB 2997* (FI, K, ♀); Lundu, *Foxworthy 344* (L). WEST BORNEO. *De Vriese s.n.*, 1857–61 (BO [labelled *Riedel s.n.*, Menado, Celebes], L); Sanggau, Nek Sawah, *bb 14307* (BO). SOUTH AND SOUTHEAST BORNEO. Pleihari, Kintap, *bb 8145* (BO, L); Puruktjahu, Muara Djaan, *bb 10506* (BO, L); Tanah Bumbu, Kampong Baru, *bb 13053* (BO, L, ♂). EAST AND NORTHEAST BORNEO. Balikpapan: S. Tunan, *bb 25588* (BO, L). Berouw: Domaring, *bb 18861* (BO). Bulungan: Salim Botu, S. Kumoh, *bb 11275* (BO, L). E. Kutei: Bengalon

Rapak, *bb 15285, 15319* (BO, L); Peridan, *bb 9862* (BO, L); Sangkulirang, Palawan, *bb 11859* (BO, L); Sangkulirang, Ronggang, *bb 7971* (BO, L); T. Leban, *bb 14685* (BO, L). W. Kutei: Blu-u, *Jaheri 1460* (BO); Ibo Antjalong, *bb 16484* (BO, P); Kahala, *bb 28365* (BO); Kelumpang, *bb 16928* (A, BO, L); Longbleh, *bb 16137* (A, BO, L), *16141* (BO), *16149* (BO, SING), *16152* (BO, P), *16488* (BO, SING); Mujup, *bb 16752* (A, BO, L). BRITISH NORTH BORNEO. Elphinstone Prov., Tawao, *Elmer 21600* (A, BM, BO, C, GH, K, L, P, SING, U, ♀); Kinabatangan Besar, Kori Timber Camp, *Cuadra A 2133* (K, SING); Mt. Kinabalu, Penibukan ridge, *Clemens 40424a, 50210* (BM); Sepilok For. Res., 15 miles w. of Sandakan, *Wood SAN 16549* (A, K, L, ♂, ♀).

This species is the only one in *Artocarpus* to have pinnate adult leaves. It was noted by Corner (1940) that these are unusual both in that they do not disarticulate when falling, as do most compound leaves, and in the arrangement of the pinnae, with longer and shorter pairs alternating and the latter lying in a plane above the former (well shown in the photograph, l.c.). The only other occurrence of pinnate leaves in the genus appears to be in saplings of *A. tamaran*; the latter can readily be distinguished (apart from the indumentum of the shoot) by the continuous narrow wing of lamina on both sides of the rachis.

A sheet at Bogor identified under an unpublished name purports to have been collected by Riedel in Menado, Celebes, but this is presumably an error of labelling, since *De Vriese s.n.*, West Borneo, at Leiden, bears the same determination.

Merrill (1921, 1923) recorded this species (as *A. superba*) from Basilan (*Hutchinson FB 3989*), Mindanao (Zamboanga, *Merrill 8280*; Port Banga, *Whitford & Hutchinson FB 9164*; both sterile) and Palawan (*Cenabre et al. FB 28009*), but no duplicates of these collections have been traced.

2. **Artocarpus lanceifolius** Roxb. Fl. Ind. **3**: 527. 1832, "*lanceaefolia*;" Wight, Ic. Ind. Or. **2**: *t. 679.* 1843; Tréc. Ann. Sci. Nat. Bot. III. **8**: 122. 1847; King in Hook. f. Fl. Brit. Ind. **5**: 543. 1888; King, Ann. Bot. Gard. Calcutta **2**: 13. *t. 11.* 1889; Renner, Bot. Jahrb. **39**: 366. 1907; Ridley, Fl. Malay Penin. **3**: 354. 1924; Foxworthy, Malayan For. Rec. **3**: 128. *2 plates.* 1927; Burkill, Dict. 256. 1935; Corner, Wayside Trees, 656. *t. 197.* 1940.

Artocarpus lanceofolia Roxb. Hort. Beng. 103. 1814, nomen nudum.

ssp. **lanceifolius**

Evergreen trees, height to 35 m., with small buttresses, bark dark grey, peeling off in flakes. *Twigs* 6–8 mm. thick, rugose, appressed-puberulent and minutely punctate; annulate stipular scars c. 1 mm. broad, inconspicuous; lenticels scattered. *Stipules* 1.5–4.5 cm. long, ovate-lanceolate, acute, exterior rugose, shortly appressed-pubescent. *Leaves* 10–33 × 5–17 cm., elliptic, varying to ovate, obovate or oblong, rarely narrowly lanceolate-elliptic, short-acuminate, acumen rounded varying acute, base cuneate, decurrent, rarely inequilateral, thickly coriaceous, glabrous, the margin entire or shallowly and distantly crenate; juvenile leaves pinnatifid; main veins prominent beneath, reticulum not or scarcely prominent; lateral veins 9–14 pairs, straight; intercostals parallel; deep green, drying pale or reddish brown with straw-coloured reticulum; hypodermis of one cell-layer present, interrupted over the areolae, cells elongate in surface view; glands deeply sunken in narrow pits, heads globose, 4–6-celled; petiole 10–30 mm. long.

Inflorescences solitary in leaf-axils or the male ones paired. *At anthesis*: *male head* 30–60 × 12–18 mm., ellipsoid to cylindric, smooth, covered by flowers and bracts; perianths tubular, 2 mm. long, shortly bilobed above, puberulent; stamen 3.5 mm. long, filament slender, cylindric, anther-cells oblong, 0.4 mm. long; bracts slenderly stalked, heads infundibuliform, to 0.5 mm. across, sparsely ciliate; peduncle 25–70 × 2.5–5 mm., shortly appressed-pubescent; *female head* with pubescent peltate bracts mostly shed and bifid styles exserted to 0.5 mm. *Syncarp* to 8 × 7 cm. (to 12 cm. across, fide Foxworthy, 1927), subglobose, olive- or chestnut-brown, drying brown, tesselated from closely set, indurated, cylindric, truncate, appressed-pubescent processes, c. 3.5 × 3 mm.; wall c. 8 mm. thick; fruiting perianths numerous, proximal free region whitish, pulpy (fide Burkill, 1935), "seeds" (endocarps) ellipsoid, 20 × 10 mm.; core c. 15 mm. across; peduncle 50–100 × 8 mm., surface as in the twigs, or shortly appressed-pubescent.

Vernacular names: *Keledang* or *Klidang* (Malay), Malaya, Riouw-Lingga Archip. Uses: the timber is valuable and the pulp surrounding the seeds is eaten by jungle tribes.

Distribution: in evergreen forest to 2000 ft., Malaya, Sumatra (West and East Coast), Banka, Riouw-Lingga Archip.

Malaya. Perak. Larut: *King 3452* (BM, CAL, K, ♂), *3826* (CAL, K, ♀); Gunong Boobo Range, *King 7631* (CAL, K, P, SING, ♀). Pahang: Kuala Lipis, *Phillips 670* (SING); Temerloh, *Hamid CF 5737* (SING). Negri Sembilan: Gunong Angsi For. Res., *Sow 23728* (SING). Malacca: *Maingay 1478* (CAL, K, ♂, ♀); Bukit Sedanan Reserve, *CF 2100* (SING, ♂); Kesang tua, *Goodenough 1328* (BM, CAL, SING, ♀). Johore: Pulau Tinggi, above Kampong Tandjong Balang, *Sinclair s.n.*, May 1954 (SING); Pinerong, *Cantley 27* (K, ♂). Penang: Batu Ferengy, *Curtis 3654* (CAL, K, SING, ♀); Highlands, *Curtis 3602* (CAL, K, SING, ♂); Penang Hill, *Nanen 35845* (SING, ♀); Puram (?) Bukit, *Curtis s.n.*, July 1893 (SING). Singapore: Bukit Timah, *Corner s.n.*, Feb. 1931 (SING, ♀); Bukit Timah For. Res., Jalan Tiup Tiup, *Sinclair SFN 40249* (K, L); Gardens Jungle, *Ridley 6541* (BM, CAL, K, SING, ♂). (Fide Foxworthy, 1927, also in Kedah, Kelantan and Trengganu.)

Sumatra. West Coast: *de Vriese & Teysmann 20* (L); Padang, Lubuk peraku, *bb 6117* (BO); Painan, Barung Belantae, *NIFS SWK/I-50* (BO); near Pajakumbuh, Mt. Sago, *Meijer 4708* (CGE, ♀). East Coast: Simelungun, Masikat, *bb 5349* (BO, L); Sibolangit, *Lörzing 5445*, (BO, L, ♀). Banka: *Teysmann 7248* (BO, C, K, L, P); Muntok, Aer Limau, *bb 7613* (BO); Sungei-elan, *Teysmann 7250* (BO, C, K, L, P, ♀); Sungei-elan, Kampong permis, *Teysmann 7251* (BO, P, ♀). Riouw Archip.: Bintang, *Teysmann 7283* (BO, CAL, K, L, P, ♀). Lingga Archip. P. Sinkep: Bakong, *bb 2045*, *13670*, *Kassim 6* (BO, L); Bakong, Santel, *bb 17400* (BO, SING); Djago, *bb 3945* (BO); Mapur, Marok Tuwa, *bb 3846* (BO); Tadjur Tandjong, *bb 8386* (BO); Tandjung Batang, *bb 4014* (BO, L).

Roxburgh's original description was very brief and no type specimen has been found, so that the identification must rest on his drawing of a leaf and a syncarp which was published by Wight in 1843 and can be recognized with certainty as representing this species.

ssp. **clementis** (Merrill) Jarrett, stat. nov.

Artocarpus clementis Merr. Jour. Str. Br. Asiat. Soc. **85**: 164. 1922. Holotype, British North Borneo, *Clemens 10770* (PNH, not seen, photograph in A); isotypes (A, BO, K).

Differs from ssp. *lanceifolius* as follows: *leaves* varying to ovate-elliptic or ovate-lanceolate; *syncarp* covered by somewhat widely spaced, indurated, slightly tapering, obtuse, appressed-pubescent processes, 1–1.5 × 1 mm., with scattered peltate bracts persistent between them; wall c. 3 mm. thick; "seeds" (endocarps) numerous, ellipsoid, 12–15 × 8 mm.; core c. 15 mm. across; peduncle 40 × 6 mm., minutely punctate.

VERNACULAR NAME: *Keledang* (Malay).

DISTRIBUTION: in evergreen forests to 3600 ft., endemic to northeastern Borneo.

Borneo. EAST AND NORTHEAST BORNEO. Balikpapan: Pemaluan, *bb 24763* (BO, L); S. Karnain, *bb 26374* (BO, L, SING). Berouw: Betemaran Tidi, *bb 19062* (BO); Domaring, *bb 18831* (A, BO), *bb 18835* (A, BO, L), *18851* (BO); Inaran, *bb 12078* (BO); Long Lanuk, *bb 18445* (BO), *18461* (BO, L, SING). Bulungan: Kabiran, S. Bengalun, *bb 11686* (BO); Mara, *bb 10750* (BO). E. Kutei: Muara Karangan, Remendai, *bb 7962* (BO); Sangkulirang, Palawan, *bb 11867* (BO); Sangkulirang, Pingadan, *bb 12992* (BO); Sangkulirang, Rantau Banan, *bb 15236, 15238, 15247* (BO); Loa Djanan, w. of Samarinda, *Kostermans 6627* (K, L, ♂); Tandjong Bangko, nr. Mahakam River estuary, *Kostermans 7096* (BO, K, L, ♀). W. Kutei: Djembajan, Sungei Djambu, *bb 24672* (A, BO, L); Kendisi, *bb 16681* (BO, L), *16695* (A, BO, L); Mo-Antjalong, *bb 16482, 16486* (A, BO, L); near Mt. Kemul, *Endert 3683* (L). Tidung: Loban, *bb 17882* (BO, L). BRITISH NORTH BORNEO. Mt. Kinabalu, *Foster & Puasa 3522* (K); Mt. Kinabalu, Gurulau Spur, *Clemens 10770*, Nov. 1915 (A, BO, K, ♀); 12 miles w. of Ranau, Bondu Tahan, *Wood & Charrington SAN 16381* (A, ♀). NUNUKAN. *bb 26174* (BO).

The description of the syncarp is based on that of the type of *Artocarpus clementis*, which is slightly decayed, but almost certainly had the processes rather widely spaced at maturity. In the other, younger, syncarps seen from Borneo the processes are also small but they are closely set and apparently separate only when the syncarp nears maturity. The three collections cited from British North Borneo have rather distinctive ovate-elliptic to ovate-lanceolate leaves, but they merely represent an extreme of the range of variation which is exhibited by the rest of the material seen from Borneo, nearly all sterile, and which is not separable from that of the species as a whole. In view of the discontinuity in the distribution of the species between a western area including Malaya and Sumatra and a smaller area to the east in northeastern Borneo, it is likely that only ssp. *clementis* is represented in the latter. The sterile collections from Borneo are tentatively listed under this subspecies, but only specimens bearing syncarps or showing the extreme leaf-shape can be assigned here with certainty.

Series **Asperifolii** Jarrett, ser. nov.

Ramuli et folia hispidi vel hispidi-pubescentes; folia sine hypoderme, glandulis subimmersis, capitibus globosis, 4–16-cellis; inflorescentiae masculae globosae ad clavatae.

TYPE SPECIES: *Artocarpus rigidus* Blume.

3. **Artocarpus melinoxylus** Gagnep. Bull. Soc. Bot. Fr. **73**: 87. 1926. "*melinoxyla*;" Gagnep. in Lecomte, Fl. Gén. Indoch. **5**: 736. 1928. Syntypes, Indochina, *Chevalier 37007, Poilane 1218, 4588, 6873, 7079, 7621* (P); lectotype *Poilane 7079* (P).

ssp. **melinoxylus**

Trees, height to 15 m. *Twigs* 3–7 mm. thick, rugose, hispid, hairs yellow, appressed (longer and patent on juvenile shoots); annulate stipular scars 0.5 mm. broad, not or scarcely prominent; lenticels scattered. *Stipules* c. 2.5 cm. long, ovate, acute, hispid-pubescent, hairs yellow, subappressed. *Leaves* 7–30 × 4–18 cm. (–35 × 25 cm.) elliptic to obovate- or ovate-elliptic, short-acuminate, base rounded, varying cuneate, margin entire; main veins only prominent beneath or intercostals slightly so; glabrous above or with scattered hairs on the main veins, appressed subhispid-pubescent on the main veins beneath; lateral veins 6–13 pairs, straight, intercostals parallel; drying pale to dark red-brown, lighter beneath; hypodermis absent; glands half immersed, heads globose, 6–8-celled; petiole 8–28 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* (one only seen at maturity) 50 × 45 mm., subglobose, smooth, covered by flowers and bracts; perianths deeply 2(or 3)-lobed, 1 mm. long; stamen 1.5 mm. long, filament slender, cylindric, anther-cells ellipsoid, 0.2 mm. long; bracts stoutly stalked, heads peltate, to 0.4 mm. across, these and perianths sparsely ciliate; peduncle 50 × 3 mm., appressed hispid-pubescent; *female head* with pubescent peltate bracts mostly shed and simple styles exserted to 1.0 mm. *Syncarp* to 6 cm. across, globose, drying red-brown, covered by closely set, indurated, cylindric, obtuse, hispid processes, c. 3 × 2 mm., hairs patent and slightly crisped; wall c. 5 mm. thick; fruiting perianths numerous, proximal free region fleshy, "seeds" (pericarps) ellipsoid, 10 × 6 mm.; core 20–25 mm. across; peduncle 70–135 × 6 mm., appressed-hispid.

VERNACULAR NAME: *Cay mit nai,* Annam. USES: the wood is stated in field notes to be of good quality.

DISTRIBUTION: in forests to 5000 ft., endemic to Indochina.

Indochina. ANNAM. Near Huê, Nui Bah Ma, *Poilane 29977* (P, ♀). Near Nhatrang: Massif de Cô Ihn, *Poilane 4588*, Sept. 1922 (P, ♀); Massif de la Mère et l'Enfant, *Poilane 6873*, May 1923 (P, ♀). Quang Tri prov., Mai Lanh, *Poilane 1218*, Mar. 1920 (K, P, ♂). Near Tourane: *Clemens 3431* (P, ♂); Balete, *Clemens 4021* (K, P, ♀); Ba na, *Poilane 7079*, Aug. 1923 (A, P, ♀); Mt. Bani [Ba na], *Clemens 3510* (A, K, P, ♀); Lien Chien, *Poilane 7621*, Aug. 1923 (A, P, ♀); Thua-Luu div., Lang-co For. Res., *Chevalier 37007*, Apr. 1918 (P, ♂). LAOS. Luang Prabang prov., n.e. of M. Ngai [probably Muong Ngoi], *Poilane 20689* (P, ♂).

ssp. **brevipedunculatus** Jarrett, ssp. nov. Holotype, British North Borneo, *Wood SAN A 1733* (A); isotype (K).

Differt ab typo *inflorescentiis ad anthesin capitulis masculis* subglobosis, c. 15 mm. diametro, pedunculis, 8–17 × 2.5 mm. suffultis, *femineis* pedunculis 13–18 × 3 mm. suffultis [in syncarpio submaturo ad 25 mm. longis].

VERNACULAR NAME: *Temponek.*

DISTRIBUTION: in lowland forest, endemic to British North Borneo.

Borneo. BRITISH NORTH BORNEO: Beaufort, *Wood SAN A 1733*, May 1955 (A, K, ♂, ♀); Jesselton, *Daw Kepong FN 71664* (A, K, ♀).

This new subspecies agrees closely with the type from Indochina, except in the smaller size of the male head and in the length of the peduncles. The elongation of the latter, throughout the genus, occurs largely before anthesis and they can be assumed to be considerably shorter than in ssp. *melinoxylus*, even in the mature syncarp. In spite of the difference in the size of the male inflorescence in the two subspecies the dimensions of the flowers are the same; the perianths are unusual for this subgenus in that they are very deeply lobed.

Although taxonomically *Artocarpus melinoxylus* is very near *A. chaplasha*, it differs in a number of characters which appear to justify maintaining it as a distinct species. The male inflorescence in *A. chaplasha* has a longer, more slender peduncle and the flowers are larger in all their parts, while the perianth is only shortly bilobed. The indumentum of the syncarps is also different, being appressed on the syncarp processes in *A. chaplasha* instead of patent and slightly crisped. In *A. chaplasha* the leaves have the entire upper surface and the venation beneath subappressed hispid-pubescent, but in *A. melinoxylus* the leaves have a smooth upper surface and only the main veins are appressed hispid-pubescent beneath.

4. **Artocarpus chaplasha** Roxb. Hort. Beng. 66. 1814, nomen nudum, Fl. Ind. **3**: 525. 1832; Wight, Ic. Ind. Or. **2**: *t. 682.* 1843; Tréc. Ann. Sci. Nat. Bot. III. **8**: 112. 1847; Kurz, For. Fl. Burma **2**: 432. 1877; King in Hook. f. Fl. Brit. Ind. **5**: 543. 1888; King, Ann. Bot. Gard. Calcutta **2**: 13. *t. 12.* 1889; Renner, Bot. Jahrb. **39**: 365. 1907; Troup, Silvicult. Ind. Trees **3**: 880. *t. 325.* 1921; Parkinson, For. Fl. Andaman Is. 254. 1923; Champion, Indian For. **60**: 524. *t. 50.* 1934. Holotype, "East India," *Roxburgh s.n.* (K).

Artocarpus chama Buch.-Ham. ex Wall. Cat. no. 4657C. 1831, nomen nudum.
Urostigma chrysophthalmum Miq. Hook. Lond. Jour. Bot. **6**: 575. 1847.
Ficus chrysophthalma Miq. Ann. Mus. Lugd.-Bat. **3**: 285. 1867.

Deciduous trees, height to 40 m., bark grey, becoming brown, peeling off in flakes. *Twigs* 4–10 mm. thick, rugose, densely hispid-pubescent, hairs yellow, appressed (patent on juvenile shoots); annulate stipular scars c. 0.5 mm. broad, not or scarcely prominent; lenticels scattered. *Stipules* 1.5–2.5 cm. long, ovate-lanceolate, acute, hispid-pubescent, hairs yellow, appressed. *Leaves* 14–23 × 9–14 cm., obovate-oblong, varying obovate or elliptic, acute, base rounded or shallowly cordate, margin entire; juvenile leaves pinnatifid; main veins prominent beneath, intercostals slightly so; very shortly subappressed-hispid above, venation beneath shortly subappressed hispid-pubescent, both surfaces varying subglabrous; lateral veins 8–12 pairs, straight; intercostals parallel; green, drying pale or reddish brown, lighter beneath; hypodermis absent; glands half immersed, heads depressed-globose, c. 8-celled; petiole 8–30 (–40) mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 15–30 × 10–30 mm., ellipsoid to short-obovoid or subglobose, smooth, covered by flowers and bracts; perianths tubular, 2 mm. long, bilobed above, minutely pubescent; stamen 2.5 mm. long, filament slender, cylindric, anther-cells ellipsoid, 0.3 mm. long; bracts slenderly stalked, the heads peltate, to 0.5 mm. across, pubescent; peduncle 60–75 × 1.5 mm., shortly appressed hispid-pubescent; *female head* with pubescent peltate bracts mostly shed and simple styles exserted to 0.5 mm. *Syncarp* to 6 cm. [to 10 cm., fide King, 1889] across, subglobose, yellow, drying brown, covered by closely set, indurated, cylindric, obtuse, appressed-hispid processes, c. 1.5 × 2 mm.; wall c. 5 mm. thick; fruiting perianths numerous, proximal free region . . . , "seeds" (pericarps) ellipsoid, 7 × 4 mm. [fide King, 1889, to 20 mm. long]; core c. 20 mm. across; peduncle 55–80 × 3 mm., appressed hispid-pubescent.

VERNACULAR NAMES: *Chaplash* (Bengali), India; [4] *Taung-peing*, Burma. USES: an important timber tree and often planted, although Champion (1934) stated that elephants found the seedlings very palatable; Parkinson (1923) noted that the leaves were used for elephant fodder and the fruits were edible.

DISTRIBUTION: in evergreen, semi-evergreen and moist deciduous forest to 5000 ft., in regions with a monsoon climate (rainfall at least 80 inches), northeastern India (Sikkim to Assam and Chittagong), Lower Burma (to northern Tenasserim), Andaman and Nicobar Is.

India. Not localized: East India, *Roxburgh s.n.* (K); Dulka Thae, *Gamble 1180A*, Jan. 1873 (K); Majoojah forests, *Brandis 331*, Jan. 1862 (BM). SIKKIM: *Anderson s.n.* (BO), *Hooker f. & Thomson s.n.* (CAL, GH, P), *Kurz s.n.* (CAL); Terai, Tin sing tung, *sine nom. et num.* (K). WEST AND EAST BENGAL: Duars,

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[4] Throughout this series of papers the word India will be used in a geographical sense, to denote the Indian subcontinent, and will include the modern political subdivisions of India and Pakistan.

Talpaigwa, *Haines 529* (K); towards Ilafoo, *Griffith 4668* (K); Tipperah (Hill), near Ranir Bazar, Noagaon, *Debbarman 1096* (CAL, ♀). ASSAM: *Lister s.n.* (CAL), *Mann s.n.* (CAL, ♂), *Masters s.n.* (BO, L, P); Abor, Pilung, *Burkill 38127* (CAL); Gowhatly, *Clarke 37165A* (BM); [? =] Guwalatty, near Aber [? Abor], *Jenkins s.n.*, Apr. 1835 (CAL); Cachar, Bundookmora, *Keenan s.n.* (K); Jatookia, *Watt 11308* (BM, ♂); Kamrup, *sine nom. 942* (CAL, ♂); Khasia Hills, *Hooker f. & Thomson s.n.* (A, BM, C, L, P, U); Khasia Hills, Doodputli, *Hooker f. & Thomson s.n.*, Nov. 1856 (K); Mangeldai to foot of Bhutan Himalaya, *Schlagintweit 13480* (BM); Naga Hills, *Mohassi 214* (L); Nowgong, *Hooker f. & Thomson s.n.*, July 1850 (K); Sibsagar, Ligri Pukri, *Watt 10405* (CAL, ♀). CHITTAGONG: Kagi Ke Hath, *Hooker f. & Thomson s.n.*, Jan. 1851 (K); Kodala, *Hooper 26008* (CAL), *King 392, 487* (BM, CAL, ♀); Rangamati, *Lister s.n.* (CAL); Rangamati, Magban, *Hooper s.n.*, Nov. 1898 (CAL); Rangamati and Damara, *Wallich 4657C* (BM); Seetakoone, *Hooker f. & Thomson s.n.*, Jan. 1851 (K).

FIG. 11. Distribution of the species of sect. DURICARPUS. 1, *Artocarpus anisophyllus* (? also in the Philippines); 2, *A. lanceifolius*, a, ssp. *lanceifolius*, b, ssp. *clementis*; 3, *A. melinoxylus*, a, ssp. *melinoxylus*, b, ssp. *brevipedunculatus*; 4, *A. chaplasha*; 5, *A. odoratissimus* (probably introduced in the areas enclosed by broken lines); 6, *A. hispidus*; 7, *A. rigidus*, a, ssp. *rigidus*, b, ssp. *asperulus*.

Lower Burma. (?) *Abel s.n.* ["East Indies"] (*K*, ♂); Pegu, Tonkyeghat, *Kurz 1498* (CAL p.p., L, ♀), *1499* (CAL); Rangoon, *Dickason 5528*, *6948* (A), *McClelland s.n.* (K, ♂). TENASSERIM, Kyauktalon [not located], *Meebold 14612* (CAL, ♂). Thaton: Martaban, *Kurz 1498* (CAL p.p., ♀). **Andaman Islands.** *Kurz s.n.*, Nov. 1881 (CAL), *Parkinson 167* (DD, ♂), *Rogers s.n.*, 1904 (K, ♂, ♀); Manglutan, *Parkinson 463* (K, ♂ ♀); South Andaman, *King s.n.*, Apr. 1890 (CAL), *Kurz s.n.* (K, ♀); South Andaman, n. coast, *Kurz s.n.* (K, ♀); S. Andaman, S. Corbyn's Cove, *Kurz s.n.* (CAL). **Nicobar Islands.** *Jelinek 165* (CAL, ♂); Karnicobar, Kakena, *Kamphovener 2672* (C); Karnicobar and Chowry, *Kamphovener 2394* (C); Teressa, *Kamphovener 2741*, *2742* (C).

Cultivated. INDIA: Calcutta, Hort. Bot., *Lane 7935* (CAL, ♂), *Wallich 4657* (K, ♂), *4657D* (BM, CGE, P, ♂), *s.n.*, Apr. 1815 (C); Dehra Dun, Forest Research Institute, *Raizada s.n.*, May 1947 (DD, ♂, ♀), *s.n.*, June 1950 (DD, ♀).

Artocarpus chaplasha is somewhat similar vegetatively to *A. rigidus* ssp. *asperulus* (in addition to *A. melinoxylus*, the distinguishing characters of which have been given above), but it may be identified by the larger, typically obovate-oblong leaf, since in Tenasserim where the two entities may overlap, the leaf shape of *A. rigidus* ssp. *asperulus* tends to ovate. It is, however, of interest to note that the distributional areas of these three entities, and hence, presumably, their ecological requirements are complementary. *A. chaplasha* is restricted to areas with a moderate to well-marked monsoon climate (but a rainfall of at least 80 inches) and is recorded definitely as far south as the Thaton district of Tenasserim. *A. rigidus* ssp. *asperulus* is recorded only as far north as the adjacent Amherst district (there is one unlocalized collection by Meebold of each species) and occurs, primarily in coastal areas, in the moister peninsular regions of Burma and Siam, extending to Cambodia and southern Annam; it is replaced by *A. melinoxylus* in the mountains of Annam and northeastern Laos, which have a rather more uniform, though not more abundant, rainfall.

5. **Artocarpus odoratissimus** Blanco, Fl. Filip. 671. 1837, "*Arctocarpus odoratissima*;" Fern.-Villar, Noviss. App. 203. 1880; Elmer, Leafl. Philip. Bot. **2**. 618. 1909; Wester, Philip. Agr. Rev. **8**: 108. *t. 7d, 9b*. 1915. **17**: 24. 1924(a), Bull. Bur. Agr. Philip. **39**: 129, *t. 15b, 32b*. 1924(b); Merr. Jour. Str. Br. Asiat. Soc. **76**: 80. 1917, Sp. Blancoanae. 124. 1918, Enum. Philip. Pl. **2**: 42. 1923. Neotype, Mindoro, *Merrill SB 1019* (BM).

Artocarpus tarap Becc. For. Borneo, 626. 1902; Renner, Bot. Jahrb. **39**: 365. 1907. Syntypes, Sarawak, *Beccari PB 9*, *PB 2528*, *PB 2588*, *PB 2697* (FI); lectotype, *Beccari PB 2697* (FI).

Artocarpus mutabilis Becc. For. Borneo, 627. 1902; Renner, Bot. Jahrb. **29**: 365. 1907. Holotype, Sarawak, *Beccari PB 758* (FI); isotypes (FI, K, P).

Evergreen trees, height to 25 m. *Twigs* 4–10 mm. thick, rugose, hispid-pubescent, hairs yellow to rufous, patent; annulate stipular scars c. 0.5 mm. wide, not raised; lenticels scattered. *Stipules* 1–8 cm. long, ovate, acute, hispid-pubescent, hairs yellow to rufous, appressed or patent. *Leaves* 16–50 × 11–28 cm., broadly elliptic to obovate, obtuse to shortly acuminate, base cuneate, often slightly decurrent, margin entire or distantly and shallowly crenate, often bearing tufts of hairs towards and at apex, varying lobed in upper half, lobes one (rarely two) on each side; juvenile leaves pinnatifid; main veins and intercostals prominent beneath, reticulum slightly so; both surfaces subappressed hispid-pubescent, scabrescent above, with the main veins softly and densely yellowish pubescent; lateral veins 13–15 pairs, straight; intercostals parallel; dark green, drying reddish to blueish brown above, red-brown beneath; hypodermis absent; glands slightly sunken, heads globose (8–)16-celled, cells in two tiers; petiole, 20–30 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 40–90 × 25–35 mm., ellipsoid to clavate, smooth, covered by flowers and bracts; perianths tubular, 1.8 mm. long, shortly bilobed above, minutely pubescent; stamen 2.0 mm. long, filament slender, cylindric, anther-cells subglobose, 0.15 mm. long; bracts slenderly stalked, heads peltate, to 0.4 mm. across, pubescent; peduncle 25–70 × 3–5 mm., indumentum as shoot; *female head* with pubescent peltate bracts mostly shed and simple styles exserted to c. 1.5 mm. *Syncarp* to 16 × 13 cm., subglobose, greenish yellow, drying pale red-brown, covered by closely set, rigid, cylindric, hispid processes, 8–13 × 1 mm., fluted below, the tips clavate; wall c. 8 mm. thick; fruiting perianths numerous, proximal free region white, juicy (fide Wester, 1915), "seeds" (pericarps) ellipsoid, 12 × 8 mm.; core c. 15 mm. across; peduncle 55–140 × 8 mm., indumentum as shoot.

Vernacular names: *Oloi* or *Loloi*, Mindoro; *Marang* or *Madang*, Mindanao, Basilan, Sulu; *Terap* (Malay), Borneo. Uses: the syncarp is esteemed, particularly in the Philippines, for the sweet, juicy, aromatic perianths surrounding the seeds, which may also be roasted; according to Wester (1915) the flavour is better than that of the Jack.

Distribution: in evergreen forest to 3000 ft., Borneo; in regions with abundant and equally distributed rainfall (? introduced), Philippines (Mindoro, Mindanao, Basilan, Sulu Archip.).

Borneo. *Korthals s.n.* (L, U). Sarawak. *Haviland 3116C* (CAL, ♂, ♀); Upper Rejang River, Gat, *Clemens s.n.*, July 1922 (NY); Gunong Mattan, *Beccari PB 2528*, Nov. 1866 (FI, K), *2588*, Nov. 1866 (FI, K, P, ♂, ♀); Kuching, *Beccari PB 2697*, Nov. 1866 (FI, K, ♀), *Haviland 2190* (CAL, K, SING, ♂, ♀), *Haviland & Hose 3316* (K, ♂, ♀), *3316B* (BM, L, ♂, ♀); base of Santubong, *Sinclair SFN 38372* (K, SING, ♀); Siul, nr. Kuching, *Beccari PB 758*, Oct. 1865 (FI, K, P, ♂, ♀). West Borneo. *De Vriese s.n.* (K); Landak, *s. nom. et num.* (BO); Liang gagang, *Hallier 2577* (BO); Melawie, Tjatil B. Tengkujung, *bb 26328* (BO, L). South and southeast Borneo. Muara Teweh, Lué Katjang, *bb 10926* (BO); Puruktjahu, Muara Djaan, *bb 10514* (BO). East and northeast Borneo. Berouw: Dedemuaer, *bb 19103* (A, BO, L); Tandjong-redeb, Labanan, *bb 11520* (BO). Tidung: *bb 17732* (BO); G. Muara Tagel, *Amdjah 136* (BO, L, ♀). W. Kutei: Blu-u, *Jaheri 1488* (BO). British North Borneo. *Burbridge s.n.*, 1877–78 (BM, K); Kabili-Sepilok For. Res., *Puasa Herb. For. Dept. B.N.B. 7037* (SING); Mt. Kinabalu, Dallas, *Clemens 26228* (A, BM, BO, L, NY, SING, ♀); Tenom, Pangie mile 80, *Cuadra A 3282* (L, SING). Sibatik. St. Lucia, *Cuadra*

A 2403 (K, L). NUNUKAN. *bb 26196* (BO, L). TARAKAN. N. E. Kalimantan, Passanggrahan, *Meijer 1851* (K, L, ♀).

Philippine Islands. MINDORO. Calapan, *Merrill 2583* (US, ♂), *SB 1019*, May 1916 (A, BM, BO, GH, K, L, P, ♀); Pinamalayan, *Ramos BS 41090* (A, ♀); Upper Sinariri River ("near house"), *Conklin PNH 17522* (A, L, PNH, ♀). MINDANAO. Davao: *Wester BS 19356* (K, ♀). Lanao: near Abaga ("probably planted"), *Lynn Zwickey 243* (A, ♂). Zamboanga: *Ramos & Edano BS 37469* (A, BM, L, ♀). BASILAN. *Hallier 4504* (L), *Merrill SB 1018* (A, BM, BO, GH, K, L, P), *Miranda FB 17880* (K, P, ♂), *Reillo FB 15416* (L), *Wester BS 38345* (A); San Rafael, Moro, *Hutchinson s.n.*, May 1906 (NY). SULU ARCHIP. Jolo, *Vidal 3846* (K). **Cultivated.** BORNEO. Sarawak, *Beccari PB 9*, May 1865 (FI, K, P, ♂); Sandakan, *Villamil Herb. For. Dept. B.N.B. 200* (L). MAURITIUS. *Chapelier s.n.*, *Commerson s.n.* (P).

Apart from the very characteristic inflorescences, this species can be recognized by the length of the indumentum on both surfaces of the leaves. In *Artocarpus elasticus*, which may be confused with *A. odoratissimus* when sterile, the leaves are also markedly scabrid above, but from very short appressed hairs.

Although this species was described from and is better known in the Philippines, its distribution there is limited and it was probably introduced to the islands from Borneo, where it was described under the names *A. mutabilis* and *A. tarap* by Beccari. The second of these was reduced to *A. odoratissimus* by Merrill (1917) and later he stated (1924) that the species apparently was always planted in the Philippines, which is confirmed by such field notes as are available (quoted above). Wester (1924a) also noted a tradition of the Moros in the southwestern Philippines that the Marang was introduced by them from the west.

6. **Artocarpus hispidus** Jarrett, sp. nov. Holotype, Singapore, *Corner SFN 37035* (SING); isotype (K).

Differt ab *A. rigido* capitulis masculis longiore pedunculatis, ramulis juvenilibus pedunculisque dense hispidi-pubescentibus, pilis patentibus.

Arbores [ad 20 m. altae]. *Ramuli juniores* 4–7 mm. crassi, plus minusve rugosi, dense hispidi-pubescentes, pilis rufis patentibus; cicatrices stipularum annulatae, 0.5 mm. latae, non prominentes, nec conspicuae; lenticellae rarae. *Stipulae* 0.5–1[–2] cm. longae, ovatae, acutae, dense subappresseque hispidae, pilis rufis. *Folia* 15–19 × 7–8 [12–23 × 5–10] cm., obovati-elliptica [vel elliptica], acuta [vel breviter acuminata] basi cuneata, margine versus apicem denticulata [vel integra], supra scabrida, pilis brevissimis appressis praefractisve, basibus inflatis tuberculatis, costa nervis lateralibusque dense appresseque pubescentibus, subtus hispidi-pubescentia, saturata virida, in sicco rubri-brunnea, vel supra canescentia; folia juvenilia pinnatifida; costa nervi lateralesque subtus prominentes; nervi transversales venulaeque subtus prominuli; nervi laterales utrinque [11–]14–15, recti; nervi transversales paralleli; hypodermis absens; glandulae subimmersae, capitibus globosis, 4–8-cellis; petiolus 10–15[–20] mm. longus.

Inflorescentiae axillis foliorum solitariae [vel geminae]. *Ad anthesin: capitula mascula* [15–]30 × [15–]20 mm., obovoidea, plana, floribus bracteisque numerosissimis obtecta; perianthia tubulosa, 0.6 mm. longa, supra bilobata, minute pubescentia; stamina 0.7 mm. longa, filamentis tenuis, cylindricis, cellis antherum globosis, 0.1 mm. longis; bracteae tenuiter stipitatae, capitibus peltatis, ad 0.3 mm. latis, pubescentibus; pedunculus 25[12–30] × 2 mm., indumento ut ramulis; *capitula feminea* bracteis peltatis pubescentibus subdeciduis, stylis simplicibus 1.5 mm. longis exsertis. *Syncarpia* ad 5.5 cm. diametro, globosa, in sicco fulvi-brunnea, echinata, processibus crebris, rigidis, teretibus, obtusis, hispidis, 5–6 × 1 mm.; stratum externum syncarpii c. 2 mm. crassum; "semina" (pericarpia indurata) numerosa, ellipsoidea, 13 × 10 mm., perianthiis liberis carnosisque inclusa; axis syncarpii c. 15 mm. diametro; pedunculus 25–35 × 5 mm., indumento ut ramulis. (Inflorescentiae typi spiritu vini conservae descriptae.)

Distribution: in evergreen forest to 1000 ft., endemic to Malaya.

Malaya. Perak: Goping, *Scortechini 1979* (BM, CAL, K, SING, ♂, ♀). Trengganu: Kg. Binjai, on road to K. Brang, *Corner s.n.*, Apr. 1937 (SING). Selangor: Sungei Buloh For. Res., *Ja'amat & Jackson SFN 39416* (A, L, ♂). Malacca: *Cantley s.n.* (SING, ♂). Penang: Government Hill, *Curtis s.n.*, Mar. 1894 (SING). Singapore: Bukit Timah, *Corner SFN 37035*, June 1940 (K, SING, ♂, ♀). *Corner s.n.*, Mar. 1941 (SING, ♂); Changi, *Ridley 3357* (BM, CAL, SING, ♀); 11½ miles Mandai road, *Sinclair SFN 40051* (L); Reservoir jungle, Thompson Reach end, *Corner s.n.*, Jan. 1937 (SING); Sangli, *Ridley 6756* (SING, ♂). **Cultivated.** Singapore: Hort. Bot., *Ahmad s.n.*, Mar. 1926 (SING, ♂).

The syncarps of *Artocarpus hispidus* and *A. rigidus* are very similar but the two species are quite distinct in the length of the male peduncles and the indumentum of the shoot and peduncles, and the differences were noted by Corner on the type. *Artocarpus hispidus* also differs from *A. rigidus* ssp. *rigidus* in the scabrid upper surface of the leaf, and from ssp. *asperulus* in the leaf shape. King's description of *A. rigidus*, under which he cited *Scortechini 1979*, also included this species.

7. **Artocarpus rigidus** Blume, Bijdr. 482. 1825, "*rigida*;" Tréc. Ann. Sci. Nat. Bot. III. **8**: 114. 1847; Miq. in Zoll. Syst. Verz. Ind. Archip. **2**: 89, 95. 1854; Miq. Fl. Ind. Bat. **1**(2): 286. 1859, Suppl. 418. 1861, Ann. Mus. Lugd.-Bat. **3**: 211. 1867. Kurz, For. Fl. Burma **2**: 431. 1877; King in Hook. f. Fl. Brit. Ind. **5**: 540. 1888; King, Ann. Bot. Gard. Calcutta **2**: 8. *t. 3.* 1889; Koord. & Val. Bijdr. Boomsoort. Java **11**: 17. 1906; Renner, Bot. Jahrb. **39**: 366. 1907; Ridley, Fl. Malay Penin. **3**: 352. 1924; Corner, Wayside Trees, 657. *t. 198, 199.* 1940; Backer, Beknopte Fl. Java **6**: 14. 1948. Holotype, Java, *Blume 1364* (L); isotype (CAL).

Artocarpus runcinata Reinw. ex Blume, Cat. Bog. 101. 1823, nomen nudum.
Artocarpus echinata Roxb. Hort. Beng. 66. 1814, nomen nudum. Fl. Ind. 3:

527. 1832; Wight, Ic. Ind. Or. **2:** *t. 680.* 1843; Tréc. Ann. Sci. Nat. Bot. III. **8:** 113. 1847. Holotype, *Roxburgh s.n.* (BM).

Artocarpus cuspidatus Griffith, Not. Pl. Asiat. **4:** 400. 1854. Holotype, Malacca, *Griffith 4664* (K).

Artocarpus kertau Zoll. ex Miq. in Zoll. Syst. Verz. Ind. Archip. **2:** 89, 95. 1854; Miq. Fl. Ind. Bat. **1**(2): 287. 1859; Koord. Exkursionsfl. Java **2:** 95. 1912. Holotype, Java, *Zollinger 1009* (P); isotypes (L, U).

Artocarpus dimorphophylla Miq. Fl. Ind. Bat. Suppl. 417. 1861, Ann. Mus. Lugd.-Bat. **3:** 211. 1867. Holotype, Sumatra, *Teysmann HB 3369* (U); isotype (BO).

Artocarpus varians Miq. ll.cc. Holotype, Sumatra, *Teysmann HB 4358* (U); isotypes (BO, L).

Artocarpus muricata Hunter ex Ridley, Jour. Str. Br. Asiat. Soc. **53:** 114. 1909, pro syn.

ssp. **rigidus**

Evergreen trees, height to 35 m., buttressed, bark grey, peeling off in flakes. *Twigs* 2–6 mm. thick, smooth or rugose, densely to sparsely hispid, hairs rufous, appressed; annulate stipular scars c. 0.5 mm. broad, inconspicuous; lenticels few, scattered, or none. *Stipules* 0.5–3 cm. long, ovate-lanceolate, acute, hispid-pubescent, hairs yellow or rufous, appressed. *Leaves* 9–32 × 5–15 cm., elliptic to ovate-, obovate- or oblong-elliptic, apex acute or short-acuminate, varying obtuse, base cuneate, varying narrowly rounded, margin entire or distantly and shallowly crenate; juvenile leaves pinnatifid; main veins and intercostals prominent beneath, reticulum slightly so; glabrous and smooth above, or rarely slightly scabrid from sparse, very short, appressed hairs, except the appressed-pubescent main veins, venation appressed-hispid beneath; lateral veins (9–)12–20 pairs, straight; intercostals parallel; dark green, drying blue-grey to red-brown above, red-brown beneath; hypodermis absent; glands slightly sunken, heads globose, 8-celled, cells in two tiers; petiole 10–25 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 13–20 mm. across, short-obovoid to globose, smooth, covered by flowers and bracts; perianths tubular, 1.2 mm. long, shortly bilobed above, minutely pubescent; stamen 1.3 mm. long, filament slender, cylindric, anther-cells globose, 0.1 mm. long; bracts slenderly stalked, heads peltate, to 0.3 mm. across, shortly ciliate; peduncle 2–6 × 2.5 mm., densely appressed hispid; *female head* with pubescent peltate bracts being shed, and simple styles exserted to c. 5 mm. *Syncarp* to 7 cm. across (to 13 cm. fide Corner, 1940) globose, dull orange, drying pale brown, echinate from closely set, rigid, tapering, fluted, acute, hispidulous processes, 7–9 × 1.5 mm.; wall c. 10 mm. thick; fruiting perianths numerous, proximal free region orange, fleshy, "seeds" (pericarps) ellipsoid, 12 × 7 mm.; core c. 20 mm. across; peduncle 8–25(–40) × 8 mm., appressed hispid.

VERNACULAR NAMES: *Perian*, Malaya, *Purian* or *Surian*, Sumatra, *Pujan*, Borneo (Malay); *Tempunai* or *Tempunih*, Malaya, *Tempunit*, Sumatra (Malay); *Pussar*, Java (Sundanese). USES: the tree is cultivated for its fruit in Malaya and Java, the edible portion being the sweet, pulpy, waxy perianths surrounding the seeds; it also provides timber.

Distribution: in evergreen forest to 1500(–3000) ft., noted several times as occurring near streams, Tenasserim, Malaya, Sumatra, Simalur, Banka, Billiton, Riouw-Lingga Archip., Borneo, Java (except the eastern province).

Lower Burma. Tenasserim: *Helfer 4669* (CAL, K, ♂). **Malaya.** Kedah: Bukit Rombang, *Dmat Kepong FN 27377* (K, ♂); Cherok Perah, *Meh CF 17779* (SING); Katumbah, *Meh CF 17882* (SING). Perak: *King 6921* (CAL, K, ♂, ♀); Batang Padang district, *King 7755* (CAL, K, L, P, ♀); Bikum Sungei, *Murdoch 376* (BM); Larut, *King 6727* (CAL, K, ♂); Larut, Turu, *King 6751* (CAL, L, P, ♂); Larut, Turu, Gunong Bubu range, *King 7612* (CAL, SING, ♀), *7679* (CAL, K, ♂, ♀); Matang Jambu, *Wray 2528* (CAL, SING, ♀); Teluk Anson, *Allen 37244* (A, BO, K, SING). Trengganu: Ulu Brang, *Moysey & Kiah 33745* (SING). Pahang: Gat, near Raub, *Burkill & Haniff 16929* (SING); Kuala Lipis, *Nong CF 1258* (SING); Temerloh, *Awang CF 2398* (SING), *Kassim CF 0731* (SING, ♂). Selangor: Bukit Badat res., Rawang, *Bahsin CF 32403* (SING); Kuala Lumpur, *Hose CF 4599* (K, SING, ♀); Sungei Buloh For. Res., *Hashim 37* (K, ♂); Weld Hills Res., *Hamid CF 4575* (K, ♀). Negri Sembilan: *Franck 1197* (C). Malacca: *Alvins 590, 1070, 1234, 1317* (SING), *1624* (SING, ♀), *Maingay 1474* (CAL, K, L, ♂, ♀), *1475* (K), *1476* (CAL, GH, K, L, ♂, ♀); Batu Tiga, *Holmberg 766* (SING); between Roombiya and Aloor Gafah, *Griffith 4664*, Sept. 1842 (K); 14–14½ miles Sungei Udan For. Res., *Sinclair SFN 40597* (K, SING). Johore: Gunong Pantai, *Corner s.n.*, Jan. 1937 (SING); Sungei Pelepah Kiri, *Corner s.n.*, June 1937 (SING). Penang: Government Hill, *Curtis s.n.*, Mar. 1894 (SING, ♀); Penaea Bukit, *Curtis 1984* (SING); Penang Hill, *Nanen s.n.*, June 1940 (SING); Waterfall, *King s.n.*, Aug. 1879 (CAL); Waterfall Quarry, *Curtis 3603* (CAL, K, SING, ♀). Singapore: Changi, *Ridley 3357* (K), *4437* (CAL, SING, ♂, ♀); Garden Jungle, *Ridley 6542* (BM, CAL, K, ♂, ♀).

Sumatra. *De Vriese 23* (L), *De Vriese & Teysmann 18* (L). Tapanuli: Barus, Pardamuan, *bb 31402* (A, BO, L); Padang Lawas, Gunong Tua Djulu, *bb 6443* (BO). West Coast: Ayer Waringun, *Burck s.n.*, Aug. 1883 (BO, L); Priaman, *Diepenhorst HB 7292* (BO, P), *Teysmann 754* (BO); Sinkara, *Teysmann HB 756* (BO, CAL, L, U). East Coast: Huta Padang, Asahan, *Krukoff 4376* (A, BO, L, SING, ♀); Karolanden, Lao Pengulu, *bb 12503* (BO); Langkat, Sungei Sedapan, *bb 9132* (BO); Tasik, *Koorders 10456* (BO). Indragiri: Keritang, *bb 28660* (BO, L, SING); Kuantan, Djake, *bb 26487*, *26491* (BO, L); Kuantan, Sungei Besar, *bb 24028* (BO, L); Peranap, *bb 30102*, *30120* (A, BO, L). Djambi: Muara Pidjuan, *bb 12273* (BO, L, ♂). Benkulen: Redjang, Penandjung pandang, *bb 2735* (BO, L). Palembang: *Praetorius s.n.* (L); Banjuasin and Kubustreken, *Grashoff 809* (BO, L); Banjuasin and Kubustreken, Bajunglintjir, *NIFS T 27* (BO, L, ♂, ♀), *195* (BO, K, L, SING, ♂, ♀); Komering Ulu, *Grashoff 575* (BO); Lematang Ilir, Gunong Magang, *NIFS T 284* (BO, L, P, SING, U, ♂, ♀), *300* (BO, L, ♂), *522* (BO, ♂); Lematang Ilir, Semangus, *bb 32245* (BO, L); Muara Dua, *Grashoff 461* (BO, L); Muara Dua, Kisau, *bb 9630* (BO); Muara Mengkulem, *Forbes 3041* (A, BM, CAL, L, P, SING, ♂, ♀); Musi Ilir, Ipil, *NIFS T 1071* (BO, L); Rawas, *Grashoff 1032* (BO, L); Pasemahlanden, Djangkar, *bb 8106* (BO). Lampongs: Mangala, *Gusdorf 47* (BO, ♂, ♀), *Teysmann HB 4358* (BO, L, U), *4369* (P), *4393* (BO, L, U), *4419* (BO, U); Seputik, Suwikis, *bb 2844* (BO, L); Seputik, Tulangbawang, Gunong Sugit, *Gusdorf 140* (BO, ♀). Simalur: *Achmad 814* (BO); Landschap

Tapah, Defajan, *Achmad 1429* (BO, K, L, U). BANKA: *Teysmann HB 3296* (BO), *6844* (BO, K, L, P); Blinju, *Grashoff 14* (BO, L, ♂, ♀); Blinju, foot of Gunong Rengkuk, *Berkhout 149a* (BO); Djebus, *Teysmann HB 3369* (BO, U), *7243* (L), *7252* (C, L, P); Lobok-besar, *Kostermans & Anta 824* (A, K, ♂); Muntok, Majang, *bb 7596* (BO); Toboali, *Teysmann HB 7265* (BO, P); Tohrin, *sine nom. HB 296* (U). BILLITON: *Rossum 20* (BO, K, L, ♂), *76* (BO), *Teysmann HB 17580, 17583* (BO); Tandjong Pandjang, *bb 6778* (BO). RIOUW ARCHIP.: Tandjong Pinang, Bintan, *Teysmann HB 7284* (BO, C, L, P). LINGGA ARCHIP. NIFS Ri./I–128 (BO). P. Singkep: Marok Tuwa, near Sungei Lorong, *Amat 12* (L); Ulu Sungei Marok Tuwa, *Amat 34* (BO, L).

Borneo. SARAWAK. *Beccari PB 2478* (K, P, ♂), *2998* (K, P, ♀); near Kuching, *Haviland 1888* (CAL, K, ♀); Mt. Poi, *Clemens 20305* (K, NY); Sibu Sungei Assan, *For. Dept. Sarawak S 0502* (SAR). WEST BORNEO. Melawie, Tjatit B. Tangkujung, *bb 26439* (BO, L); Sadakan, Pait, *bb 8048* (BO, L). SOUTH AND SOUTHEAST BORNEO. Martapura, Djungur, *bb 10384* (BO); Pleihari, Sungei Sangga, *bb 9950* (BO); Tanah Bumbu, Kampong Baru, *bb 13356* (BO, L, ♂, ♀). EAST AND NORTHEAST BORNEO. E. Kutei: Sangkulirang, Ranggang, *bb 7968* (BO); Tandjong Bangko region, mouth of Mahakam River, *Kostermans 7186* (K, L, ♀). W. Kutei: Djembajan, Sungei Kelasan, *bb 25122* (BO, L); Djembajan, Sungei Gitan, *bb 12766* (BO); Tandjong Tsue, *Endert 1953* (A, K, L). BRITISH NORTH BORNEO. Elphinstone prov., Tawao, *Elmer 21514* (A, BM, BO, C, GH, K, L, P, SING, U, ♀). P. LAUT. Sungei Paring, *bb 12897* (BO, U, ♂, ♀), *13258* (BO).

Java. *Blume 1364* (CAL, L, ♀), *Reinwardt s.n.* (L), *De Vriese 1655* (L). WEST JAVA. Batavia: Depok, *Beumée 6021, Hallier s.n.*, Aug. 1896 (BO), *Koorders 31077* (BO, L), *41048* (BO, ♀), *42776* (BO), *42792* (BO, ♂), *44119* (BO), *Van Steenis 12750* (L); between Kota Bambu and Djembatan duren, *Backer s.n.*, 1902 (BO, ♂); Leeuwiliang, Pasir Angsana, *Bakh. van den Brink 6974* (BO, K, L, ♂, ♀); Leeuwiliang, Pasir Tjihideung, *Bakh. van den Brink 6386* (BO, L); Leeuwiliang, Tjibata, *Bakh. van den Brink 6796* (BO, L, ♀); Tjiampea, *Koorders 30364, 30365* (BO), *30366* (A, BO, L, ♂). Buitenzorg: Handjere, Janglappa, *NIFS Ja 6206* (L). Cheribon: Kuningan, *Houter 67, 138* (BO). Preanger: Palabuanratu, *Koorders 8738* (BO, L), *12561, 12562* (BO, L, ♂), *12570* (A, BO, L, P, ♂, ♀), *15677* (BO, L, ♂), *33049* (BO); Palabuanratu, Buniwangi, *sine nom. et num.*, Mar. 1873 (BO); Palabuanratu, Tjibareno, *Winckel 1858* (BO, L, U, ♀); Sanggrawa, *Koorders 8739* (BO). CENTRAL JAVA. Pekalongan: Loutresten, E. Tegal, *Beumée 1889* (BO); Pemalong, *Bruscomps 8* (BO). NUSA KAMBANGAN: Tjilatjap, *Koorders 27032* (BO, ♀). **Lesser Sunda Islands.** Bali: [? cult.] *sine nom. et num.* (L).

Cultivated. INDIA: Calcutta, Hort. Bot., *Wallich 2142* (P), *4658D* (BM, CGE, K), *s.n.*, 1819 (BM, ♂, ♀). JAVA: Bantam, *Zollinger 1009* (A, L, P, U); Bogor, Hort. Bot., *Zollinger 2982* (BM, P, U, ♀). Unlocalized collections: *Abel s.n.* (East Indies) (K, ♀); *Kurz 2084* (CAL); *Roxburgh s.n.* (BM).

The synonyms given above all refer exclusively to *Artocarpus rigidus* ssp. *rigidus*, as do the references, except for King's descriptions (1888, 1889) which include *A. hispidus*. Merrill (Jour. Arnold Arb. **19**: 331. 1938) reduced *A. rigidus* to *A. rotunda* (Houtt.) Panzer, Pflanzensyst. **10**: 380. 1783, based on *Rademachia rotunda* Houtt. Nat. Hist. II. Pl. **11**: 455. 1779, which was very briefly described from Javan material as having leaves of the same shape as *Artocarpus integer* but without "roughness" except on the fruit, which was round and grew, so Houttuyn was told, to the size of a child's head. This could be a crude description of *A. rigidus* but, in fact the leaves in this species are more or less scabrid beneath, the twigs and peduncles are appressed-hispid and the syncarp is smaller. Since no type has been found at Leiden, the identification would have to be based primarily on the vernacular name *Mandelique* given by Houttuyn, which is cited by Teysmann and Binnendijk (Cat. Bog. 85. 1866) and by Koorders and Valeton (1906) as a Javan name for *A. rigidus*. The description does not fit any other species occurring in Java and it seems preferable to treat *A. rotunda* as a *nomen dubium*.

The specimen listed above from Bali is probably from a cultivated tree, since there are no other records of *A. rigidus* from eastern Java or the Lesser Sunda Islands as an indigenous plant. One of the collections from Penang, *Curtis s.n.*, May 1894, has the syncarp processes softly pubescent, but otherwise agrees with *A. rigidus* ssp. *rigidus*.

ssp. **asperulus** (Gagnep.) Jarrett, stat. nov.

Artocarpus calophylla Kurz, Prelim. Rep. For. Pegu App. A, 124, App. B, 82. 1876. in clavis, For. Fl. Burma **2:** 431. 1877, non Teysm. & Binnend., 1866, quae est nomen nudum; King in Hook. f. Fl. Brit. Ind. **5:** 540. 1888; King, Ann. Bot. Gard. Calcutta **2:** 8. *t. 2.* 1889. Holotype, Burma, *Kurz s.n.* (CAL).

Artocarpus asperula Gagnep. Bull. Bot. Soc. Fr. **73:** 86. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5:** 734. *fig. 90.* 1928. Syntypes, Indochina, *Chevalier 30083, Herb. For. Cambodge 36930, Pierre 15, 1851, Poilane 6644, Thorel 1067* (P); lectotype, *Poilane 6644* (P).

Artocarpus asperula var. *hirta* Gagnep. Bull. Soc. Bot. Fr. **73:** 87. 1926; Gagnep. in Lecomte, Fl. Gén. Indoch. **5:** 735. 1928. Syntypes, Indochina, *Pierre 3377, 3777, Thorel s.n.*, 1862–66 (P); lectotype, *Pierre 3777* (P).

Artocarpus chaplasha auct. non Roxb., Gagnep. in Lecomte, Fl. Gén. Indoch. **5:** 735. 1928.

Differs from ssp. *rigidus* as follows: *twigs* rather softly and densely subappressed hispid-pubescent, juvenile shoots with long patent hairs; *leaves* obovate-oblong to ovate, base rounded or shallowly cordate, rarely cuneate; very shortly appressed-hispid above, rarely nearly smooth, indumentum beneath as on shoot; lateral veins 9–12 pairs; *syncarp* with processes hispid from spreading hairs c. 0.5 mm. long.

VERNACULAR NAMES: *Taung peing*, Burma; *Kanun pan*, Siam; *Knol prey* or *Knor prey*, Cambodia; *Cay mit nai* or *Mit nai*, Annam. USES: as in ssp. *rigidus*.

DISTRIBUTION: in evergreen forest to 3000 ft., Burma, Siam, Indochina.

Burma. Kyauktwin [not located], *Meebold 15599* (CAL). TENASSERIM. Amherst: *Falconer 1015* (CAL, ♀); Mekhrein chaung, *Parkinson 5205* (DD, ♀); Moulmein, *Kurz s.n.* (CAL). Tavoy: Kalemaung Res., *Ba-Pe 864* (CAL, DD, ♀); Kadwe For. Circle, *Manson 762* (CAL, ♀). **Siam.** Chanburi [Chantaburi ?], Makham, Khao sabap, *Put 2368* (CGE); Rayawng, Ban Pe, *Kerr 2734* (BM, ♀); Kaw Chang (island off se. coast), Klawng Mayom, *Kerr 6923* (BM, P, ♀), *Marcan 1329* (BM, ♀). PENINSULAR SIAM. Surat, *Sman 2365* (CGE, ♂, ♀); Surat, Panom, *Kerr 12375* (BM, ♀). Island off w. coast: P. Terutao, *Kerr 14198* (BM, ♀). Islands off e. coast: Kaw Pa-ngan, *Kerr 1235* (BM, ♀); Kaw Tao, *Kerr 12799* (BM, K, ♂).

Indochina. CAMBODIA: *Hahn 61* (P); Kamput, *Pierre 15* (P); Phom-ba, Nem-Tram-Kok, *Müller 350* (P); Pursat Prov., Pnom Barong, Roleap, *Herb. For. Cambodge 36930* (P). COCHINCHINA. *Thorel 1067* (A, BM, K, P, ♂, ♀), *Thorel s.n.*, 1862–6 (P). Baria prov.: *Chevalier 36637* (P), *Commission de la Gutta 4* (P); Xuon moc, Chevalier *36606* (P, ♀). Bien Hoa prov.: *Commission de la Gutta s.n.*, 1866 (P); Bao Chiang, *Pierre 1851*, p.p. (A, BM, K, P, ♀); Song lu, *Pierre 3777* (A, P); Trang-bom, *Chevalier 30083* (P, ♀), *Chevalier 36761* (P), *Fleury 39323* (P, ♀). Budot, *Müller 1728* (P). Saigon [? cult.], *Pierre 3377* (P, ♀). Tay ninh prov., Cay Cing, *Pierre 1851*, p.p. (L). ANNAM: Massif de la Mère et l'Enfant, *Poilane 6644* (K, P, ♀). P. CONDORE: *Perry 4699* (P).

This subspecies is consistently distinguished from the type by the hispid and not hispidulous syncarp processes, and usually also by the rounded or shallowly cordate base and rough upper surface of the leaves. In indumentum and leaf shape it is rather variable, though the hairs are usually denser and softer on both shoot and leaf than in ssp. *rigidus*. The latter feature is most marked in Burma, where, in addition, the leaves are frequently ovate. This form was described by Kurz as *A. calophylla* and is shown in King's plate (1889), drawn from *Falconer 1015* and not Kurz's own collection, as stated by King, who reversed these two collections in his discussion of the species. In Siam and Indochina the leaf shape is usually obovate-oblong and the form was described by Gagnepain as *A. asperula*. However, since the variation between the two forms is continuous, they are here united. Both species were distinguished by their authors from *A. rigidus* by the indumentum of the leaf, but, since the differences in this and in the leaf shape are not constant and those in the syncarp are so slight, it is preferable to treat the continental entity as a geographical subspecies of *A. rigidus*. The northern boundary of Malaya appears to separate the two subspecies, with the exception of Helfer's collection of ssp. *rigidus* from Tenasserim, but more material from this area is desirable to show whether there is any intergrading of characters.

Gagnepain's *A. asperula* var. *hirta* was described from sapling collections with long patent hairs on the shoot. Two Indochinese collections of *A. rigidus* ssp. *asperulus* at Paris, *Comm. de la Gutta s.n.*, 1866, and *Pierre 15*, were labelled *A. polyphema* Pers., but the native species which may have been included by Loureiro in his confused description of *Polyphema champeden*, on which this name is based, is not identifiable, although it will be further discussed under *Artocarpus integer*. The identification was not mentioned by Gagnepain in 1928.

(*To be continued*)

A YELLOW-FLOWERED FORM OF RHODODENDRON CAROLINIANUM

LEONARD F. FRISBIE

Rhododendron carolinianum Rehder f. **luteum,** forma nova.

A low, evergreen shrub of medium-compact growth. Branchlets brown with scattered scales. Leaves lanceolate, acuminate to acute at the apex, cuneate at the base, the blade to 6.3 cm. long, 2.5 cm. wide, yellowish green, glabrous above, reticulate, densely scaly below with scales separated by one-half their width, the petioles to 1.2 cm. long, scaly. Inflorescences terminal, the rachis 2 cm. long, about 6-flowered, the pedicels about 1 cm. long, scaly. Calyx-lobes 5, ca. 2.7 mm. long, scaly; corolla rotate-funnel-shaped, 4 cm. across, mimosa yellow [Horticultural Color Chart 602/1], nearly self-colored, scaly on the outside, the lobes obtuse, the tube 1.0 cm. long; stamens 10, ca. 1.5 cm. long, slightly exserted, hairy at the base; ovary oblong, ca. 1 cm. long, scaly; style glabrous. Capsule narrowly oblong, 1.3 cm. long, scaly.

Frutex humilis sempervirens, compacto-mediocriter incremens. Ramuli fusci squamis sparsis. Folia lanceolata, acuminata vel acuta, basi cuneata, lamina 6.3 cm. longa, 2.5 cm. lata, flavo-viridia, reticulata, dense squamosa. Inflorescentia terminalis, rachis 2 cm. longus, sex-floribus intextus; pedicelli ca. 1 cm. longi; corolla rotato-infundibuliformis, 4 cm. lata, "mimosa flava," prope uniformiter colorata, extus squamosa, lobis obtusis, tubulo 1.0 cm. longo; stamina 10, ca. 1.5 cm. longa, parum exserta, basi pilosa; ovarium squamosum, stilus glaber. Capsula 1.3 cm. longa, squamosa.

TYPE: Plant in cultivation, 2728 Lemons Beach Road, Tacoma 66, Washington; known only to have come from "the mountains of western North Carolina," *L. F. Frisbie*, May 15, 1958 (Herb. Arnold Arboretum).

This very handsome and distinctly different color-form of *Rhododendron carolinianum* was one of a group of native plants obtained about 1945 by Halfdan Lem of Seattle, Washington. The plants were offered to Mr. Lem as being "yellow-flowered carolinianum." He accepted the small plants, but had such small faith in the possibility of the claim that he promptly forgot about the plants in the press of other matters. In the spring of 1957 this writer on a visit to Mr. Lem's garden was attracted by one of the plants in flower. Due to my keen interest Mr. Lem let me have the form and it was brought to Tacoma. Subsequent efforts to gain information as to the exact natural location of the plants have met with no success. The possible collectors whom we have contacted have all given negative answers, and seemed to know nothing of such a form of the species, so it has proved impossible to obtain more exact information than that given above.

At the present writing the plant is thriving, is making excellent growth, and has adapted itself very well to this climate. It will make an excellent addition to the series of evergreen rhododendrons, and will be a valuable horticultural subject wherever rhododendrons are grown. Here in western Washington, where a wide range of types of the genus is grown, we are very much pleased with this new color form. The hybridizing potential of the *luteum* form is intriguing, especially so in the light of such acceptable hybrids of the typical form as 'Conewago' and 'Conestoga.'

This yellow-flowered form of *Rhododendron carolinianum* is being propagated by ground layering and every effort will be made to see that it is generally available through the Washington Rhododendron Society, Inc.

In addition to this color variation the typical form of the species with clear pink flowers is highly valued for decorative garden purposes, and a special place is reserved for the white-flowered form, *R. carolinianum* var. *album* Rehder. Good foliage, compact habit, and free flowering with chaste trusses of multiple flowers make this form a favorite which sometimes wins in rhododendron shows over all other species exhibited. The three color forms of *Rhododendron carolinianum* make a delightful combination in the garden, a grouping of true distinction. But we have found that it pays to be selective, especially with the pink and white forms of the species. Collected plants are not difficult to obtain, and persistent culling will turn up a very few plants of outstanding quality. Here in the West where the genus grows so well, some shaping and pruning are essential if one is to have compact plants.

These distinctive forms of native American rhododendron species, both evergreen and deciduous solidly substantiate the importance of the work of the selective collector, a field in which the Washington Rhododendron Society has made a notable contribution.

2728 LEMONS BEACH ROAD
TACOMA 66, WASHINGTON

ANDRODIOECISM IN THE FLOWERS OF TROCHODENDRON ARALIOIDES

HSUAN KENG *

EXISTING DESCRIPTIONS of *Trochodendron aralioides* Sieb. et Zucc., the sole living representative of the vesselless angiospermous family Trochodendraceae (Smith 1945, Lawrence 1951), are based primarily on herbarium specimens. In all the botanical works consulted the flowers are described as hermaphrodite. The literature is reviewed in detail by Smith (1945).

In the spring of 1957, from January to June, the author visited Bamboo Lake, forty miles northwest of Taipeh, Formosa, every two weeks to collect flowering buds, flowers, and fruits of *Trochodendron*. A number of trees growing naturally in the valley and on the hill slopes were examined. About half of them were found to be protandrous: during the maturation of the stamens, the styles are clasped together (*Figs. 1, 2*). The other half were found to be protogynous, with the styles recurved distally, exposing the ventral stigmatic surfaces, at a time when the stamens had not yet dehisced (*Fig. 3*). All the flowers of any one tree without exception presented the same condition, *i.e.*, they were either all protandrous or all protogynous.

In mid-April the trees were in full bloom and were being frequented by honey bees (*Apis mellifica, A. indica*) and snake-eyed butterflies (*Ypthima motschulski*). The carpels and filaments of open flowers are pale yellowish green, while the anthers are bright yellow in color. A shining, viscid fluid coats the external surface of the gynoecia in a great majority of both protandrous and protogynous flowers, although no nectar has been found. The sweet, pleasant fragrance is detectable from some distance away, especially on a sunny morning. Occasionally a few flowers appear to lack a coating of viscid fluid and remain dry.

In protogynous flowers the stamens possess well developed anther-sacs which dehisce subsequently to release normal pollen. In addition, the gynoecia are also well developed. On the other hand, in protandrous flowers, with an equally normal androecium, the styles are at first tightly clasped, only opening slightly later. The trees which bear protogynous flowers produce normal follicles and fertile seeds. However, the author failed to find a single normal follicle on those trees which bore protandrous flowers. Thus, the species appears to be androdioecious, a condition which Darwin (1896, p. 13) pointed out as being exceedingly rare among flowering plants. It would be most interesting to have reports on the floral biology of *Trochodendron* from other parts of its range, particularly from the islands of Japan.

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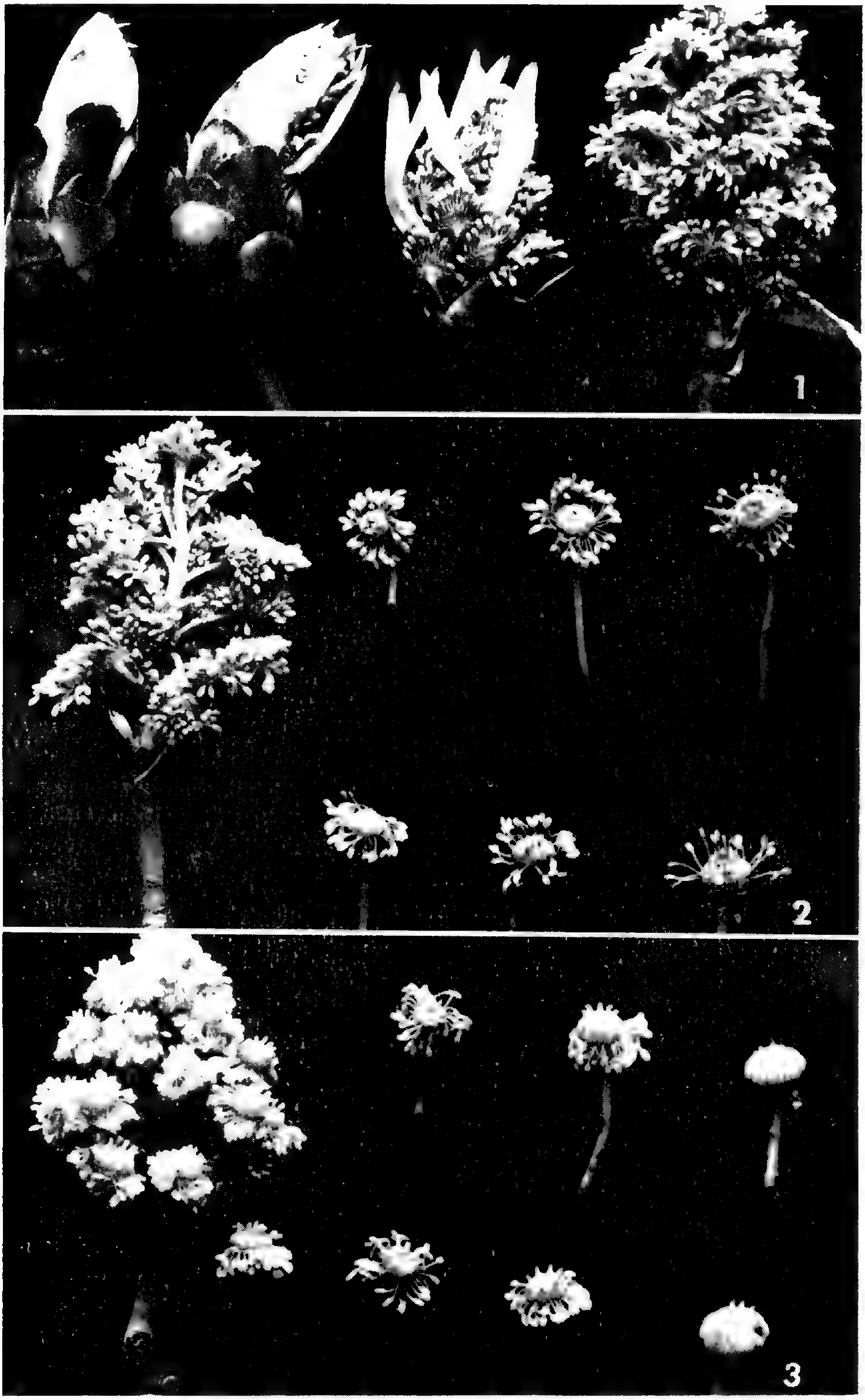
* The author wishes to express his thanks to Dr. Lincoln Constance and Dr. Herbert G. Baker for their helpful suggestions.



Trochodendron araliOIDES Sieb. & Zucc.

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UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA

EXPLANATION OF THE PLATE

FIG. 1. Stages in the unfolding of the inflorescence of *Trochodendron.* FIG. 2. Development of protandrous flowers. FIG. 3. Development of protogynous flowers. (All natural size.)

THE EMPETRACEAE AND DIAPENSIACEAE OF THE SOUTHEASTERN UNITED STATES

C. E. Wood, Jr. and R. B. Channell

The studies of Empetraceae and Diapensiaceae, two small families of both biosystematic and phylogenetic interest considered below, are part of a generic flora which is in preparation for the southeastern United States.[1] The genera of these families provide examples on a different level of complexity from those of nine families of Ranalian affinities, the treatments of which have been published previously (Jour. Arnold Arb. **39**: 296–346. 1958; **40**: 94–112. 1959). Further examples of the diversity of the plants of this area and of the problems which they present will be published as space permits in order that some of this material may be

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[1] Preliminary to a manual of the species of seed plants of this area, generic treatments of this type are intended to call attention to problems of various kinds which will require the talents of all available workers before it will be possible to understand thoroughly the plants of this large area; to bring together a large part of the information available concerning the genera which occur there; to focus attention where possible on the biosystematic aspects of each group; and to examine and clarify the confused generic lines so often found among groups of plants in the southeastern United States. Although to some the approach from the generic level may seem a roundabout one, we are confident that, by bringing together in one place information of the kind presented in the treatments below, the widest interests of taxonomy and taxonomists will be served in both research and teaching and that the ultimate goal of an understanding of the plants of the area will be reached more quickly through this approach than through the traditional one.

While one may speak of "alpha" and "omega" taxonomy and insist that one precede the other, in times such as the present with the ever increasing destruction of the natural areas of the earth — a process all too evident in the southeastern United States — it is important as never before that taxonomic problems be approached simultaneously on all levels, from the alpha to the omega, and from all directions, and that the taxonomist have the knowledge and viewpoint to do this. It is not sufficient to say "Collect now — study later." The very items the monographer or careful student of evolution may need to know are the ones which may easily be overlooked (and often are) by the well-meaning but uninformed collector. Provided with a guide to some of the critical features which need observation, with some idea as to the basis of the taxonomic complexities of a group, or with a knowledge of the gaps in the information available concerning a group of plants, a worker is in a much more favorable position to obtain critical information in the field, and to look at plants with an awareness which is lacking among those whose aim is only to collect and identify. If taxonomy as a science is to command the respect of workers in other disciplines, if it is to be both analytic and synthetic, and if a modern flora of any area is to have a firm basis in an understanding of the plants involved, the approach must be one of understanding plants as living organisms and the information considered must come from all branches of botany and from all levels — from the alpha to the omega. Generic treatments of the kind presented here may serve the interests of workers on any of these levels. Certainly a number of taxonomic and phylogenetic, as well as morphological and biological, problems will be apparent to the thoughtful reader of the descriptions, notes and references which follow. — C. E. W.

made more immediately available to those interested in the plants of eastern North America.

The general scheme of these studies is outlined in the first paper of this series (see above). It should be pointed out again, however, that the southeastern United States as defined here is bounded by and includes North Carolina, Tennessee, Arkansas and Louisiana; that the descriptions are based primarily upon the species occurring within our area, any supplementary material added for clarity being included in brackets; that the abbreviations used for periodicals are the very useful ones of Lazella Schwarten and H. W. Rickett (Abbreviations of titles of serials cited by botanists. Bull. Torrey Bot. Club **76**: 277–300. 1958); and that references which we have not seen are marked by an asterisk. All of this work, which is being conducted as a joint project of the Gray Herbarium and the Arnold Arboretum, has been made possible through the kind support of George R. Cooley and through a grant from the National Science Foundation.

The detailed drawings of the four genera are the careful work of Dorothy H. Marsh. We are indebted to H. L. Blomquist, of Duke University, and to R. K. Godfrey, of Florida State University, for their respective kindness in sending for study and use in illustration a large series of specimens of *Pyxidanthera brevifolia* and excellent fresh specimens of *Ceratiola* in fruit.

EMPETRACEAE (CROWBERRY FAMILY)[2]

A small family of evergreen shrubs of ericoid habit with numerous pulvinate leaves, inconspicuous apetalous flowers of few stamens and drupaceous fruits. Three genera of disjunct distribution and about eight species: *Empetrum* L., bicentric, with about four boreal species, primarily of arctic to subalpine distribution, and a single species in the subantarctic; *Corema* D. Don, with *C. Conradii* (Torrey) Torrey ex Loud., in widely separated areas from the Magdalen and Prince Edward islands and Nova Scotia to New Jersey, and *C. alba* (L.) D. Don in Portugal and the Azores; and the monotypic *Ceratiola* Michx. confined to our area.

The systematic position of the Empetraceae has been the subject of considerable controversy. The family has been variously allied with the Celastrales, Ericales and Sapindales. The erect ovule and ventral raphe have been considered to indicate affinities with the Sapindales. A natural group, it is perhaps best regarded as a reduced apetalous and polygamous or dioecious derivative of the Ericaceae. This view is supported by the embryological data of Samuelsson and is confirmed by the morphological studies of Hagerup. A whole series of well-marked embryological features characterizes the Ericales. These represent standard stages in Ericalean embryology and constitute a combination unknown in any other order. The Empetraceae show close correspondence in all respects. The embryol-

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[2] By R. B. Channell.

ogy of the Celastrales and Sapindales differs in so many ways as to render any link with the Empetraceae obscure indeed. The 3-colporate pollen grains are united in tetrahedral tetrads as in Ericaceae.

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1. **Ceratiola** Michx. Fl. Bor.-Am. 2: 221. 1803.

Dioecious shrubs of dry sand strands and sand hills, emitting a characteristic odor. Leaves linear-acicular, in "decussate" whorls, with a longitudinal groove on the lower surface, jointed at the base of the short petiole. Old stems roughened by petiolar sterigmata. Flowers axillary, sessile, hypogynous, the perianth consisting of 5–6 bracts and sepals. Male flowers of 2 exserted stamens, the 2-loculed anthers longitudinally dehiscent; pollen in tetrads. Female flowers with a single pistil, the 3–4 exserted stigmas divergent, flabellate-incised-pinnatifid, united into the single style arising from the summit of the ovoid, 2-locular ovary. Fruit small, greenish-yellow, drupaceous with 2 pyrenes, the seeds with a straight embryo. TYPE AND SOLE SPECIES: *Ceratiola ericoides* Michx. (*C. falcatula* Gandoger, *Empetrum aciculare* Bertol.) (Name from Greek *ceras*, horn, apparently alluding to the flabellate style-branches.) — ROSEMARY.

Often covering extensive areas, *Ceratiola* is associated with pines and oaks throughout its range from Florida to South Carolina and Mississippi, and is a more or less characteristic shrub of the *Pinus clausa*-scrub in Florida. It does not occur on the Florida Keys. In some areas, especially on coastal sand dunes, it is associated with a shrub of similar habit and stature, *Solidago* (*Chrysoma*) *pauciflosculosa* Michx. Inhabiting extremely dry situations in pinelands, in sand hammocks and on inland sand dunes, often in almost pure sand with *Selaginella arenicola* Underw. and *Cladonia*, *Ceratiola* is often ravaged by fire. In southern Florida it may be seriously parasitized by the lauraceous woevine, *Cassytha filiformis* L.

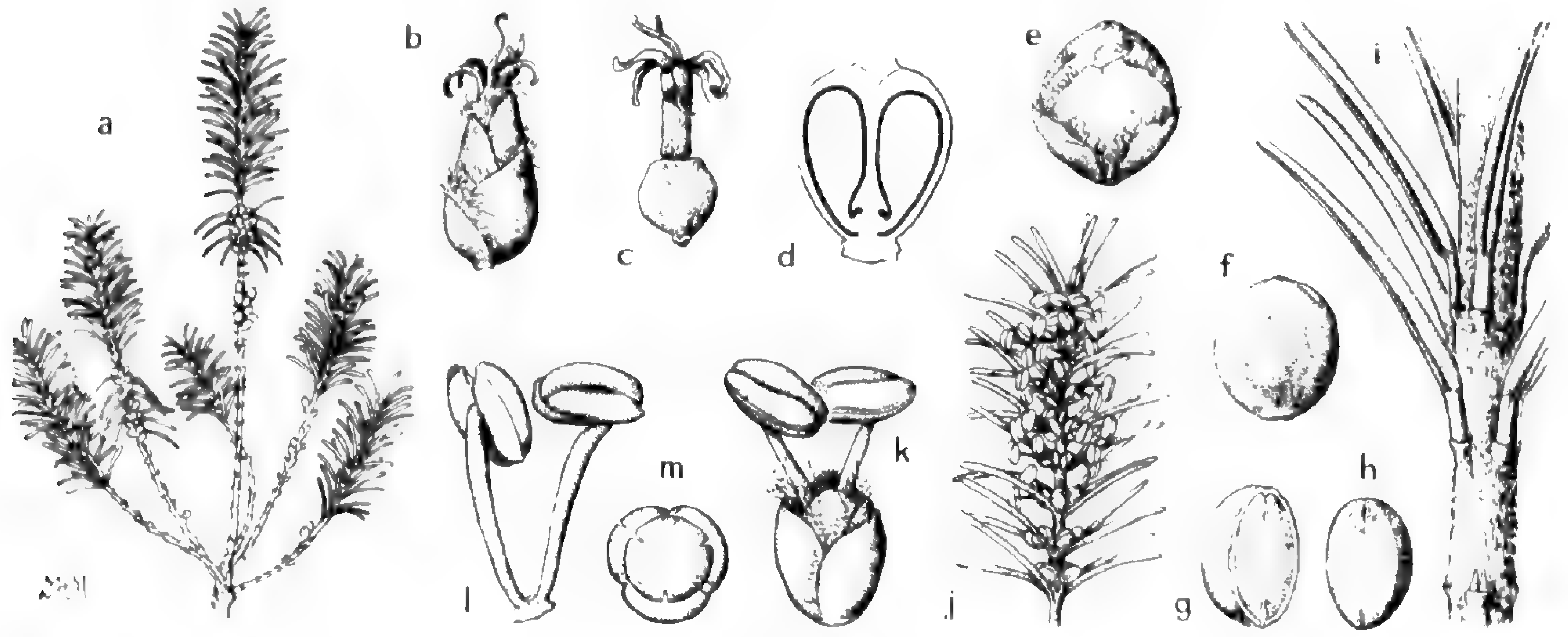

FIG. 1. **Ceratiola.** a–m, *C. ericoides*: a, habit, ♀ plant, × ½; b, ♀ flower, × 6; c, pistil, × 6; d, young ovary, semi-diagrammatic vertical section, showing two locules each with a single ascending ovule, × 12; e, mature fruit inclosed in weathered bracts and sepals, × 6; f, mature fruit free of bracts and sepals, × 6; g, pyrene inclosed in ovary wall, × 6; h, pyrene, × 6; i, portion of vegetative shoot showing position and arrangement of leaves — note articulate, pulvinate, appressed petioles, × 6; j, portion of ♂ shoot in flower, × 1; k, ♂ flower, × 6; l, stamens of a single ♂ flower, × 6; m, pollen tetrad, ca. 30 μ diameter, × ca. 300.

Usually a well-formed shrub, *Ceratiola* is very exacting in habitat and, like *Empetrum* and *Corema*, is difficult to cultivate, presumably because of a mycorrhizal relationship. The common name rosemary refers to the superficial resemblance to *Rosmarinus officinalis* L.

Little is known concerning the agent of pollination (wind?), germination and other biological features of the species.

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DIAPENSIACEAE (DIAPENSIA FAMILY)[3]

Low, evergreen herbs or subshrubs of acid soils, tufted or creeping, with simple exstipulate, alternate leaves. Flowers regular, the sepals 5, free, imbricate, the petals 5, separate or united, the corolla campanulate or funnel-shaped. Androecium typically of two whorls: an outer of 5 connivent fertile stamens, and an inner (when present) of 5 staminodia oppo-

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[3] By C. E. Wood, Jr.

site the petals; filaments adherent to the petals (and sometimes monadelphous, as well); pollen grains single, 3-colporate. Style simple, the stigma 3-lobed, the ovary 3-loculed, superior, lacking a disc at the base; ovules 2-integumented, the placentation axile. Fruit a loculicidal capsule; seeds as in Ericaceae. (Including Galacaceae of Small's Manual.)

A small family of five genera, primarily of eastern America and eastern Asia (with the exception of the circumpolar *Diapensia lapponica* L.), forming a natural group with numerous reticulate relationships. Two tribes, DIAPENSIEAE Gray and GALACINEAE Gray, generally are recognized, although variously delimited (see Gray, Drude, Diels).

The group is usually agreed to be related to the Ericales but differs from most in the simple pollen grains, the epipetalous stamens and the absence of a disc. In view of the importance accorded embryological evidence in allying the Empetraceae with the Ericales it should be noted that the embryological features of *Diapensia lapponica* do not fit with those of other members of the Ericales. Further embryological studies of other genera are highly desirable. The family is currently placed either with the Ericales or in a separate order Diapensiales. Chromosome structure and basic number are similar throughout those members of the family thus far examined. The stamens and staminodia present interesting problems in function and morphology.

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KEY TO THE GENERA OF DIAPENSIACEAE

A. Plant with small awl-like leaves; prostrate, creeping; staminodia lacking; anthers 2-locular, apparently transversely dehiscent, each locule awned on the lower side; capsule with a persistent but easily broken columella. .... 1. *Pyxidanthera*.

A. Plant rhizomatous with shining oval to orbicular leaves; 5 staminodia present.
  B. Flowers large, solitary; petals connate, crenate-undulate-toothed; anthers large, oval, 2-locular; staminodia distinct, near base of corolla; capsule with a persistent columella; seeds ovoid or spherical. .... 2. *Shortia*.

B. Flowers small, numerous, in wand-like racemes on naked scapes; petals entire, distinct; stamens and staminodia monadelphous, forming a tube adnate to the petals; anthers 1-locular; capsule without a columella; seeds angular. . . . . 3. *Galax*.

1. **Pyxidanthera** Michx. Fl. Bor.-Am. 1: 152. *pl. 17.* 1803.

Creeping, prostrate, evergreen subshrub from a woody root, the small leaves alternate, oblanceolate, awl-pointed, sessile and hairy on the upper side (at least near the base). Flowers solitary and sessile on short, densely leafy branches. Sepals concave, oblong, reddish. Corolla white, about 5–10 mm. broad, the petals united by the broad stamen-filaments to form a tube, the lobes broadly spatulate, cuneate or obovate-cuneate. Stamens alternating with the petals, the filaments white, almost petal-like, the anthers bent inward; anther locules 2, each apparently dehiscing transversely and awned at the base; staminodia lacking. Style as long as the corolla tube, increasing somewhat in length in age; ovules 4–6 in each locule of ovary. Fruit with a persistent but brittle and easily broken columella; seeds globular, regularly pitted (seldom collected). $2n = 12$. TYPE SPECIES: *P. barbulata* Michx. (Name from the Greek *pyxis*, a small box, and New Latin *anthera*, for anther, from the appearance and dehiscence of the anthers.) — PIXIE, FLOWERING-MOSS.

One or two species: *Pyxidanthera barbulata*, of sandy pine barrens, usually seasonally wet, on the coastal plain from New Jersey to Virginia, and North and South Carolina, and *P. brevifolia* Wells, of the inner coastal plain, Harnett Co., N. C. to Darlington Co., S. C. The status of this second species, which is associated with *Quercus laevis* Walt. and *Pinus australis* Michx. f. on the rolling sand hills, needs careful study, for it appears to intergrade in moister habitats with the more widespread plant. Although *P. brevifolia* when well developed is characteristic in aspect, its only distinctive features are the smaller size of all parts and the greater hairiness of the leaves and stems, characteristics which may well be attributable to the more xeric habitat and which are matched or approached by various smaller specimens from New Jersey and North Carolina.

The mechanical operation of the awned, connivent anthers, which are apparently transversely dehiscent, is probably significant in the biology of the small, white flowers which are borne abundantly in March and April. Pollen is not discharged from the anther unless the awned tip is pushed downward. A comparison with the stamens of *Diapensia* suggests that the orientation of the anther-locules has changed from vertical to horizontal in the inwardly bent anthers of this plant so that the dehiscence is not truly "transverse."

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2. **Shortia** Torrey & Gray, Am. Jour. Sci. Arts I. **42**: 48. 1842; II. **45**: 402. 1868, nom. cons.

Low, evergreen, perennial herb, forming dense clumps or carpets, the foliage combining the aspect of *Galax* and *Pyrola*. Plants spreading by horizontal rhizomes bearing clustered long-petioled, broadly elliptic to sub-orbicular truncate-emarginate, cordate, lustrous leaves, toothed along the margin, and much smaller leaves or scales. Flowers 2–3 cm. high, solitary on bracted peduncles, nodding. Sepals ovate, imbricate. Corolla open-campanulate, white, pale pink or pale blue, the petals united, the lobes undulate-crenate notched. Fertile stamens with conspicuous, 2-loculed anthers bent sharply inward and connivent in the tube; staminodia borne near the base of the corolla and incurving over the ovary. Style elongate; capsule globular, 3-valved and with a persistent columella bearing the globular or ovoid seeds. $2n = 12$. (*Sherwoodia* House; not *Shortia* Raf., 1840, nom. rejic.) TYPE SPECIES: *Shortia galacifolia* Torrey & Gray. (Dedicated to Charles Wilkens Short, 1794–1863, of Kentucky, "whose attainments and eminent services in North American botany are well known and appreciated both at home and abroad.") — SHORTIA, OCONEE-BELLS, LITTLE COLTSFOOT.

In North America a single species and in Japan, Formosa and China perhaps 9–11 species, depending upon specific and generic concepts. *Shortia galacifolia*, *S. uniflora* Maxim., of Japan, and *S. sinensis* Hemsl. form a closely related group of species with solitary flowers and staminodia. Other species with several-flowered inflorescences and partially developed, although sterile, stamens have been treated as the genus *Schizocodon* Sieb. & Zucc., while four species described from Formosa with several-flowered inflorescences and no staminodia would be placed in *Shortiopsis* Hayata. All of these species appear to be closely related, however, and are best treated as a single genus, *Shortia*. The nearest ally is the Sino-Himalayan *Berneuxia* Decne.

Shortia galacifolia, a handsome plant with an intriguing history shares in our area the special fame of *Franklinia* and "Bartram's Ixia" (*Sphenostigma coelestinum* (Bartr.) R. C. Foster). Collected by André Michaux in the Carolina mountains in 1787, the specimen was seen by Asa Gray in Paris in 1839 and was later described as a new genus. All searches for the plant were futile, but a second species described from Japan was recognized by Gray as belonging to the genus. *Shortia galacifolia* finally was rediscovered by George M. Hyams, in McDowell Co., N. C., in 1877, and, in 1886, was found by Sargent and Boynton near the junction of the Horsepasture and Toxaway Rivers in Oconee Co., S. C.

The plant is now known from two limited areas some 60 miles apart: var. *galacifolia*, primarily in the drainage of the Keowee River in Oconee and Pickens counties, S. C., Rabun Co., Ga., and Transylvania Co., N. C., and var. *brevistyla* P. A. Davies, in McDowell and Burke counties, N. C.

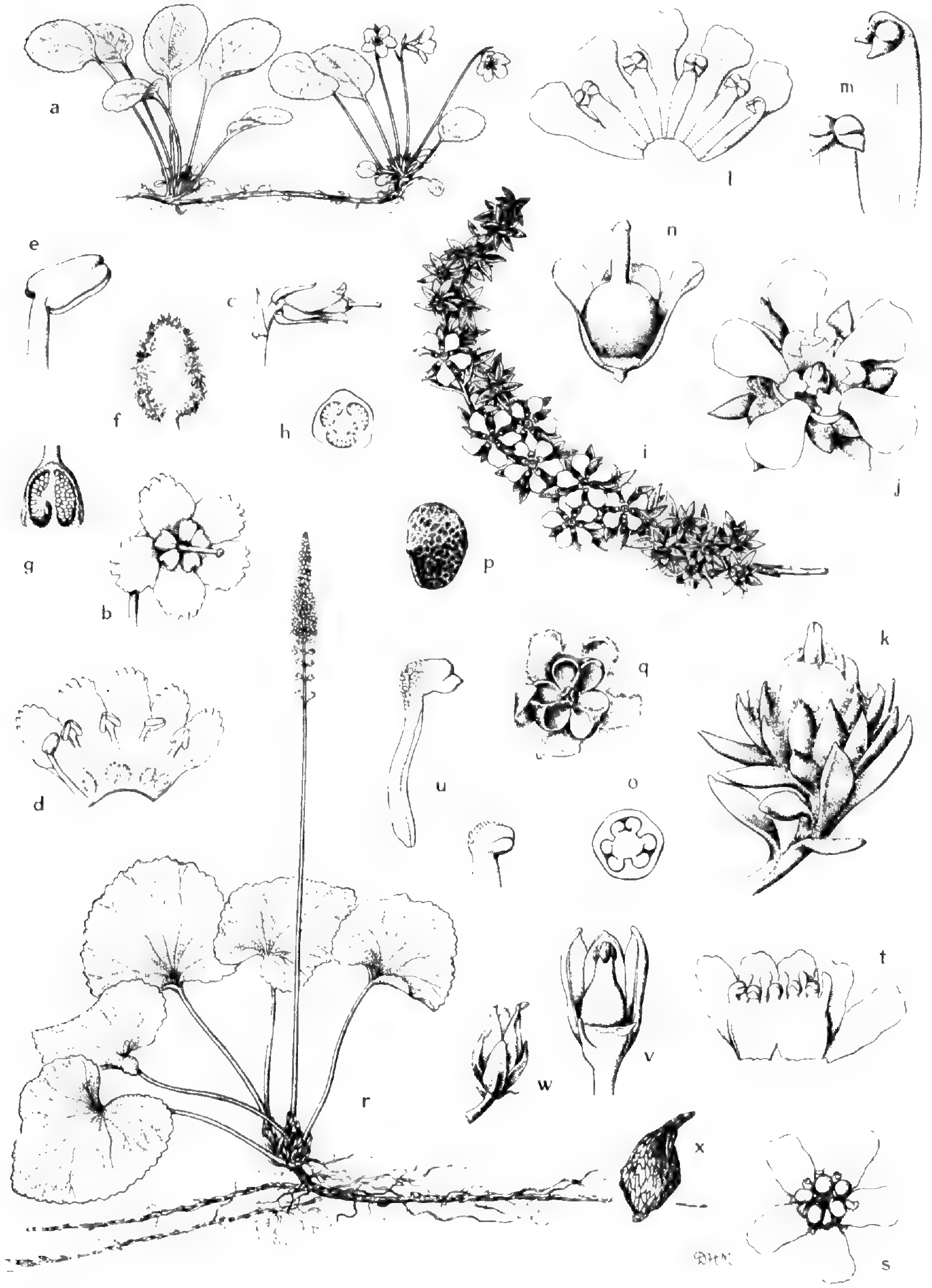

FIG. 2. DIAPENSIACEAE. a–h, **Shortia.** *S. galacifolia*: a, habit, × ¼; b, flower, × 1; c, lateral view of flower, corolla removed to show calyx and bracts, × 1; d, opened corolla, × 1; e, stamen, lateral view, × 4; f, staminodium, × 6; g, ovary, vertical section, semi-diagrammatic, × 4; h, ovary, cross section, × 4. i–q, **Pyxidanthera.** i–p, *P. barbulata*: i, habit, branchlet from above, × 1; j, flower, × 4; k, tip of flowering branchlet with flower after fall of corolla, × 4; l, opened corolla, × 4; m, stamens, × 10; n, immature fruit with calyx (2 lobes removed), × 4; o, ovary, cross section, × 10; p, seed, × 20. q, *P. brevifolia*: opened capsule from above, showing persistent but easily dislodged columella in

The two varieties differ in petal-length, -notching and -venation, length of staminodial hairs and length of styles. The ratio of length of style to length of mature ovary is 1:2.4 in the Keowee area and 1:1.3 in McDowell County. On this and other bases it appears that Michaux' specimen came from near the spot where Sargent and Boynton first found it.

Shortia is still abundant in a part of the Keowee area but should be protected from vandalism and excessive commercialism. It occurs in moderately acid soils with good aeration and usually with abundant moisture, growing best under *Rhododendron maximum* or *Tsuga*, but often in association with *Pinus Strobus*, *P. rigida*, *Liriodendron*, *Liquidambar* and *Kalmia latifolia* and various other Ericaceae. The altitudinal range is from about 600 feet (180 m.) to well above 1600 feet (500 m.) but the plant is hardy far to the north of its restricted range. The proterogynous flowers are borne in March and early April and the seeds mature from late April to May (or June). It has been suggested that the restricted distribution is related to the lack of a dispersal mechanism and to limited reproduction by seeds, for the seeds often germinate even within the capsule. However, natural reproduction by seeds is reported in Amherst Co., Virginia, and in the Keowee region.

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center, × 4. r–x, **Galax.** *G. aphylla*: r, habit, × ¼; s, flower, from above, × 4; t, opened corolla and staminal tube, × 4; u, stamen and anther, × 10; v, ovary with 3 sepals and bracteole, × 5; w, fruit, × 4; x, seed, × 20.

3. **Galax** L. Sp. Pl. 1: 200. 1753, partim, emend. Nutt. Gen. 1: 145. 1818, nom. cons.

Low herbs with scaly-bracted rhizomes forming a thick, matted tuft bearing long-petioled, round-cordate, crenate-toothed, lustrous evergreen leaves, the plant spreading by slender cord-like rhizomes which later become branched, thickened, and leaf-bearing at the tips. Flowers small (4–5 mm.), white, each with minute bracts at the base, borne in a wand-like raceme on a slender, naked scape in May (or July at higher altitudes). Sepals 1/3–1/2 the length of the oblong-spatulate petals. Petals distinct to the base, nearly erect or spreading. Filaments of 5 fertile stamens and 5 staminodia united, forming a tube adnate to the petals at the base, falling with the petals; free tips of the staminodia fleshy, nearly erect, the fertile anthers bent at right angles to the tube, connivent, each anther apparently 1-loculed and opening horizontally (actually across the top), the lower (inner) half tapering to an obtuse point. Pistil about as long as the calyx, the style short, the stigma 3-lobed. Capsule obpyriform, about 3 mm. long, without a columella, the seeds numerous, small, brown, angular, tapering, with a cellular seed coat. $2n = 12, 24$. (Not *Galax* L., 1754, nom. rejic.) TYPE AND SOLE SPECIES: *G. aphylla* L. (Name from Greek, *gala*, milk, presumably from the white flowers.) — GALAX, GALAXY, WAND-FLOWER, COLTSFOOT, BEETLEWEED, BEETLE-PLANT, SKUNK-CABBAGE.

A handsome and distinctive monotypic genus ranging from northern West Virginia and northwestern Maryland to the coastal plain of eastern Virginia and eastern North Carolina, to central Georgia, central Alabama and central Tennessee, in acid soils, generally in mesophytic associations with *Kalmia* or *Rhododendron* and other Ericaceae. The plant reaches its best development in rich, acid, humus-covered soils in the piedmont and Blue Ridge where, from North Carolina to Georgia, great quantities of the leaves, which become bronzed in winter, are gathered and sold to florists.

Galax provides one of the clearest, simplest and best studied cases of autoploidy in wild populations. Diploids occur throughout the range of the species, except in the Virginia coastal plain, where only the tetraploids are known. Tetraploid plants grow in the same habitats and areas as diploids, but are especially concentrated in the region from southern Virginia through the North Carolina mountains into South Carolina and Georgia. They appear to be absent from the northern and western parts of the range. Under the most favorable conditions the leaves of tetraploids may reach 15 cm. wide, while those of diploids attain only 10 cm. The plants are usually indistinguishable in the field, however, and no morphological distinctions other than those of size are known. No triploids and no meiotic irregularities have been reported in either diploids or tetraploids.

The apparently one-loculed anthers are strongly reminiscent of those of *Pyxidanthera* and suggest a similar mode of development. The flowers are most like those of *Pyxidanthera* (except for the presence of staminodia) but in vegetative features *Galax* suggests *Shortia*. The genus has been treated either as the sole member of the tribe GALACINEAE or has been placed there with *Shortia* and *Berneuxia*.

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ARNOLD ARBORETUM
AND
VANDERBILT UNIVERSITY

THE EFFECT OF JUVENILITY ON ROOTING OF CUTTINGS FROM APPLE SEEDLINGS

DONALD L. SMITH

IT HAS LONG BEEN KNOWN that cuttings from young seedlings can be rooted much more readily than can cuttings from mature trees. Extensive tests conducted by Gardner (1929) with seedlings of apple, pear, cherry, elm, locust, pine and spruce showed that cuttings from one-year-old seedlings rooted easily. He obtained some rooting from cuttings from two-year-old seedlings, but as the seedlings grew older it was difficult or impossible to root the cuttings taken from the upper branches.

It also has long been known that the basal part of the tree remains in the juvenile stage. More than 150 years ago Thomas Andrew Knight observed that shoots from the base of a seedling pear tree possessed juvenile characters and that scions from such shoots, when grafted on pear rootstocks, were much slower to come into fruit than scions from the bearing branches.

It is also known that cuttings taken from the lower branches of seedling trees will root more easily than cuttings taken from the tops of the mature trees (Grace, 1939; O'Rourke, 1951). The basal part of the tree appears to remain in the juvenile stage and a seedling tree can be kept in the juvenile stage indefinitely by cutting it back to the ground each year (Blair, 1955).

These observations on the relation of juvenility to ease of rooting of cuttings are of considerable significance in the clonal propagation of trees and shrubs. Clonal propagation of certain species by cuttings is essential to maintain a uniform root system. It is also essential in species such as the lilac, which suckers from the roots, if the clone is to be maintained true to type by the amateur horticulturist.

Seedling trees can be grown to maturity so that the flowers and fruits can be evaluated, but can still be propagated readily by cuttings by forcing sucker shoots from the base of the trunk. This can be done by girdling the bark near the base of the trunk or cutting the tree back nearly to the level of the ground. Less drastic methods are bark inversion or "scoring" the bark of the trunk near the base of the tree.

Tests were made on four-year-old seedlings of an ornamental apple, *Malus* 'Henry F. duPont,' grown in the Bussey Institution nursery during the summer of 1958. In June 1957 every other tree in the nursery row had a short ring of bark inverted to induce earlier flowering. The bark-inverted trees did not fruit earlier than the controls, but they did produce profuse suckering from the base of the tree. In some cases the sucker shoots bore leaves which were tri-lobed, even though the mature branches bore only entire leaves. In other cases there was little morphological difference between the juvenile and adult leaves. All of the trees tested fruited for the first time in 1958.

Cuttings from sucker shoots and from fruiting branches were taken in June. The cuttings, which were about eight inches long, were cut in half to provide basal and tip cuttings. Half of the cuttings were treated with Hormodin No. 2, while the other half were planted with no hormone treatment. The cuttings were set in wet sand in greenhouse flats, a wire frame was placed over them, and the entire flat and wire frame were enclosed in polyethylene film. The enclosed flats were set in the shade under the greenhouse bench and given no further attention until examined for rooting. The results are shown in TABLE I.

The juvenile cuttings of tree number 16155–4 rooted rather well with or without hormone treatment, but the adult cuttings rooted poorly or only moderately well, even with hormone, and very poorly, or not at all, without hormone. The juvenile cuttings of tree 16155–14 also rooted much better and earlier than did the adult cuttings. With tree 16155–21 the adult basal cuttings rooted comparatively well with hormone. In general the basal cuttings of either juvenile or adult branches rooted better than the terminal cuttings and the juvenile cuttings from the basal suckers rooted much better than the adult cuttings from fruiting branches. The cuttings which

TABLE I. **Rooting of Cuttings from Juvenile and Mature Branches**

TREE NUMBER	TYPE OF CUTTINGS	HORMONE	NUMBER OF CUTTINGS	PER CENT ROOTED AFTER WEEKS				
				2	3	4	5	6
16155–4	J,T*	+	10	40		40	50	
"	J,T	–	10			40		50
"	J,B	+	10	80		90	90	
"	J,B	–	10			80		80
"	A,T	+	10	20		20	20	
"	A,T	–	10			0		0
"	A,B	+	10	0		50	50	
"	A,B	–	10			0		10
16155–14	J,T	+	8	75	87		100	
"	J,T	–	10			20		30
"	J,B	+	8	87	87		100	
"	J,B	–	10			100		100
"	A,T	+	8	0	0		0	
"	A,T	–	10			0		10
"	A,B	+	8	0	12		62	
"	A,B	–	10			20		40
16155–21	J,T	+	9	0	33		77	
"	J,B	+	9	11	77		77	
"	A,T	+	9	0	0		22	44
"	A,B	+	9	0	44		77	

* A = Adult; J = Juvenile; T = Terminal; B = Basal.

rooted in two weeks were more likely to thrive when transplanted than those which required a longer time.

Cuttings from root suckers were also found to root more easily than cuttings from mature fruiting branches, even when the root suckers had developed six or seven feet from the base of the tree. Suckers from the roots were numerous on a *Malus sargentii* f. *rosea* hybrid (3340) which was 18 years old and growing in sod. Cuttings were made in the same manner as previously described. The results are shown in TABLE II. No rooting was obtained from the cuttings from the fruiting branches, but moderate rooting, with hormone, was produced in four weeks by cuttings from the root suckers. Evidently the roots retain their juvenility for a greater distance from the base of the tree than do the branches.

In the summer of 1957 Dr. Karl Sax found a seedling of Hopa Crab (*Malus baccata* × *pumila niedzwetzkyana*) which appeared to be promising as a dwarfing rootstock because of its thick bark — a characteristic of the extremely dwarfing rootstock varieties used in Europe. Cuttings from the original three-year-old seedling gave 91 per cent rooting in two weeks, and cuttings from lateral branches of the Hopa Crab seedling budded on *M. sargentii* f. *rosea* gave 100 per cent rooting in two weeks, using hormone (TABLE II). Even without hormone 85 per cent rooted in four weeks. These rooted cuttings were transplanted to soil, with no loss, for testing as a dwarfing rootstock and to see if they can be kept as permanent juveniles (as a source of cuttings) by keeping them cut back to the ground level each year.

TABLE II. **Rooting of Cuttings from Juvenile and Adult Seedlings**

TREE NUMBER	TYPE OF CUTTING	HORMONE	NUMBER OF CUTTINGS	PER CENT ROOTED AFTER WEEKS 2	3	4	5	6
33340	A.T.*	+	25	0		0		
"	A.T.	–	25	0		0		
"	R.T.	+	15	13		53		
Hopa Sdlg.	T	+	12	91				
"	S	+	12	100				
"	S	–	20	40		85		

* A.T. = Adult Terminal; R = Root sucker; T = Terminal; S = Secondary.

SUMMARY

Juvenile shoots from the base of fruiting seedling apple trees, induced by bark inversion, were found to root more readily than cuttings taken from the fruiting branches. Root suckers of a mature apple tree rooted well, although cuttings from the fruiting branches produced no roots, even with hormone treatment. A three-year-old seedling of Hopa Crab rooted very readily from cuttings to be tested as a dwarfing rootstock clone. The production and retention of juvenility in clonal varieties of trees and shrubs should be of value in clonal propagation.

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STUDIES IN THE GENUS COCCOLOBA, VII. A SYNOPSIS AND KEY TO THE SPECIES IN MEXICO AND CENTRAL AMERICA

Richard A. Howard

The only complete monograph of the genus *Coccoloba* was prepared by Gustav Lindau and published in Engler's Botanische Jahrbücher **13**: 106–229. 1890. Since that time many additional species have been described in the genus as the result of extensive collecting by botanists in Mexico and in the several countries of Central America. Paul Standley revised *Coccoloba* as it occurs in Mexico in his treatment of the trees and shrubs of Mexico published in 1922. More recently Standley with Julian Steyermark treated the species of Guatemala as part of their series of papers on the flora of Guatemala. In addition, lists of species, some with critical notes, will be found in the following papers. Other papers and citations are included in the text.

Allen, P. Preliminary index to the trees of the Golfito-Palmar area, Costa Rica. 37. 1952.

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In general, the genus *Coccoloba* has been overdescribed in Mexico and Central America. Of the eighty names which have been applied in published form, only thirty-three species are recognized in this paper. In large part this tendency to excessive description is due to floristic treatments which deal individually with the many small countries of Central America. Many species which were considered endemic in adjacent countries have proved to be identical instead. Several West Indian species are now recognized in the Central American flora and the corresponding Central American name has been reduced to synonymy. Seven species had been described on the basis of sterile branches from adventitious shoots. All of these have now been associated with fertile material and these names placed in synonymy. Fortunately only one such name had to be retained with a sterile holotype specimen. The failure to recognize the unisexual condition of the plants led to the duplication of specific names and several such species have now been properly associated. Two new species are described and one species has been removed from synonymy and re-established at the species rank.

Lindau in his monograph treated the species from Mexico and Central America in three sections of the genus. While these sections are useful in a preliminary assignment of species within the genus, the sections can not be maintained. When sufficient material is examined, intermediates are found and the sections grade indistinguishably into one another.

In the previously published studies[1] of the genus *Coccoloba* in the West Indies I had the advantage of extensive field work and an intimate knowledge of the variation found in the living plant. Much of the information gained in studying the West Indian species has been applied to the current study.

Many of the experienced field botanists who have described species of *Coccoloba* in Mexico and Central America have regarded the flowers as being perfect. The extensive group of herbarium specimens I have seen, as well as the living plants I have studied in Mexico and Honduras, clearly indicates, however, that the flowers are unisexual or functionally so. The pistillate flowers are normally borne singly at each nodule of the inflorescence rachis or rarely in clusters of two or three. The stamens of such flowers are rudimentary and included. The staminate flowers with pollen-producing, exserted stamens are borne in clusters of three or more.

Only a few species of Mexico and Central America have heavily coriaceous leaves or leaves much reduced in size. The leaves tend to be more pubescent than those of West Indian species. The variation in size between leaves of normal shoots and/or adventitious shoots is similar in the West Indies and in Central America. The leaves of adventitious shoots are larger, thinner and on longer petioles than those of normal shoots. Short-shoots, or at least shoots of limited growth, occurring laterally on the branches may also produce leaves smaller in size than those of shoots of normal growth. Pubescence varies with age of the leaf.

An adequate understanding of the species is best obtained from a study of staminate and pistillate flowers, fruits and leaves from both normal and adventitious shoots. I am grateful to the several collectors indicated in the text who made special efforts to get complete material for me. I have also been fortunate to be able to study nearly all the types of the species considered in this paper. I am particularly grateful to the directors and curators of the Botanisches Museum, Berlin; the Jardin Botanique de l'État, Brussels; the Royal Botanic Gardens, Kew; the Chicago Natural History Museum, Chicago; the Botanische Staatssammlung, Munich; and the University Herbarium, University of Michigan, Ann Arbor, for the significant materials sent for this study. Equally valuable but less authen-

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[1] Jour. Arnold Arb. **30**: 388–424. 1949; **37**: 317–339. 1956; **38**: 81–106. 1957; **38**: 211–242. 1957; **39**: 1–48. 1958; **40**: 68–93. 1959.

tic specimens were received on loan from the other herbaria designated by the standard abbreviations given in Index Herbariorum.

Distribution of recognized species of Coccoloba in Mexico and Central America

	GREATER ANTILLES	MEXICO	GUATEMALA	BR. HONDURAS	EL SALVADOR	HONDURAS	NICARAGUA	COSTA RICA	PANAMA	SOUTH AMERICA	LESSER ANTILLES
acapulcensis		×	×	×		×		×			
acuminata			×			×	×	×	×		
barbadensis		×	×		×						
belizensis			×	×		×	×				
caracasana		×	×		×		×	×	×		
chiapensis		×				×					
cozumelensis		×	×	×			×				
darienensis									×		
diversifolia	×	×	×								
goldmannii		×									
hondurensis		×	×	×		×					
humboldtii		×									
lasseri									×		
lehmannii								×	×	×	
liebmannii		×									
lindeniana		×									
lindaviana						×					
× *lundellii*				×							
manzanillensis									×		
matudai		×									
montana		×	×	×	×						
nicaraguensis							×				
novogranatensis			×						×	×	×
obovata								×	×	×	
padiformis								×	×	×	
parimensis									×	×	
reflexiflora		×	×	×		×					
spicata		×		×							
standleyana								×			
swartzii	×			×		×					×
tuerckheimii			×			×	×	×	×		
uvifera	×	×	×	×	×	×	×	×	×	×	×
venosa	×	×	×		×	×	×	×		×	×

The following list contains the names used for species of *Coccoloba* in Mexico and Central America. These names either were used in floras, lists or monographic treatments or apply to taxa based on specimens collected in this area. The generic name *Coccoloba* has been conserved. *Coccolobis* is regarded as an orthographic variant and all binomials published under this spelling are also known as *Coccoloba.* The many transfers made by Otto Kuntze to the genus *Uvifera* have been omitted. All of the names in this list are discussed in the text under the recognized specific name. Varieties which are treated as distinct from the species are listed below. Varieties not listed are transferred with the species.

Campderia floribunda = **Coccoloba venosa**
C. lindeniana = **Coccoloba lindeniana**
C. mexicana = **Coccoloba venosa**
C. nematostachya = **Coccoloba manzanillensis**
Coccoloba acapulcensis Standley
C. acuminata HBK.
C. alagoensis major = **C. venosa**
C. allenii = **C. lehmannii**
C. anisophylla = **C. chiapensis**
C. barbadensis Jacquin
C. belizensis Standley
C. bracteolosa = **C. parimensis**
C. browniana = **C. acapulcensis**
C. cardiophylla = **C. acapulcensis**
C. caracasana Meisner
C. changuinolana = **C. lehmannii**
C. chiapensis Standley
C. colonensis = **C. reflexiflora**
C. coronata = **C. spicata**
C. corozalensis = **C. swartzii**
C. cozumelensis Hemsley
C. darienensis Howard
C. diversifolia Jacquin
C. emarginata = **Neomillspaughia emarginata** (Gross) Blake
C. escuintlensis = **C. montana**
C. excelsa glabra = **C. parimensis**
C. excoriata = **C. venosa**
C. floribunda = **C. venosa**
C. fluviatilis = **C. barbadensis**
C. gentlei = **C. swartzii**
C. goldmannii Standley
C. grandifolia Standley = **C. liebmannii**
C. guatemalensis = **C. tuerckheimii**
C. hirsuta = **C. belizensis**
C. hondurensis Lundell
C. humboldtii Meisner
C. jurgenseni = **C. barbadensis**
C. lancifolia = **C. diversifolia**
C. lapathifolia = **C. liebmannii**
C. laurifolia = **C. diversifolia**
Coccoloba lasseri Lundell
C. latifolia = **C. tuerckheimii**
C. lehmannii Lindau
C. leptostachya = **C. barbadensis**
C. liebmanni = **C. liebmannii**
C. liebmannii Lindau
C. lindaviana Howard
C. lindeniana (Bentham) Lindau
C. lundellii = **C. × lundellii**
C. × lundellii Standley
C. macrophylla = **C. rugosa** Desfontaines
C. manzanillensis Beurling
C. manzinellensis = **C. manzanillensis**
C. marginata = **C. hondurensis**
C. masoni = **C. barbadensis**
C. matudai Lundell
C. mayana = **C. barbadensis**
C. molinae = **C. venosa**
C. montana Standley
C. nematostachya = **C. manzanillensis**
C. nicaraguensis Standley & L. Williams
C. nivea = **C. venosa**
C. novogranatensis Lindau
C. oaxacensis = **C. barbadensis**
C. obovata HBK.
C. orizabae = **C. humboldtii**
C. padiformis Meisner
C. parimensis Bentham
C. petrophila = **C. humboldtii**
C. pubescens = **C. liebmannii**
C. roseiflora = **C. padiformis**
C. reflexiflora Standley
C. riparia = **C. obovata**
C. sessiliflora = **C. barbadensis**
C. schiedeana = **C. barbadensis**
C. schippii = **C. montana**
C. spicata Lundell
C. steyermarkii = **C. montana**
C. standleyana Allen
C. strobilulifera = **C. acuminata**
C. suborbicularis = *C. × lundellii*
C. swartzii Meisner

Coccoloba tuerckheimii Donnell Smith
C. umbilicata = **C. pyrifolia** Desfontaines
C. uvifera Linnaeus
C. venosa Linnaeus
Coccoloba *waittii* = **C. novogranatensis**
C. wercklei = **C. acapulcensis**
C. yucatana = **C. cozumelensis**
Uvifera lehmanni = **Coccoloba lehmannii**

The following is a synoptic key to the species of Mexico and Central America. To be fully applicable, the key requires both flowers and fruit. It does not apply to sterile material, particularly that of adventitious shoots.

Following the key, the species are listed in alphabetical order with a citation of specimens seen and a discussion of the nomenclature adopted. The countries are considered in order from north to south, with the states, provinces, districts, etc., in each country being listed alphabetically.

KEY TO THE SPECIES

1. Petioles arising from above the base of the ocrea, the diameter of the leaf scar smaller than the distance from the base of the leaf scar to the base of the ocrea.

(Species inadequately known: Leaves lanceolate-ovate, deciduous, the young leaves turning black on drying. .... *C. nicaraguensis*.)

2. Inflorescence paniculate.

3. Inflorescence branches few; leaf base rounded or cordate; fruit spherical, rounded at the base. .... *C. lasseri*.

3. Inflorescence many-branched; leaf blade acute at the apex, the base decurrent on the petiole; fruit oval, stalked at the base. .... *C. tuerckheimii*.

2. Inflorescence racemose or spicate.

4. Inflorescence racemose.

5. Leaves narrowly oblong to narrowly elliptic. ..... *C. lindaviana*.

5. Leaves cordate, elliptic or obovate-elliptic.

6. Leaves cordate, the base strongly cordate, occasionally peltate; flowering and fruiting pedicels 5–15 mm. long; fruit globose, 1 cm. diameter, or abnormally obovoid and 2.5 cm. long; ocreae splitting longitudinally, flaring, the petiole appearing winged at the base; the inflorescence ocrea often appearing spathe-like. .... *C. acapulcensis*.

6. Leaves elliptic to obovate-elliptic, flowering and fruiting pedicels shorter; ocrea not flaring if split.

7. Leaves usually narrowed to a cordate-auriculate base; ocreolae conspicuous, papery, flaring; flowers never reflexed; fruit globose, conspicuously coronate. .. *C. novogranatensis*.

7. Leaves rounded at the base or narrowed to an obtuse base; ocreolae small and inconspicuous, the flowers commonly reflexed; fruit narrowed at the base and obtuse, at most slightly coronate, at the apex. .... *C. reflexiflora*.

4. Inflorescence spicate, the fruits essentially sessile.

8. Leaves tan-colored when dry, the petioles usually grayish green; leaf blades acute to obtuse at the apex; fruit globose, obtuse at the apex. .... *C. spicata*.

8. Leaves and petioles turning dark brown or black on drying; leaf blades acuminate at the apex; fruit elongate, the achene stoutly coronate at the apex. . . . . *C. obovata.*

1. Petioles arising from the base of the ocrea, the base of the leaf scar at or close to the base of the ocrea.
   (Species inadequately known: . . . . *C. standleyana.*)
   9. Inflorescence paniculate.
      10. Flowering pedicels stout, not exceeding the ocreolae; young stems, ocreae and inflorescence rachis conspicuously puberulent or tomentose to pilose on adventitious shoots, the pubescence golden or chestnut-colored; the terminal buds large, conspicuously club-shaped, swollen and rounded at the apex, the ocrea of the terminal bud commonly subcalyptrate; fruit globose, not narrowed to a stalk at the base, obtuse or rounded, not coronate, at the apex. . . . . *C. belizensis.*
      10. Flowering pedicels tenuous, exceeding or up to twice the length of the ocreolae; young stems, ocreae and inflorescence rachis puberulent, the pubescence commonly noticeable only with a lens; the terminal bud slender, acute at the apex, the ocrea splitting laterally; mature fruits not known. . . . . *C. matudai.*
   9. Inflorescence racemose or spicate.
      11. Inflorescence racemose; the flowers and fruits borne on pedicels which exceed the bracts and the ocreolae.
         12. Lianas; leaf blade umbonate between the veins. . . *C. parimensis.*
         12. Trees or shrubs, at most the ends of the branches rarely scrambling.
            13. Leaves as broad as or broader than long, orbicular to broadly oblong, apex rounded to emarginate.
               14. Fruits 1–2.5 cm. long, obtuse or rounded at the apex, at most very slightly coronate, usually slightly stalked at the base.
                  15. Leaves usually much broader than long, the base strongly cordate with one lobe of the blade usually slightly overlapping the petiole. . . . . . . *C. uvifera.*
                  15. Leaves usually orbicular, the base of the blade essentially rounded or obtuse. . . . . *C.* × *lundellii.*
               14. Fruits less than 1 cm. long.
                  16. Fruit strongly coronate at the apex, the base rounded; leaf blades persistently pubescent only along the midrib and primary veins or glabrate. . . . . *C. barbadensis* hybrid.
                  16. Fruit elongate, the perianth lobes distinct on the upper 1/3 or 1/2 of the fruit; leaf blades persistently pubescent on the lower surface. . . . . *C. goldmannii.*
            13. Leaves noticeably longer than broad.
               17. Leaves elliptic-lanceolate in outline, acuminate to long-acuminate at the apex, cuneate or rounded to an obtuse asymmetrical base; petioles 2–6 mm. long. . . . . *C. chiapensis.*
               17. Leaves not of this type.
                  18. Foliar ocreae 3–5 cm. long, membranaceous or

chartaceous, silky pubescent, fruit coronate at the apex, the crown surrounded by the distinct perianth lobes, these fused below. . . . . . . *C. manzanillensis.*

18. Foliar ocreae 1–2 cm. long, coriaceous, or if chartaceous, not silky pubescent.

19. Achene surrounded by the expanded perianth lobes, these free nearly to the base.

20. Leaves elliptic to elliptic-oblong, the flower clusters distinct on the inflorescence rachis. . . . . *C. lehmannii.*

20. Leaves narrowly oblong or obovate-oblong, the inflorescence of closely associated flower clusters and these not clearly distinct on the rachis and not appearing interrupted.

21. Leaves obovate-oblong, broadest above the middle; midrib and veins usually pubescent below, blades persistently barbate in the axils of the primary veins. . . . . *C. venosa.*

21. Leaves narrowly oblong, broadest at middle; leaves glabrous below. . . . . *C. darienensis.*

19. Achene surrounded by the expanded hypanthium, the perianth lobes coronate or surrounding the upper third of the achene.

22. Fruit conspicuously coronate.

23. Leaves lanceolate-ovate in outline, ocreae glabrous; pedicels in fruit several times as long as the thickness of the inflorescence rachis. . . . . *C. diversifolia.*

23. Leaves broader, ovate-oblong to obovate-elliptic in outline, ocreae puberulent; fruiting pedicels not longer than the thickness of the inflorescence rachis.

24. Fruiting pedicels shorter than the ocreolae; leaves usually rounded or with a short, bluntly acute apex, concolorous. . . . . *C. barbadensis.*

24. Fruiting pedicels slightly longer than the ocreolae; leaves usually with a short but sharply acuminate apex, dark or black on the upper surface and lighter below. . . . . *C. hondurensis.*

22. Fruit obtuse at the apex, the perianth lobes imbricate over the obtuse apex of the achene.

25. Leaves persistently pubescent below, the margin entire but usually conspicuously crispate to undulate. .... *C. liebmannii.*

25. Leaves glabrous, the ocreae or petioles puberulent or glabrous, margin of the blade entire or flat or slightly recurved but not crispate-undulate.

    26. Ocreolae conspicuous in flower and fruit, membranaceous and flaring; fruit as broad as or broader than long, rounded to slightly stalked at the base, slightly acute at the apex. .... *C. montana.*

    26. Ocreolae small and inconspicuous, appressed and not flaring; fruit longer than broad, rounded or obtuse at the apex and the base.

        27. Upper leaf surface with the ultimate venation conspicuously reticulate when dry, the ocreae and petioles puberulent. . . *C. humboldtii.*

        27. Upper leaf surface plain between the primary veins, the ultimate venation not evident; ocreae and petioles glabrous. .... *C. padiformis.*

11. Inflorescence spicate, the pedicels shorter than the bracts and ocreolae in flower and fruit or, if protruding beyond the ocreolae, the visible portion less than the diameter of the inflorescence axis.

    28. Inflorescence rachis swollen at the flower clusters and tapering below them, the flowers appearing at an acute angle to the axis; the lobes of the perianth expanded in fruit and covering at least the upper half of the achene. .... *C. acuminata.*

    28. Inflorescence rachis of uniform thickness and not expanded to each flower cluster, the flowers borne flat or at right angles to the axis.

        29. Ocreolae conspicuous in flower and fruit, membranaceous or chartaceous.

            30. Leaves narrowly oblong, acute to acuminate at the apex; fruit not known. .... *C. lindeniana.*

            30. Leaves broadly oblong to orbicular, often broader than long, the apex rounded or emarginate; the lobes of the perianth expanded in fruit and covering more than half of the achene. .... *C. caracasana.*

        29. Ocreolae small, not conspicuous in flower or fruit; the

hypanthium surrounding the achene in fruit, the perianth lobes imbricate or coronate.

31. Leaves narrowly ovate to ovate-lanceolate, generally cordate at the base, rarely rounded or obtuse, acuminate at the apex, generally drying to a pale tan color, the petioles usually grayish when dry, the petioles and ocreolae puberulent but rarely tomentose; the blades 3–9 cm. long. .... *C. cozumelensis.*
31. Leaves rounded or obtuse at the base, acute or obtuse at the apex, the blades turning dark on drying, the petiole almost black when dry; glabrous (in Central America).
    32. Leaves of fertile branches generally with blades 12–20 cm. long and 8–12 cm. broad; inflorescences densely flowered; fruit obtuse at the apex and only slightly coronate. .... *C. hondurensis.*
    32. Leaves of fertile branches usually with blades 7–11 cm. long and 5–6.5 cm. broad; inflorescence axis sparsely flowered, the flower clusters distinct and separated; fruit rounded at the apex and distinctly coronate. .... *C. swartzii.*

Coccoloba acapulcensis Standley, Proc. Biol. Soc. Wash. **33**: 66–67. 1920.

Coccoloba cardiophylla Standley, Publ. Field Mus. Bot. **8**: 8. 1930.
Coccoloba browniana Standley, Trop. Woods **10**: 4. 1927.
Coccoloba wercklei Standley, Publ. Field Mus. Bot. **4**: 304. 1929.

It is unfortunate that the oldest name applicable to this species is based on anomalous material. To the present, *Coccoloba acapulcensis* has been distinguished by the peltate leaves and the large fruits. The collections cited below, made since the type collection of the species, show clearly that leaves with peltate, cordate or rounded bases may be found on the same shoot. Miranda (Anal. Inst. Biol. México **14**: 29. 1943) reports that peltate leaves appear abundantly on all young specimens of *C. acapulcensis* but that the cordate base is more frequent on older plants. The fruits of this species are larger than is usual in the genus *Coccoloba*; however, the fruits of the holotype appear to be abnormal, the probable result of an insect attack. Similar abnormal pedicels also occur on the type specimens of the other species which I have examined and which I now consider to be synonymous with *C. acapulcensis*.

Lundell (Lloydia **2**: 83. 1939) placed *Coccoloba cardiophylla* in the synonymy of *C. browniana* and reported the affinities of the species to be with *C. wercklei*, of Costa Rica, and *C. acapulcensis*, of Guerrero, Mexico. In the original description of *C. wercklei* Standley suggested that his new species is a relative of the Honduran *C. browniana* but distinct from it in that *C. browniana* bears pedicels only 5 mm. long. The series of specimens cited, however, shows the full range of variation in the length of the pedicel between flowering and mature fruiting conditions, as well as the differences in the pedicel length of the male and female flowers. It is clear to me that all four species must be grouped together under the oldest accepted name, which is *C. acapulcensis.*

México. GUERRERO: Acapulco, *MacDaniels 249* (F), *Haenke 1120* (F), *1125* (F), *Palmer 399* (US-type of *C. acapulcensis*; GH, NY); Tecpán de Galiana, *Hinton 14118* (F, GH). YUCATÁN: Chichén Itzá, *Bequaert 28* (A, F), *C. L. & A. A. Lundell 7471* (DS, F, MICH), *7513* (A, DS, F, MICH); Kancabdzonot, *Gaumer & sons 23865* (DS, F, GH), *23905* (F); Quintana Roo, *C. L. & A. A. Lundell 7644* (MICH); Ebtún, *C. L. & A. A. Lundell 7534* (A, DS, F, MICH); without specific location, *Gaumer 24013* (F-type of *C. cardiophylla;* A, GH). **Guatemala.** EL PROGRESSO: Barranquilla, *Steyermark 46428* (F). HUEHUETENANGO: Between Democracia and canyon of Chamusú, *Steyermark 51229* (F); Paso del Boquerón, *Steyermark 51152* (F). JUTIAPA: Quebrada above Ovejero, *Standley 77647* (F). **British Honduras.** ORANGE WALK DISTRICT: Honey Camp, *Lundell 514* (A, DS, F, GH). **Honduras.** COMAYAGUA: Comayagua, *Standley & Chacón 5126* (F), *5383* (F), *5484* (F), *6012* (F); El Banco, *Rodriguez 2374* (F, GH); Río Selguapa, *Rodriguez 2616* (F, GH); Siguatepeque, *Yuncker, Dawson & Youse 6138* (F, GH, MICH). YORO: Coyoles, *Yuncker, Koepper & Wagner 8071* (F, GH, MICH); Olanchito, *Record & Kuylen H–54* (US-type of *C. browniana;* GH, Y). **Costa Rica.** El Coyolar, *Wercklé s.n.* (US 865109-type of *C. wercklei*); San Pedro de San Ramón, *Brenes 21872* (F).

Coccoloba acuminata HBK. Nov. Gen. 2: 176. 1817.

Coccoloba acuminata var. *pubescens* Lindau, Bot. Jahrb. 13: 193. 1890.
Coccoloba acuminata var. *glabra* Lindau, l.c. 194.
Coccoloba strobilulifera Meisner, Fl. Bras. 5(1): 25. 1855.

Lindau was correct in concluding that *Coccoloba strobilulifera* Meisner is the same as *C. acuminata*. I have examined the specimens cited by Meisner and Lindau and have also seen this species in the field. On the basis of these observations, I find it impossible to recognize the two varieties that Lindau established on a characteristic of the pubescence. The variation in the amount of pubescence seems to be related to the age and vigor of the plant. Pubescence is present on the young leaves and shoots but is less conspicuous, or the hairs are broken off so that only the clear hair bases remain, on older specimens. Certainly all intermediate stages can be found between the material cited by Lindau as *C. acuminata* var. *pubescens* and that cited as var. *glabra*.

In addition to the material cited below, I have seen collections from Colombia, Venezuela, British Guiana, Brazil, Ecuador and Peru. The type is *Humboldt 1479*, collected along the Río Magdalena, near Mompox, Colombia. Lindau did not select a type for his var. *glabra*, but the type of *C. strobilulifera* Meisner is *Moritz*, without number and without definite locality in Colombia. Lindau places this species in synonymy under his var. *glabra*.

Guatemala. IZABAL: Quebradas, *Pittier 8592* (GH); between Bananera and Sioux Station, *Steyermark 38986* (F, MICH). **Honduras.** ATLÁNTIDA: Near Tela, *Mitchell 82* (F, GH); near Tela, *Standley 54710* (A, F); La Fragua, *Standley*

55720 (F); vicinity of Tela, *Standley 56867* (F); vicinity of San Alejo, *Standley 7771* (F); between Tela and Lancetilla, *Yuncker 4645* (A, F, GH, MICH). CORTÉS: La Lima, *Johansen 45* (A, F); Río Piedras near San Pedro Sula, *Molino 3417* (F); La Lima, *Standley & Chacón 7556* (F), *Williams & Molina 12485* (F). YORO: Near Progresso, *W. D. Hottle 1* (F), *Record & Kuylen H–44* (GH), *Standley 55013* (A, F); Coyoles, *Yuncker, Koepper & Wagner 8034* (F, MICH), *8061* (F, GH, MICH). Department unspecified: Coyol, *Carleton 495* (A, GH); Highland Creek, Pto. Sierra, *Wilson 84* (F). **Nicaragua.** ZELAYA: La Esperanza, Río Grande, *Molina 2109* (F), *2136* (F, GH). Department unspecified: Region of Braggman's Bluff, *Englesing 183* (F, Y), *229* (F, Y). **Costa Rica.** ALAJUELA: Vicinity of Capulín, Río Grande de Tárcoles, *Standley 40189* (F). PUNTARENAS: Canton de Osa, Palmar Norte to Cañablancal, *Allen 5226* (GH, MICH). **Panamá.** CANAL ZONE: Barro Colorado Island, *Aviles 74, 976* (F), *L.H. & E.Z. Bailey 616* (GH), *Bangham 378* (A, F), *Starry 223* (F), *Wilson 22, 140* (F), *Woodworth & Vestal 397* (A, F); Juan Mina, Chagres River, *Bartlett & Lasser 16321* (MICH); Gamboa Reach, *Maggs II 39* (F); Frijoles, *Maxon 4707* (F, GH); Gamboa, *Pittier 2608* (F, GH, MO); Upper Chilibre River, *Seibert 1510* (MO); Quebrada Bonita, *Steyermark & Allen 17194* (MICH, MO). DARIEN: Tucuti, Chepigana, *M. E. & R. A. Terry 1381* (A, F, MO); Yape, *Allen 850* (F, GH, MO); location unspecified, *MacBride 2676* (F). Province unspecified: Maume & Gorgone, *Wagner s.n.* (M); Marraganti, *Williams s.n.* (NY). Location unspecified: *Weddell s.n.* (GH, P).

Coccoloba barbadensis Jacquin, Enum. 36. 1760, Obs. Bot. 1: 18. *pl. 8.* 1764; Howard, Jour. Arnold Arb. 37: 317–339. 1956.

Coccoloba barbadensis var. *mexicana* Meisner, DC. Prodr. **14**: 153. 1856.
Coccoloba schiedeana Lindau, Bot. Jahrb. **13**: 187. 1890.
Coccoloba jurgenseni Lindau, Bot. Jahrb. **13**: 188. 1890.
Coccoloba leptostachya Bentham, Bot. Sulph. 159. 1856.
Coccoloba oaxacensis Gross, Repert. Sp. Nov. **12**: 219. 1913.
Coccoloba mayana Lundell, Bull. Torrey Club **64**: 547. 1937.
Coccoloba masoni Lundell, Lloydia **2**: 8. 1939.
Coccoloba fluviatilis Lundell, Contr. Univ. Mich. Herb. **7**: 8. 1942.

In the second paper of this series (Jour. Arnold Arb. **37**: 317–339. 1956), I considered the correct identification and application of the names *Coccoloba swartzii* Meisner and *C. barbadensis* Jacq. The former name had been overlooked by recent workers on the floras of the Antillean Islands and the latter name had been misapplied. I concluded that the material which is properly called *C. swartzii* was first identified by Lindau as *C. barbadensis* and that later he and all recent authors on the West Indian flora used the name *C. diversifolia* Jacq. for the same material.

Coccoloba barbadensis Jacq. was described twice by Jacquin, first in his Enumeratio, and later, supported by an illustration, in his Observationum Botanicarum. A definite location was not given for the species and recent authors have assumed from the name that the island of Barbados was implied. However, in the British Museum (Natural History) there are two sheets which can be referred to the Jacquin description and illustration and these are significant in the correct application of the name. One of these, from the Miller herbarium, is obviously the material illustrated by Jacquin. Moreover, it bears the Houston catalogue reference which Jacquin cites in the synonymy of his *Coccoloba barbadensis*. Houston collected in Campeche (Yucatán) and his specimen is accurately matched in many of the collections cited below.

In his monograph of the genus *Coccoloba* for De Candolle's Prodromus, Meisner assumed that *C. barbadensis* came from the West Indies and so created a variety, *C. barbadensis* var. *mexicana*, for a Schiede specimen from Mexico. Lindau (Bot. Jahrb. 13: 187. 1890) recognized the variety as a species which he named *Coccoloba schiedeana*, citing in synonymy *C. barbadensis* var. *mexicana* Meisner. Lindau cited additional material, all of which, with the exception of one collection, I have now seen. These are all clearly comparable to the original Jacquin material; thus, *C. barbadensis* Jacq. must henceforth be considered in the flora of Mexico and Central America.

Of the two old specimens in the British Museum (Natural History), one represents a sterile adventitious shoot and the other a vigorous shoot with an old inflorescence from which the fruits have fallen. In all probability, therefore, it will be impossible to describe the fruit which accompanied this original sheet. However, with a knowledge of the variation found in other species of *Coccoloba* in such characteristics as leaf shape, size of petiole, presence or absence of pubescence and length of fruiting pedicels, it is possible to make an accurate comparison with more recent collections. It is clear that *C. barbadensis* has puberulent to tomentose ocreae and inflorescence rachises, although in age these become glabrous. Also, the leaves are coriaceous and the leaf shape, particularly at the base, is variable. As in other species of *Coccoloba*, the plants are dioecious and the pistillate flowers, and later the fruits, are borne on short pedicels which in length barely exceed the ocreolae. The fruit, coronate at the apex, is rounded at the base and not attenuated into a stipe.

The variations with age and environment in these characteristics have caused *Coccoloba barbadensis* to be described many times. Seven species are assigned to the synonymy of *C. barbadensis* in this paper alone. Three additional apparently unpublished names have been applied to the specimens in various herbaria. The original variety which Meisner described is also placed in synonymy with the species. Three of these newly recognized synonyms represent only sexual variations, i.e., staminate versus pistillate plants, in the comparisons given by the original authors. Two species were originally distinguished through the failure of the author to recognize the loss of, or to see the residual, pubescence. One species was based on an abnormal fascination of the inflorescence and two others were based on size and texture differences of the leaves. When considered alone or with only the material cited by the original authors, several of the species which I have reduced to synonymy might well represent clones or local populations. When considered with the wealth of material cited below, the differences become of little taxonomic value. It appears desirable to treat *Coccoloba barbadensis* as a widespread species of central and southern Mexico and northern Central America, recognizing the considerable variation in leaf size, shape and texture.

Two excellent series of collections by Dr. Robert Dressler made in the states of Veracruz and Guerrero, Mexico, show the variation in leaf-size, -shape and -pubescence to be found on single plants.

Coccoloba leptostachya Bentham has been a troublesome name. Bentham described this plant, without citing a collection, in reporting on the Botany of the Sulphur Expedition. The locality was given as Libertad in Colombia, and recent collections from Colombia and Panama have been assigned to this species. However, examination of the type material in the Herbarium at the Royal Botanical Gardens at Kew shows clearly that the specimen on which Bentham based the species is a Barclay collection which represents *C. barbadensis.* Other species from the Sulphur voyage reportedly collected in "Libertad in Colombia" have more recently been recognized as Central American and, in several instances, the collection is believed to have come from Libertad in El Salvador. *Coccoloba leptostachya* appears to me to be a similar example of the incorrect citation of a locality. The recent collection *Carlson 563* (F) from "Finca Santa Emilia west of La Libertad at or near sea level" in El Salvador is a perfect match for the Barclay specimen. No material comparable to the type of *C. leptostachya* has been seen from Colombia.

In his monograph Lindau distinguishes *Coccoloba jurgenseni* from *C. schiedeana* on the basis of a glabrous inflorescence rachis in the former and a pubescent one in the latter. The distinction is inadequate, especially since the holotype of *C. jurgenseni*, *Jurgensen 157* (G) shows a slight puberulence within the range of variation expected in this genus.

Coccoloba oaxacensis Gross was reduced to the synynomy of *C. schiedeana* by Standley in his treatment of the trees and shrubs of Mexico. He reported at the time that he had "seen no material of *C. oaxacensis*, and it may be a distinct species." I have examined the holotype in the Berlin herbarium but find no reason to maintain *C. oaxacensis* as a species.

Coccoloba mayana Lundell was based on a staminate flowering specimen collected by Lundell on the bank of the Río San Pedro de Martir above El Paso in the Department of Petén, Guatemala. Lundell reported that the species was found only in wet soils on river banks and around "aguadas." *Coccoloba mayana*, he states, "is related to *Coccoloba schiedeana* Lindau, from which it differs in having longer racemes, nodes 1- or 2-flowered, larger flowers, and suborbicular perianth lobes." None of these characteristics is of specific value. At best, *C. mayana* as conceived by Lundell is an ecological variation, distinct only in having smaller and thinner leaves, but it does not seem to be worth a subspecific category. *Coccoloba barbadensis* is a variable species and, judging from the collections seen, occurs primarily in drier areas. Plants from other departments in Guatemala show larger leaves of thinner texture and are thus intermediate between the type collection of *C. mayana* and *C. barbadensis.*

Coccoloba masoni Lundell was based on a collection by H. L. Mason from Maria Magdalena Island of the Tres Marias Islands off the coast of

Nayarit, Mexico. Lundell recognized the dioecious condition of the flowers, the obovate or oval leaf shape and the pilose pubescence in the axils and on the veins of the leaves as distinguishing characteristics of this species. Two other collections from the same island group, one made earlier and one made later than the Mason specimen, show more clearly the range of variation in leaf-shape and -pubescence and indicate that *C. masoni* and the Mason collection on which it is based are the same as *C. barbadensis.* Only a few recent floras have recognized the dioecious nature of *Coccoloba.* At present it appears that all species are functionally unisexual and the dioecious character is not of specific value in the case of *C. masoni.*

In describing *Coccoloba fluviatilis,* Lundell placed his new species in a group which included *C. jurgenseni* and *C. mayana,* both of which are here included in *C. barbadensis.* Lundell felt that *C. fluviatilis* was distinct because of "large glabrous leaves, subcordate at the base, the stout petioles up to 1.7 cm. long, the glabrous rachis of the inflorescences, and the subsessile fruits." However, all of the size and shape characteristics mentioned by Lundell can be found in many of the single collections cited. The "glabrous" characteristic, however, is an error, for pubescence can be found on the terminal buds and in the axils of the leaves on the holotype, although the plants do become glabrate in the clonal material which Lundell studied.

Seler 1642 from Arroyo de San Carlos, in Mexico, was designated by Gross as the type of an apparently unpublished species named for the large, fasciated inflorescence axis. Many of Gross' new species have been published in obscure papers, so it is possible that this name may be in print. The fasciated inflorescence rachis is relatively common in other species of the genus and has been seen in three additional collections cited below. The Seler collection is clearly identical with the material assigned to this species.

The collection by Edward Palmer which was distributed with the letter "G" in place of a collector's number bears an unpublished name attributed to Rose. This name refers to the sessile flowers, but the collection is not distinct from *C. barbadensis.*

The specimen attributed to Galeotti and numbered *7218* has been cited and annotated by Lindau as *C. schiedeana.* The material, however, is a mixed collection containing in part *C. barbadensis* and *C. venosa.*

México. CAMPECHE: Champotón, *Flores 1934* (F); Mundo Nuevo, *Karwinsky 733b* (LE). CHIAPAS: Escuintla, *Matuda 2028* (A, DS, F, MICH); Javalinero, Palenque, *Matuda 3634* (A, F, MICH); Malpaso, near Siltepec, *Matuda 4517* (MICH-type of *C. fluviatilis*; A, F); Chicomuselo, *Matuda 15627* (F); Montecristo, *Matuda 15948* (F); Nandolopez, Acapetahua, *Matuda 16642* (BR, F); Mojarra, Tonalá, *Matuda 17139* (F); Mapastepec, *Matuda 17517* (F); Monserrate, *Purpus 275* (LE, US). COLIMA: Paso del Río, *Emrick 168* (F); Manzanillo, *Ferris 6209* (DS), *Palmer "G"* (B, GH, NY); Colima, *Palmer 90* (A, C, MICH). GUERRERO: La Mina near Atoyac, *Dressler 1798a, 1798b, 1798c* (GH); Vallecitos, Montes de Oca, *Hinton 10209* (DS, MICH), *10221* (DS, LE, MICH); Vallecitos, Llano de Oca, *Hinton 11781* (DS, LE, MICH); Sierrita, El Limón, Galeana, *Hinton 14137* (F, GH); Chilpancingo, *Kenoyer C–277* (MICH); La Copradilla, *Langlassé 134* (B, GH); El Trienta, *C.L. & A.A. Lundell 12588* (MICH); Dos Arroyos, *Nelson 7029* (GH, NY); Acapulco, *Palmer 344* (A, GH), *602* (A, F, GH, MICH). Jalisco: Navidad, *McVaugh 11903* (MICH); Tuxpan, *Mexia 1051* (A, F, GH). Michoacán: San Naranjillo, Coalcomán, *Hinton 13943* (GH); La Placita, *Turner 2028* (MICH). Nayarit: Acaponeta, *Rose 1414* (NY), *Rose, Standley & Russell 14399* (NY); Magdalena Island, Tres Marias Islands, *Elmore 1B3* (F, MICH), *Nelson 4315* (GH), *Mason 1806* (F-holotype of *C. masoni*; A, DS, GH, MICH), *Maltby 167* (NY); San Blas, *Ferris 5331* (A, DS); Ixitlán, *Viereck 1193* (US). Oaxaca: Rincón San Antonio, *Endlich* (B-holotype of *C. oaxacensis*); Dunes del'Oc. Pacifique, *Galeotti 7218*, in part (BR, K, P); Pinotepa Nacional, *Jurgensen 157* (G-type *C. jurgenseni*; F-photo & fragment; B, K); Between Llano Grande and Pinotepa, *Nelson 2334* (GH); Puerto Angel, *Reiche 574* (M); Arroyo de San Carlos, *Seler 1642* (B, GH); Almoloya, *L. Williams 9906* (F, W). Sinaloa: Labradas, *Ferris & Mexia 5291* (A, DS). Veracruz: Laguna Encantada, east of San Andrés Tuxtla, *Dressler 1804a, 1804b, 1804c* (GH), *Nelson 452* (A); Tantoyuca, *Ervendberg 364* (GH, K, P); Savana de Mata de Don Juan, *Karwinsky 734, 735* (LE); Tajín, Papantla, *Kelley 65a* (GH); Laguna Tamiahua, south of Tampico, *LeSueur 100* (F); location unspecified, *Liebmann s.n.* (B); Mirador, *Ross 802* (M); Tierra Blanca, *Ross 883* (M); Zacualpan, *Purpus 12022* (F, MICH); Rancho Camarón, *Purpus 13068* (A, F, GH, MICH); Fortin, near Zacualpan, *Purpus 2428* (A, F, GH); Papantla, *Schiede s.n.* (LE-type of *C. barbadensis* var. *mexicana* and *C. schiedeana* by implication; B). State unspecified: location unspecified, *Houston s.n.* (BM-type of *C. barbadensis*); *Sessé & Mociño 950, 5434* (F).

Guatemala. Escuintla: Naranjo, *J. Donnell Smith 2496* (F, GH); San José, *Standley 63998* (F); Río Guacalate, northwest of Escuintla, *Standley 89345, 89350* (F, MICH); Río Michatoya, southeast of Escuintla, *Standley 89054, 89060* (F, MICH). Huehuetenango: Ciénaga de Lagartero below Miramar, *Steyermark 51488* (A, F). Petén: La Libertad, *Aquilar 275* (F, MICH, W), *313* (A, MICH), *Lundell 3230* (F, GH, MICH), *3212, 3340* (F, MICH); El Paso, *Lundell 1498* (MICH-holotype of *C. mayana*; DS, GH). Quezaltenango: Río Ocosito, *J. Donnell Smith 1481* (F, GH). Retalhuleu: Champerico, *Standley 66593, 66602, 66631* (F); between Nueva Linda and Champerico, *Standley 87699, 87721* (F); Retalhuleu.*Standley 88818* (F). San Marcos: Ocós, *Steyermark 37780* (F). Santa Rosa: Guazacapán, *Standley 78603* (F); Chiquimulilla, *Standley 78785, 79175, 79243* (F); La Sepultura, west of Chiquimulilla, *Standley 79378* (F). Suchitepéquez: South of Tiquisate, *Steyermark 47807* (F).

Salvador. Ahuachapán: Ahuachapán, *Standley & Padilla 2615* (F), *Standley 20313* (GH, MICH). La Libertad: Libertad, *Barclay s.n.* (K-type of *C. leptostachya*), *Carlson 563* (F). Santa Ana: Santa Ana, *Standley 20404* (GH). Sonsonate: Acajutla, *Standley 21895, 21974* (GH).

The following collections are also assigned to *Coccoloba barbadensis*, but probably represent a hybrid complex. The specimens are all staminate, with sterile, insect-infested fruits on tenuous pedicels twice as long as the ocreolae. The leaves appear to be more coriaceous and the margins are revolute. The leaves are shiny on the upper surface, although this may be an artifact of preservation.

Guatemala. Alta Verapaz: Laguna Sapalá, *Steyermark 44899* (F). Petén:

Laguna Petexbatúm, *Steyermark 46224* (A, F); Along Río Santa Mónica between Cedral and Ceibal, *Steyermark 46040* (F, MICH), *46160* (F).

The series of collections cited below appears to represent a different hybrid population limited to the state of Sinaloa and found only in the coastal areas. The probable parents are *Coccoloba barbadensis* Jacq. and *C. uvifera* L., although in general the leaves are smaller than in either of these. Leaf texture, as well as the size and shape of the fruit, indicate a relationship to *C. barbadensis*. The leaf shape, especially at the base and apex of the blade, and the venation show similarities to *C. uvifera*. However, in contrast with most of the recognized *C. uvifera* hybrids from the West Indies and with *C.* × *lundellii* of Central America, *C. uvifera* seems to be the less dominant parent in this hybrid. Fruits of two types have been found, one essentially globose but strongly coronate and the other more or less oblong and obtusely to slightly coronate at the apex. The first type closely approaches the fruit of *C. barbadensis* and all fruits opened have fully developed embryos and endosperm. The second type shows the influence of *C. uvifera* and all fruits examined had either rudimentary seed development or were sterile.

Mexico. SINALOA: Altata, *Rose 1359* (NY); Culiacán, *J. Gonzalez Ortega 6583* (DS, GH, M), *Palmer 1518* (GH, NY); Elota, *J. Gonzalez Ortega 5879* (DS, GH, M); La Concha, *Gentry 6804* (F, GH); Mazatlán, *Howell 10559* (A), *Rose, Standley & Russell 14035* (NY); Villa Union, *Rose, Standley & Russell 13953* (NY); locality unspecified, *J. Gonzalez Ortega 7203* (F).

Most of these specimens were identified as *Coccoloba goldmanii* or *C. masoni*. The former is a distinct species, but is known from the type and one other collection. It may, in fact, be related here as part of this hybrid population or be one of the parents in place of *C. barbadensis*. *Coccoloba* needs a special study in Sinaloa and southern Chihuahua. *Coccoloba masoni* Lundell is clearly referable to typical *C. barbadensis* Jacq.

Coccoloba belizensis Standley, Trop. Woods **16**: 38. 1928.

Coccoloba hirsuta Standley, Publ. Field Mus. Bot. **4**: 303. 1929.

Coccoloba belizensis Standley is a clearly defined species and one which is easily recognized. The relatively large, globular terminal buds with tawny to chestnut-brown pubescence are distinctive even on sterile or adventitious shoots. The pubescent inflorescence is branched and consists of racemes arranged as a panicle of nearly equal branches. The leaf size varies considerably in fertile material as well as on sterile shoots which are presumably adventitious. Both staminate and pistillate plants are represented in the collections cited. The mature achene is surrounded by a fleshy perianth which seems to be formed by the equal enlargement of the perianth lobes and the hypanthium.

In the Berlin Herbarium there is a specimen studied by Gross which bears an unpublished herbarium name honoring the collector, Campbell. Much of Gross' work on *Coccoloba* appeared as small notes in miscellaneous papers. Thus it is possible that this specific name has been published and, if so, it antedates *C. belizensis*.

Coccoloba hirsuta Standley was based on sterile material. The type, *Standley 54802*, as well as the cotype *52823*, was collected in the Lancetilla Valley, near Tela, Honduras. Standley noted the undesirability of basing species on sterile material, but felt that this species was easily recognizable by the "copious long pubescence of the leaves." In their treatment of the genus *Coccoloba* for the Flora of Guatemala (Fieldiana Bot. **24**: 114. 1946) Standley and Steyermark continued to recognize *C. hirsuta* as a distinct species, referring to, but not citing additional specimens from, Guatemala and thus extending the range. I have seen two collections from the Department of Izabal, *Steyermark 38185* and *Standley 72945*, which are among those which must have been seen by Standley and Steyermark. These authors suggest that *C. hirsuta* "will be found to have panicled racemes, and to be closely related to *C. Tuerckheimii*." I am unable to distinguish between material annotated "*C. hirsuta*" by Standley and Steyermark and cited by Standley and that of occasional sterile specimens which the same authors assigned to *C. belizensis*. Such collections as *C. & W. von Hagen 1344* from the Department of Colón, Honduras, and *Lundell 2756* from the Department of Petén, Guatemala, approach *C. hirsuta* in the amount and type of pubescence. The Von Hagen collection is sterile and was taken from a 75–100-foot tree. This specimen may be an adventitious shoot comparable to the type of *C. hirsuta*, for the terminal bud is the same in size and shape, but there is less copious pubescence on the stem and much less on the leaves. The Lundell collection grades easily into fertile material which can be clearly defined as *C. belizensis* and which is found in the same area.

Guatemala. ALTA VERAPAZ: Chirreacté, *Standley 91620, 91672* (F); between Sachaj and Sacacac, *Steyermark 45157a* (F). IZABAL: between Bananera and La Presa in Montaña del Mico, *Steyermark 38185, 38186* (F); Escoba, *Standley 72945* (F). PETÉN: La Libertad, *Lundell 3463* (F, MICH); Monte Santa Teresa, *Lundell 2736* (F), *2756* (MICH). **British Honduras.** COROZAL DISTRICT: San Roque, *Gentle 554* (F); Corozal, Orange Walk Rd., *Gentle 4967* (F, MICH); Corozal, Pachacan Rd., *Lundell 4784* (A, F, MICH). EL CAYO DISTRICT: San Agustin, *Lundell 6812* (F, GH, MICH). ORANGE WALK DISTRICT: Honey Camp, *Lundell 637* (DS, F, GH, MICH, US). STANN CREEK DISTRICT: Carib Reserve, *Gentle 3088* (MICH); Mullins River, *Gentle 3365, 3369* (A, MICH); Silk Grass Creek Reserve, *Gentle 2982* (MICH); Stann Creek, *Gentle 2964* (A, MICH); Stann Creek Valley, *Stevenson 7* (US-holotype; A, F, Y). TOLEDO DISTRICT: Jenkins Creek, *Gentle 4080* (A, MICH). District unspecified: Belize, *Campbell 117* (B); Crique Negra, *Stevenson 104* (F, Y); All Pines, *Schipp 794* (A, F, GH, MICH); Tower Hill Estate, *Karling 14* (F, GH). **Honduras.** ATLÁNTIDA: Lancetilla Valley near Tela, *Howard, Briggs, et al. 451* (A), *Standley 52823* (F), *53555* (A, F), *54802* (F-type of *C. hirsuta*; A); San Alejo, *Standley 7971* (F); San Juan near Tela, *Yuncker 4817* (A, F, MICH); Tela, *Standley 53402* (A, F). COLÓN: Guarunta, *C. & W. von Hagen 1344* (F). **Nicaragua.** Eastern Nicaragua, *Shank 93* (Y).

Coccoloba caracasana Meisner, DC. Prod. **14:** 157. 1856.

Coccoloba caracasana forma *glabra* Lindau, Bot. Jahrb. **13:** 211. 1890.

This species was formerly considered to have orbicular leaves, but the large number of specimens examined indicates that a broadly oblong leaf is more characteristic than a strictly orbicular one. Considerable variation in leaf size and shape is found in the species. Leaves of adventitious shoots may have nearly ovate blades up to 34 cm. long and 28 cm. wide on petioles to 4 cm. long. The straw-colored ocreolae are membranaceous, with several occurring at each nodule because of the presence of numerous flowers, several of which are frequently aborted. In fruit the lobes of the perianth expand to cover more than the upper half of the achene.

The forma *glabra* which Lindau described is scarcely worthy of recognition since the density and persistence of the pubescence varies in single collections and on single plants.

In addition to the specimens cited below, the species is known from Venezuela and Colombia and possibly farther south along the Andes. The type has been cited both as *Humboldt 732* and as *Bonpland 732*. One collection cites only Caracas, Venezuela, as the locality, while another bears a label referring to the "valley of Araguensibus."

México. CHIAPAS: Las Garzas, Acapetagua, *Matuda 2677* (A, DS, F, MICH), *2806* (A, MICH); Mapastepec, *Matuda 17516* (F); Tapachula, *Matuda 17704* (F). **Guatemala.** ESCUINTLA: Iztapa, *J. R. Johnston 1171* (F); San José, *Standley 64232* (F, MICH), *64019*, *64190* (F). JUTIAPA: Between Trapiche Vargas & Asunción Mita, *Steyermark 31792* (F). RETALHULEU: Between Nueva Linda and Champerico, *Standley 87673* (F). SANTA ROSA: Santa Rosa, *Ørsted 668* (M); Capulín, *Standley 79592* (F); Los Cerritos region, Capulín, *Standley 79607*, *79563* (F, MICH). SUCHITEPÉQUEZ: Tiquisate, *Steyermark 47700* (F). **El Salvador.** LA PAZ: Zacatecoluca, *Calderon 305* (GH). LA UNIÓN: Laguna de Maquigüe, *Standley 20977* (GH). SAN MIGUEL: San Miguel, *Standley 21139* (GH); Laguna Jaguay, San Miguel, *Fassett 28813* (A); Laguna de Olomega, *Standley 20990* (GH). SAN SALVADOR: San Salvador, *Renson 139* (NY), *Standley 23611* (F, GH). SAN VICENTE: San Vicente, *Standley 21261* (F, GH), *Standley & Padilla 3702* (F). SANTA ANA: Hacienda la Barra, *Carlson 1031* (F). SONSONATE: San Antonio del Monte, *Standley 22171* (GH). **Nicaragua.** CHINANDEGA: Chichigalpa, *Standley 11187*, *11334* (F). CHONTALES: Juigalpa, *Standley 9302*, *9305* (F). GRANADA: Granada, *Baker 2435* (A, MICH). LEÓN: La Paz, *Baker 2272* (GH). Locality unspecified: *C. Wright s.n.* (GH); *Ørsted 670*, *671* (C). **Costa Rica.** GUANACASTE: between Bebedero and Taboga, *Brenes 12562* (F); Filadelfia, *Echeverria 295* (F); Nicoya, *Tonduz 13799* (F, G, GH), *13974* (G, GH); Isla de Chira, *Valerio 1467* (F); Santa Ana de Nicoya, *León 989* (F). Province unspecified: Los Loros, *Brenes 22056* (F). Locality unspecified: *Hoffmann 292* (B), *Warscewicz s.n.* (B). **Panamá.** CANAL ZONE: Ancón, *Pittier 2730* (US); Gorgas Memorial Laboratory grounds, *White 106* (F, GH, MO); Río Agua Salud near Frijoles, *Piper 5848* (GH); Victoria Fill near Miraflores Locks, *Allen 1701* (F, GH, MO, NY). CHIRIQUÍ: Progreso, *Cooper & Slater 270* (F). LOS SANTOS: La Jagua, *Bartlett & Lasser 16382* (MICH). PANAMÁ: Sabanas Road, *Gillespie P-34*, *P-34a* (DS); Chepo, *Kluge 25* (F, NY).

Coccoloba chiapensis Standley, Proc. Biol. Soc. Wash. **33**: 67. 1920.

Coccoloba anisophylla Standley, Publ. Field Mus. Bot. **4**: 303. 1929.

Coccoloba anisophylla was based on sterile material, but Standley reported that "the form of the leaves is quite different from that of any other Central American species." On studying the material cited by Standley and being unable to distinguish *C. chiapensis* from *C. anisophylla*, I have referred the latter to the synonymy of *C. chiapensis*. This species is distinct in having leaves which are oblong to elliptic, broadest near the middle, tapering to an acuminate apex and narrowing to an abruptly obtuse and asymmetrical base. Only staminate flowers are known for this species and additional material is needed. Sterile specimens may resemble *C. novogranatensis* but can be distinguished by the basal origin of the petiole and by the pubescence.

México. CHIAPAS: Finca Irlanda, *Purpus 7699* (US-holotype of *C. chiapensis*; B, GH, NY); location unspecified, *Purpus 7599* (GH, NY). **Honduras.** ATLÁNTIDA: Lancetilla Valley near Tela, *Standley 53260* (F-holotype of *C. anisophylla*; A), *53364*, *54840* (A, F).

Coccoloba cozumelensis Hemsley, Biol. Am. Centr. **4**: 108. 1887.

Coccoloba yucatana Lindau, Bot. Jahrb. **13**: 190. 1890.

Coccoloba cozumelensis is readily recognized but difficult to define and separate in a key. The species seems amply distinct on the basis of the pale tan color of the leaves which often dry a lighter yellow-brown on the lower surface, and the sessile fruits which are obtuse at the apex with the perianth lobes not at all coronate. Also, the petioles are puberulent and along the midrib and veins on the lower leaf surface there is a characteristic crispate pubescence.

Some specimens of *Coccoloba cozumelensis* grade into the Central American phase of *C. swartzii* and it is possible that a hybrid complex exists in coastal areas where these species occur together. Since I have insufficient material to resolve this problem, the key characteristics used here apply to plants represented by the distinctive holotypes of each.

Two recent collections from the state of Chiapas are referred here. One collection, *Margery C. Carlson 2071*, made at Tuxtla Gutiérrez, is annotated as a new species by Standley and Williams. The name used refers to the tenuous spike. This collection, in flowering condition, is intermediate between typical material of *C. cozumelensis* and specimens referred to *C. spicata*, but other than the larger leaves of *Carlson 2071*, I find no reason for recognizing the collection as a new species. The second collection, *Dressler 1408*, from El Real, Chiapas, is intermediate between typical *C. cozumelensis* and the Carlson collection.

Standley placed *Coccoloba yucatana* in the synonymy of *C. cozumelensis*. I have re-examined authentic material of this and confirm his decision.

México. CAMPECHE: Tuxpeña, *Lundell 853* (A, DS, F, GH, MICH). CHIAPAS:

Tuxtla Gutiérrez, *Carlson 2071* (F, NY); El Real, east of Ocosingo, *Dressler 1408* (GH). Quintana Roo: Cozumel, *Gaumer 18* (B-holotype of *C. yucatana*; GH, K); Cobá, *C.L. & A.A. Lundell 7804* (A, DS, F, M, MICH), *7830* (A, DS, F, MICH). Tabasco: Reforma, Balancán, *Matuda 3173* (A, MICH). **British Honduras.** Belize District: Maskall, *Gentle 1068* (A, F, GH, MICH), *1349* (A, F, MICH). Corozal District: San Antonio, *Bartlett 13031* (A, F, MICH), *Lundell 4815* (A, F, MICH); Corozal, *Gentle 524* (F, MICH). El Cayo District: Little Mountain Pine Ridge, *Bartlett 13060a* (MICH); Mountain Pine Ridge, San Agustín, *Lundell 6648* (DS, F, GH, MICH). Orange Walk District: Honey Camp, *Meyer 50 (F)*. **Guatemala.** Izabal: Río Dulce, *Wilson 387* (F). Petén: Carmelita, *Egler 42–249* (F); La Libertad, *Lundell 3570* (F, GH, MICH).

Coccoloba darienensis, sp. nov.

Arbor, 12 m., ramulis teretibus, glabris; ocreis chartaceis, oblique truncatis, 1 cm. longis, glandulis (?) resinosis, adpressis; petiolis ad basem ocreis gerentibus, teretibus, supra canaliculatis, glabris, 7–11 mm. longis; laminis anguste oblongis vel lanceolati-oblongis, apice acutis vel breviter acuminatis, basi acutis, 10.5 × 3.5 vel 14.5 × 5 cm. longislatisque glabris, tenuiter coriaceis, nerviis primariis 9 vel 10, arcuato-adscendentibus; inflorescentibus racemosis, 8–14 cm. longis, floribus crebris, nodulis confluentibus, pedunculis 1 cm. longis, rachis striatis, puberulentibus; floribus ignotis, bracteis ovatis vel oblongis, apice obtusis, 1 mm. longis, puberulentibus vel breviter pilosis, ocreolis membranaceis, raro bracteolisque puberulentibus vel apice ciliatis; pedicellis fructiferis 1 mm. longis, glabris; fructu ovoideo basi rotundato, 5–6 mm. longo, 5 mm. diametro, obtuse trigono, hypanthio non manifesto, lobis perianthii ad basem distinctibus, late ovatis, imbricatis, acheniis nitidis, nigris.

Panamá. Darien: Pinogana, *P. H. Allen 934* (GH-type; F, MO).

This collection had been identified as *Coccoloba acuminata*, which is certainly a related species. The strongly divided fruiting perianth would allow this species to be placed in Lindau's section *Campderia*. *Coccoloba darienensis* is distinct from *C. acuminata* on the many-flowered inflorescence in which the flowers are confluent, not clustered, and the axis is terete but striate or grooved and not swollen below each nodule. Furthermore, *C. darienensis* differs in the evident fruiting pedicels, while *C. acuminata* can be regarded as having only spicate inflorescences without evident pedicels in fruit.

Coccoloba diversifolia Jacquin, Enum. Pl. 19. 1760.

Coccoloba laurifolia Lundell, Bull. Torrey Club **66:** 594. 1939, and authors, possibly Jacquin, Hort. Schoenbr. **3:** 9. *t. 267.* 1798.
Coccoloba lancifolia Lundell, Bull. Torrey Club **66:** 593. 1939.

I have previously discussed the proper application of the epithet *Coccoloba diversifolia* Jacq. (Jour. Arnold Arb. **30**: 421–424. 1949). All recent publications, however, have used *C. laurifolia* Jacq. for material more properly called *C. diversifolia*. *Coccoloba laurifolia*, based on material from Caracas, Venezuela, was described and illustrated by Jacquin, but I have been unable to find any collections from northern South America which exactly duplicate the characteristics which he illustrated. It is probable that *C. laurifolia* is the same as *C. diversifolia*, described by Jacquin twenty-eight years earlier. Oddly enough, no specimens of this which could be attributed to Jacquin have been seen in European herbaria, although a few specimens collected from cultivated plants and labelled "*C. laurifolia* Jacq." are present in the herbaria at Berlin, Leningrad and Geneva. However, all of these are true *C. diversifolia* and fail to compare favorably with the original illustration of *C. laurifolia* Jacq.

Lundell compares *Coccoloba lancifolia* with the original description of *C. laurifolia*, reporting that his new species differs in its small, lanceolate and pointed leaves. *Coccoloba diversifolia*, as its name implies, is a variable species in respect to leaf shape, but in all the characteristics which I can observe, it is the same as *C. lancifolia*. In their treatment of the genus for Guatemala (Fieldiana Bot. **24**: 114. 1946), Standley and Steyermark placed *C. lancifolia* Lundell in synonymy of *C. laurifolia*, but without comment. I concur with their decision, but call the species *C. diversifolia* Jacq. The small leaf size and the pointed apex can be found in many populations of *C. diversifolia*, especially in Cuba, the Bahamas and the Florida Keys.

This is the first time that this common West Indian species has been recognized in Central America and Mexico.

México. QUINTANA ROO: Lago San José, *Frère Arsène s.n.* (B). SAN LUIS POTOSÍ: Tamazunchale, *Edwards 921* (F). **Guatemala.** ALTA VERAPAZ: Cerro Cinajá, *Steyermark 45669* (A, F, MICH). IZABAL: Bay of Santo Tomás, *Steyermark 39232* (F), *39351* (F, MICH), *39357*, *39363* (F).

British Honduras. COROZAL DISTRICT: Location unspecified, *Gentle 231* (F, MICH, NY); Consejo, *Lundell 4945* (F, MICH). District unspecified: Jacinto Hills, *Schipp 1200* (MICH-holotype of *C. lancifolia*; A, GH, W).

Coccoloba emarginata Jacquin, Enum. Syst. Pl. 37. 1760.

This species was described by Jacquin in 1760 and illustrated in his Observationum Botanicarum in 1764 (*tab. 9*). It is based on a specimen from the herbarium of Mygind but no locality is given. The species was compared with the Hispaniolan *Coccoloba leoganensis* Jacq., which I have recognized (Jour. Arnold Arb. **39**: 28–30. 1958), but which is better known in that flora as *C. rotundifolia* Meisn., a later homonym. Lindau was unable to place the Jacquin species and so listed it as of uncertain identity.

The situation here is similar to that of *Coccoloba barbadensis*. The specimen which Jacquin described must have come from the Yucatán Peninsula of Mexico. The illustration, although of a sterile plant, is an excellent one and is obviously the same as *Neomillspaughia emarginata* (Gross) Blake (Bull. Torrey Club **48**: 84. 1921), the basionym of which is *Podopterus emarginatus* Gross (Repert. Sp. Nov. **12**: 218. 1913). Gross' species is based on *Seler 5600* from Yucatán, Mexico. Since the combination has already been made, I can only add *Coccoloba emarginata* Jacquin to the synonymy of *Neomillspaughia emarginata* (Gross) Blake and thereby dispose of a troublesome and misplaced ancient epithet in the genus *Coccoloba.*

Coccoloba goldmanii Standley, Contr. U.S. Nat. Herb. **23**: 245. 1922.

This distinctive species from the drier areas of northern Mexico has not been recollected in the past sixty years. Cited below are the Goldman collection made in 1898 and the Hartman collection made in 1891. The latter was misidentified as *Coccoloba orizabae. Coccoloba goldmanii* is recognized by the nearly orbicular leaves which are persistent short pubescent below and which possess a conspicuous network of veins on the lower surface. The flowers are unknown. The ellipsoidal fruits are not coronate and the lobes of the fruiting perianth cover the upper half of the achene, the hypanthium the lower half.

México. CHIHUAHUA: Apajcachi, *Hartman 535* (GH). SINALOA: Valley of Río Fuerte, *Goldman 245* (US-holotype; GH).

Coccoloba hondurensis Lundell, Bull. Torrey Club **66**: 591. 1939.

Coccoloba marginata J. Donnell Smith, Enum. Plant. Guat. **6**: 36. 1903, not Benth.

In describing this species, Lundell states, "the specimens show considerable variation, especially in leaf shape, inflorescence, and fruits but all appear to be referable to a single species. . . . Collections of *C. hondurensis* have been referred to *C. Schiedeana* Lindau, *C. marginata* Benth., *C. barbadensis* Jacq., and *C. leptostachya* Benth. I have not been able to associate the species with any of these."

It is unfortunate that Lundell did not state how he distinguished *C. hondurensis* from the other species he lists. Standley and Steyermark (Fieldiana Bot. **24**: 116. 1946) refer *C. hondurensis* to the synonymy of *C. schiedeana* Lindau in their treatment of the genus for Guatemala. I regard *C. schiedeana* Lindau as identical to *C. barbadensis* Jacq. I hesitate to follow Standley and Steyermark in reducing *C. hondurensis,* for there is a problem here which I cannot solve, even with abundant herbarium material. I prefer to keep *C. hondurensis* as a distinct species and to call this problem to the attention of field workers for further study. Material cited below as *C. hondurensis* is easily recognized, but difficult to define or to separate in a key. For the present, *C. hondurensis* can be recognized when dry by the dark brown or black upper leaf surface which contrasts with the lighter-colored lower surface. The inflorescences are usually twice as long as the subtending leaves. The fruiting pedicels are slightly more tenuous and seem relatively longer than those of *C. barbadensis* and the apex of the fruit, while coronate, is more obtuse than is general in *C. barbadensis.* Usually such distinctions are not valid in this difficult genus and I am maintaining this as a distinct species for temporary convenience only.

Further study should be rewarding, for *C. hondurensis* may prove to be either a variety of *C. barbadensis* or of hybrid origin.

México. OAXACA: Tehuantepec, *L. Williams 9906* (Y). VERACRUZ: Fortuno, Coatzacoalcos River, *L. Williams 8701* (Y). **Guatemala.** ALTA VERAPAZ: Río Sebol, near Carrizal, *Steyermark 45785* (F). IZABAL: Quiriguá, *Standley 23867, 23988, 24547, 24601* (GH), *72249* (F); Puerto Barrios, *Standley 72143* (F); Salomón Creek, south of Bananera, *Steyermark 38934* (F). PETÉN: Río Cancuén, *Steyermark 45925* (A, F); Río Machaquilla, north of El Cambio, *Steyermark 45928* (F).

Honduras. ATLÁNTIDA: Vicinity of Tela, *Bangham 212* (A); *Chickering 233* (F, MICH), *Howard, Briggs et al. 452, 503, 504, 505, 506, 507* (A), *Salvoza 810* (A), *Standley 53716, 54476, 54481, 54752, 56598, 56659* (A, F); La Ceiba, *Yuncker, Koepper & Wagner 8295* (F, GH). COLÓN: Cuyamel, *Carleton 598* (US). SANTA BÁRBARA: San Pedro Sula, *J. Donnell Smith 5433* (A, F, GH, M). Dept. unspecified: Puerto Sierra, *Wilson 74* (NY), *562* (F, GH, NY).

British Honduras. BELIZE DISTRICT: Quamina Creek, Manatee, *Gentle 3437* (A, MICH); Cornhouse Creek, Manatee River, *Bartlett 11275* (F, MICH); Sibun River, *Bartlett 11361* (GH, MICH); Northern River, *Gentle 897* (A, F, MICH). EL CAYO DISTRICT: Little Cocquericot, Belize River, *Lundell 3995* (MICH), *3996* (MICH-holotype; F), *3997* (GH, MICH). STANN CREEK DISTRICT: Sarawee Pine Ridge, *Gentle 2699* (A, F, MICH), *2748* (A, F, MICH); Mullins River Road, *Gentle 2731A* (A, F, MICH); Carib Reserve, *Gentle 2734* (A, F, MICH), *s.n.* (A, MICH, WIS); Stann Creek Valley, *Gentle 2733* (A, F, MICH), *2735* (A, F, MICH, WIS), *2737, 2738* (A, F, MICH), *s.n.* (MICH); Middlesex, *Gentle 2820, 2874, 2878, 2887* (A, MICH), *3011, 3018* (A, F, MICH); Silk Grass Creek Reserve, *Gentle 2989* (A, MICH); Big Eddy Ridge, *Gentle 3348* (A, MICH); Mt. Cow Vayyel, *Gentle 3538* (A, MICH); Silk Grass Creek Reserve, *Record BH-20* (Y); Middlesex, *Schipp 453* (A, F, GH, MICH). TOLEDO DISTRICT: Swasey Branch, Monkey River, *Gentle 3716, 3584* (A, MICH). District unspecified: Manatee Lagoon, *Peck 255* (GH).

Coccoloba humboldtii Meisner, DC. Prodr. **14**: 163. 1856.

Coccoloba orizabae Lindau, Bot. Jahrb. **13**: 189. 1890.
Coccoloba humboldtii var. *longipedicellata* Gross, Repert. Sp. Nov. **12**: 219. 1913.
Coccoloba petrophila Brandegee, Univ. Calif. Publ. Bot. **10**: 404. 1924.

Meisner cited two collections in the original description of this species, *Humboldt 4484*, which is in the Willdenow Herbarium as No. 7705, and *Berlandier 105*, collected near Tampico. Although the Humboldt specimen in the Willdenow herbarium at Berlin bears no specific locality beyond "Mexico," this should be selected as the lectotype. A second specimen collected by Humboldt is in the Paris herbarium and bears the number *4484*, with the locality given as "Vera Cruz." Unhappily, this specimen was identified and annotated by Lindau as *Coccoloba nutans*, an entirely different species.

Coccoloba orizabae Lindau was distinguished by Lindau in a key to the species on the shape of the leaf blade, especially the narrowed base and the acuminate apex. The type of this species was *Bourgeau 2822* from Orizaba, Veracruz.

Gross distinguished his new variety *Coccoloba humboldtii* var. *longipedicellata* by the longer pedicels and the inflorescence rachis as long as the leaves. Gross failed to appreciate the dioecious character of the species and based his variety on a staminate plant, in contrast to the holotype, which is a pistillate plant. The variety is clearly included within the range of variation of the Humboldt type collection and, as more recent collections demonstrate, should be included within the species.

Coccoloba petrophila was described by Brandegee in a report on Purpus collections from Mexico. *Purpus 8872* from Camerón, Veracruz, was selected as the type. No discussion was given of the distinctions or affinities of the species. Another collection, *Purpus 8736*, made at the same time and location, was not seen, or at least not cited, by Brandegee. Subsequently Purpus collected additional material assigned to this species from near Los Conejos (*16425*, *16430*) and Rancho Remudadero (*10967*). The last number was suggested to be a wide-leaved variety in Brandegee's herbarium notes. These Purpus collections, together with *Seler 4482*, show the extremes of variation to be expected in *C. humboldtii*, as well as the intermediate forms which made a continuous series from former concepts of *C. humboldtii* to *C. petrophila* and *C. orizabae*. Several of the Purpus collections also show thin-textured immature leaves of varying sizes and shapes. It is in such specimens as *Purpus 16425* that transitions to the thin-textured acuminate-tipped leaves of *C. orizabae* can be found.

In his treatment of the trees and shrubs of Mexico, Standley places both *Coccoloba orizabae* and *C. humboldtii* in a division of his key headed "rachis of the inflorescence glabrous." In all of the material cited below, the young inflorescence rachis is subtomentose, but at maturity is puberulent or glabrate. The same is true of the ocreae. The original descriptions of the three species and the variety fail to mention pubescence.

México. San Luis Potosí: Las Canoas, *Pringle 5111* (A, GH). Veracruz: Tampico, *Berlandier 105* (A, B, LE, P), 201 (LE), *Palmer 322* (GH, NY); Veracruz, *Galeotti 109* (BR), *Juzepczuk 1116* (F, LE), *Gorrin s.n.* (LE); Colipa, *Karwinsky s.n.* (LE); Laguna Tamiahua, *LeSueur 100* (GH), *101* (F); Orizaba, *Bourgeau 2822* (B-holotype of *C. orizabae*; P); Pánuco River near Ebano, *LeSueur 102* (F, GH); Pacho, *Liebmann s.n.* (LE); Coatzacoalcos, *Orcutt 3162* (DS, F, GH); Pueblo Viejo, *Palmer 443* (F, G, GH, NY); Camerón, *Purpus 8736* (GH, NY, US), *8872* (GH-isotype of *C. petrophila*); Rancho Remudadero, *Purpus 10967* (B, F); Zacualpan, *Purpus 12022*, in part (DS); Los Conejos, *Purpus 16425* (A, F, LE), *16430* (A, F); Puerto de Alvarado, *Seler 4482* (B-holotype of *C. humboldtii* var. *longipedicellata*; GH); Mocambo, *Troll 59* (M); Alvarado, *Schubert & Rojas 1844a* (A); location unspecified, *Humboldt 4484* (B-Herb. Willd. 7705, lectotype; P).

Coccoloba lasseri Lundell, Contr. Univ. Mich. Herb. **6**: 10. 1941.

This species is regarded as endemic to Panama and is perhaps not distinct from *Coccoloba tuerckheimii* Donn. Sm. For the present, *C. lasseri* may be recognized by the paniculate inflorescence of few branches, the leaves with short, stout petioles and the blades which, while narrowed below the middle, are truncate or abruptly rounded at the base. Finally, the fruits known for *C. lasseri* are rounded at the base. In contrast, *C. tuerckheimii* has a paniculate inflorescence of many more branches, leaves with longer, tenuous petioles and blades cuneate at the base with fruits narrowed to a short stipe at the base.

Panamá. COCLÉ: Aguadulce, *Pittier 4989* (F); Penonomé, *Williams 357* (NY). HERRERA: Chitré, *Allen 1111* (F, GH, MO); Mangle Bejuco, *Steyermark, Allen & Dodge, s.n.* (F). PANAMÁ: Bejuco, *Allen 2542* (A, F); Panamá Nat. Highway, Las Lajas Bridge, *Bartlett & Lasser 16638* (MICH); Río Pacora, *Bartlett & Lasser 16946* (MICH-holotype); Balboa to Chamé, *Dodge, Hunter, Steyermark & Allen 16732* (MO); Punta Paitilla, *Standley 26265* (A). Province unspecified: *Duchassaing s.n.* (P).

Coccoloba liebmannii Lindau, Bot. Jahrb. **13**: 189. 1890.

Coccoloba lapathifolia Standley, Contr. U.S. Nat. Herb. **23**: 245. 1922.

This species is quickly and easily recognized by the persistent pubescence on the lower leaf surface. Most of the leaves show a tendency toward an undulate or wavy margin to the blade, while in some specimens this tendency is so exaggerated that the marginal folds overlap in the dried specimens. The fruit is globose and the perianth lobes are imbricate in fruit. The achene is not coronate.

Standley distinguished his new species, *Coccoloba lapathifolia*, from *C. liebmannii* on the basis of a "glabrous or very minutely puberulent" inflorescence rachis, in contrast to one densely short-pilose. Examination of the material cited below, however, including both types, indicates quite clearly that *C. lapathifolia* is the same as *C. liebmannii* and should be placed in synonymy.

México. COLIMA: Manzanillo, *Ferris 6061* (A, DS, F), *Palmer 965* (GH, NY); between Galera and Pochutla, *Liebmann s.n.* (C-holotype of *C. liebmannii*; B). GUERRERO: Acapulco, *Palmer 206* (US-holotype of *C. lapathifolia*; GH); Placeres, *Hinton 9101* (NY). OAXACA: Distrito de Tamiltepec, *Conzatti 4406½* (GH); Llano Grande & Pinotepa, *Nelson 2341* (GH); Cerro de Picacho, *Purpus 7735* (GH, NY); Tequisistlán, *Seler 1719* (B).

Coccoloba lehmannii Lindau, Bot. Jahrb. **20** (Beibl. 49): 7. 1895.

Uvifera lehmanni Lindau, in footnote, l.c.
Coccoloba lehmanni Lindau, Repert. Sp. Nov. **1**: 156. 1905.
Coccoloba changuinolana Standley, Publ. Field Mus. Bot. **8**: 9. 1930.
Coccoloba williamsii Standley, Publ. Field Mus. Bot. **11**: 148–149. 1936.
Coccoloba allenii Lundell, Contr. Univ. Mich. Herb. **6**: 8. 1941.

Lindau described this species in two papers. In the earlier publication the specific name is spelled "*lehmannii*" and in the later one, "*lehmanni.*" Two collections (*Lehmann 6109* and *7560*) were cited in the first publication, but in the second description only *Lehmann 7560* was cited. In both descriptions this new species is compared with *Coccoloba gracilis* of the section *Campderia.* Lindau's two descriptions of *Lehmann 7560* are comparable; thus one may assume that Lindau overlooked the first publication which described both of these collections. It seems desirable to select *Lehmann 7560* in the Berlin Botanic Garden Herbarium as the lectotype.

Coccoloba changuinolana was based on three collections from Panama with *Dunlap 499* being selected as the type. An examination of these specimens shows Standley's original description to be in error on the important character of "perianthii tubo accrescente inclusus." The perianth lobes, not the perianth tube, increase in size to surround the mature achene, and the species as represented by the collections cited by Standley belongs to the section *Campderia.* Although Standley stated that the new species was related to *C. schiedeana,* I can find no basis for comparison between the two. However, *C. changuinolana* is comparable in all characteristics with *C. lehmannii,* from Columbia, and is assigned in synonymy to that species.

I have seen only the type collection, *Llewellyn Williams 4803,* of the several specimens that Standley cited in his original description of *C. williamsii.* This Peruvian species must also be placed in the synonymy of *C. lehmannii. Williams 4803* is in fruiting condition and the longer fruiting pedicels are in contrast to the shorter pedicels found on the flowering specimens of the Lehmann collection which is the type of the species. Additional collections which I have seen are intermediate. Standley indicated a relationship of *C. williamsii* with *C. caracasana,* both species being assigned to the section Campderia, but these are clearly distinct in the leaf shape and nature as well as in the abundant pubescence.

Still a third species, *Coccoloba allenii* Lundell is assigned to synonymy here. Lundell correctly noted the alliance of *C. allenii* with *C. williamsii,* but distinguished *C. allenii* on the basis of a furfuraceous-lepidote indument and large apiculate spathaceous ochreolae. Additional specimens collected by Allen in Panama show many intermediate conditions in both characteristics.

Coccoloba lehmannii is currently known to occur in Columbia (type), Panamá, Peru, Costa Rica and Venezuela.

Costa Rica. La Palma, Suxaola Valley, *Dunlap 467* (F, Y). **Panamá.** BOCAS DEL TORO: Daytonia farm, Region of Almirante, *Proctor Cooper 421* (F, Y); Changuinola Valley, *Dunlap 499* (F-type of *C. changuinolana;* B, Y). COCLÉ: El Valle, *Allen 2181* (MICH-type of *C. alleni*; A, F), *Allen & Alston 1857* (F, GH, MO).

Coccoloba lindaviana, sp. nov.

Frutex, 8 m., ramulis teretibus, leviter striatis, glabris; ocreis coriaceis, dense strigosis vel glabratis, 9–12 mm. longis; petiolis supra basem ocrearum gerentibus, 8–11 mm. longis, glabris; laminis oblongis, anguste oblongis vel oblongi-ellipticis, apice acutis vel breviter acuminatis, basi rotundatis, vel truncatis, 15 × 4.5 vel 22 × 8.5 cm. longislatisque, coriaceis, glabris, nerviis primariis 11–15, adscendentibus; inflorescentiis terminalibus, racemosis 12–15 cm. longis, rachis glabris, bracteis triangularibus, minutis, minusque 0.5 mm. longis, glabris, ocreolis membranaceis, glabris vel ciliatis ad marginem, bracteis aequaliter; floribus ignotis; pedicellis fructiferis 1.5–2 mm. longis, glabris; fructu ovato, 8 mm. longo, 6 mm. diametro, ad apicem obtuse coronato; acheniis castaneis, levibus, nitidis.

Honduras. YORO: Aguan river valley, vicinity of Coyoles, *Yuncker, Koepper & Wagner 8032* (GH-holotype; F); Cortés, canyon of Rio Piedras, 3 km. from San Pedro Sula, *Molina 3430* (F); El Encanto in Montana La Cumbre, *Molina 3577* (F); Montana de Rio Piedras, *Molina 3555* (F).

The Molina collections bear an unpublished name attributed to Standley and L. Williams. I agree with them that a new taxon is represented here, even though this species is currently known only from old and fruiting specimens. *Coccoloba lindaviana* is, therefore, distinct on the basis of the leaf shape, the position of the leaves, which are borne above the base of the ocreae, and by the oval fruit which is slightly coronate at the apex. It is also similar to *C. hondurensis*, differing in the venation of the leaves and the position of the petiole base. All of the fruits I have examined had fully-formed seeds. Nevertheless, there is a possibility of a hybrid origin of this species.

The species is named in honor of Gustav Lindau who published a monograph of the genus *Coccoloba* in 1890.

Coccoloba lindeniana (Bentham) Lindau, Bot. Jahrb. 13: 82. 1890.

Campderia lindeniana Bentham, in Benth. & Hook. Gen. Pl. 3: 103. 1880.

This species is known only from the type collection made by J. Linden (*1602*) in Tabasco, near Teapa, Mexico, in May, 1840. An altitude of 300 m. is given on the collector's label. Specimens have been seen in the herbaria at Geneva, Leningrad and Paris, as well as a fragment in the Berlin herbarium.

Coccoloba lindeniana seems distinctive among Mexican and Central American species in the very pubescent leaves and inflorescence axis and the pubescence of the bracts and ocreolae. It may prove to be nothing more than the pubescent form of *C. acuminata* which Lindau described as *C. acuminata* var. *pubescens*. *Coccoloba acuminata* is widely distributed through Central America and adequately represented in herbaria, although only a few collections are available from Guatemala. The pubescent phase, which I do not recognize as a distinct taxon, is found throughout the range of the species. The abundance and persistence of the pubescence varies.

The inflorescence of *Coccoloba acuminata* is characteristically interrupted, with the axis swollen below each flower cluster. The clusters therefore appear at an acute angle to the inflorescence axis. In *C. lindeniana* the axis is not swollen and the flower clusters appear to be produced flat on the axis.

The final position of *Coccoloba lindeniana* will await the collection of more material from Mexico. It is to be hoped that some of this will be in fruiting condition.

Coccoloba × lundellii Standley (pro sp.)

Coccoloba lundellii Standley, Publ. Field Mus. Bot. **8**: 138. 1930.
Coccoloba suborbicularis Lundell, Lloydia **2**: 84. 1939.

In the original description of *Coccoloba lundellii* Standley stated, "Evidently a relative of the widespread *C. schiedeana* Lindau, but differing conspicuously in its very broad leaves, somewhat suggestive of those of the common sea grape, *C. uvifera*."

A few years later Lundell described *Coccoloba suborbicularis* and reported that "among the species of the Yucatan Peninsula, *C. suborbicularis* is unique in having the leaf conspicuously unequal at the base."

The type of *Coccoloba lundellii* bears a few fruits, two of which were opened and found to be sterile. The type specimen of *C. suborbicularis* bears a few staminate flowers. Both holotypes show many of the characteristics of *C. uvifera*. The few fruits, the clustered flowers, the puberulence and the asymmetrical leaf base are characteristics of *C. uvifera*. The broad, orbicular leaves are dominant on all specimens seen, but a few smaller oblong leaves, with a strong development of secondary veins when dry, are suggestive of some other influence.

Several hybrids of *Coccoloba uvifera* and neighboring species have been found or suggested in the flora of the West Indies and it appears that a parallel situation is present here. It is not clear from the material on hand whether the second parent is *C. hondurensis,* which may, in turn, be a variation of *C. barbadensis*, or *C. reflexiflora*. Both species are known from the area of the hybrid.

British Honduras. ORANGE WALK DISTRICT: Honey Camp, coastal region, *Lundell 649* (F-holotype; DS, GH). STANN CREEK DISTRICT: Stann Creek Railway, *Gentle 2687* (MICH-holotype of *C. suborbicularis*; A, F); Stann Creek Valley, *Gentle 2716* (A, MICH); Middlesex, *Gentle 2877* (A, MICH), *2890* (A, MICH).

(*To be concluded*)

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STUDIES IN THE GENUS COCCOLOBA, VII. A SYNOPSIS AND KEY TO THE SPECIES IN MEXICO AND CENTRAL AMERICA *

RICHARD A. HOWARD

Coccoloba macrophylla Sessé & Mociño, Fl. Mex. ed. 2. 96. 1894.

Although *Coccoloba macrophylla* appears to be published as a new epithet in the "Flora Mexicana," the name is a later homonym of *C. macrophylla* Desf. ex Hook. (see Jour. Arnold Arb. **38**: 225–227. 1957), a synonym of *C. rugosa* Desf. There are no specimens cited by number in the work of Sessé and Mociño and all of their collections I have seen which bear the name are to be referred to *C. rugosa*. *Coccoloba rugosa* is endemic to Puerto Rico and the species is attributed to Mexico in error.

Coccoloba manzanillensis Beurling, Prim. Fl. Portobello in Kongl. Vetensk. Akad. Handl. 142. 1854; Lindau, Bot. Jahrb. **13**: 209. 1890.

Campderia nematostachya Grisebach, Bonplandia **6**: 4. 1858.
Coccoloba nematostachya Lindau, Bot. Jahrb. **13**: 208. 1890.

The original description of *Coccoloba manzanillensis* cited *Billberg 234* as the type collection and Lindau reported seeing specimens from the Berlin herbarium and from Stockholm. The fragment at Berlin which Lindau annotated is *Billberg 230*, although the Stockholm specimen, presumably the origin of the fragment, is correctly numbered *Billberg 234*. The collection was made on the island of Manzanilla near the port which Lindau called Puerto Belo, known on modern maps as Porto Bello.

The name of this species was originally spelled "manzinellensis" by Beurling, but the spelling was changed to "manzanillensis" by Lindau. While the island where Billberg collected the type specimen is not on modern maps, Beurling's intention in describing the species is obvious. "Manzanillo," or "little apple" in Spanish, is commonly applied to the widespread and infamous strand plant *Hippomane manchineel* and although Lindau failed to comment on his correction of an orthographic error or to cite the original spelling, it seems desirable to allow this correction to stand.

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* Continued from vol. XL, p. 203.

Campderia nematostachya Griseb., transferred to *Coccoloba* by Lindau, is based on an unnumbered Andersson specimen from Panama. A specimen from the Meisner herbarium, now at the New York Botanical Garden, appears to be identical with the Göttingen specimen and part of the Andersson collection. A label bears Grisebach's handwriting, but unfortunately it carries the legend, "*Coccoloba fagifolia* Guadeloupe? coll. Duchassaing." The label is obviously incorrect.

Lindau recognized both *Coccoloba nematostachya* and *C. manzanillensis.* He distinguished them by placing *C. manzanillensis* in a group of species having glabrous leaves, while associating *C. nematostachya* with species having persistent pubescence. However, examination of the specimens cited shows the distinction which Lindau established to be untenable, since it is based on the age of the specimen. *Coccoloba nematostachya*, therefore, must be considered to be the same as *C. manzanillensis.* A long foliar ocrea distinguishes this species which is further characterized by having long, almost silky, hairs.

The Shattuck specimen cited carries a plant of *Oryctanthus cordifolius* as a parasite.

Bailey 42 is the first mature specimen with fruit.

Panamá. CANAL ZONE: Barro Colorado Island, *L.H. & E.Z Bailey 42* (F), *Shattuck 425* (F); between Gatún and Lion Hill, *Pittier 2570* (NY). COLÓN: Porto Bello, *Billberg 230* (B). DARIÉN: La Palma, *Pittier 6599* (GH). PANAMÁ: Pacora, *Allen 3450* (A, BRUX, F, MO). Province unspecified: location unspecified, *Andersson s.n.* (GOET-type of *C. nematostachya*; B, NY), *Billberg 234* (F-photo; S).

Coccoloba matudai Lundell, Contr. Univ. Mich. Herb. **7**: 8. 1942.

Further study of populations in the field may prove this species to be a hybrid, possibly of *Coccoloba belizensis* and *C. montana*. However, the collections assigned here show an even greater range of leaf size, shape and texture than is normally found in either species. Lundell described both staminate and pistillate flowers, the former apparently from *Matuda 2002* and the latter from *Matuda 4315.* No fruits were formed. The species at present is recognizable only through the character of the branched inflorescence.

México. CHIAPAS: Finca Olvido, Mapastepec, *Matuda 2002* (A, MICH, NY, US); Saxchanal, Sierra Madre, *Matuda 4315* (MICH-holotype; A); Cascada, Siltepec, *Matuda 5144* (F, GH).

Coccoloba montana Standley, Jour. Wash. Acad. **13**: 368. 1923.

Coccoloba escuintlensis Lundell, Phytologia **1**: 213. 1937.
Coccoloba schippii Lundell, Bull. Torrey Club. **66**: 594. 1939.
Coccoloba steyermarkii Standley, Publ. Field Mus. Bot. **22**: 138. 1940.

It is unfortunate that the oldest name to be applied to this taxon is based on a sterile, fast-growing shoot. In describing *Coccoloba montana* Standley suggested that the "leaves of this *Coccoloba* are so distinct from those of other Central American species that it seems desirable to give it a name for purposes of reference."

In the Flora of Guatemala (Fieldiana Bot. **24**: 115. 1946) Standley and Steyermark suggested that the material represented is from "*C. escuintlensis* or perhaps of one of the other species listed." The specimens cited below include sterile shoots, as well as fertile specimens, but unfortunately no collections of both sterile, fast-growing shoots and fertile branches have been made from a single plant. Nevertheless, it appears certain that only one species is represented here. A pubescence in the axils of the veins and along the midrib appears in some of the specimens cited, but the leaves are usually glabrous when mature.

Coccoloba schippii was described by Lundell and the suggested relationship was with *C. guyanensis* Meisner. This was apparently made on the basis of the sessile flowers which were in bud, appearing in a "spicate" inflorescence. In their key to the Guatemalan species, Standley and Steyermark distinguished *C. schippii* on the characters of sessile flowers, conspicuous nerves and short racemes, but the type of *C. schippii* is obviously a branch with an immature inflorescence. Comparable inflorescence branches can be found on many of the other specimens cited. I believe the mature inflorescence of *C. schippii* as defined by Lundell would be elongated and the flowers would be borne on longer pedicels. *Coccoloba schippii*, with *C. escuintlensis*, seems properly referred to the synonymy of *C. montana*.

In describing *Coccoloba steyermarkii* Standley noted "the species is remarkable for its narrow leaves, more elongate and narrower than those of any other Central American species except *C. acuminata* HBK., to which it is not closely related. It is similar to *C. escuintlensis* Lundell [*C. montana*], of the Pacific slope of Guatemala and of Chiapas, but that has broader leaves, almost concolorous and with much fewer nerves." I have examined sufficient material of *C. montana* to be certain that the type specimen of *C. steyermarkii* can safely be included in *C. montana*. The few specimens which have been assigned to *C. steyermarkii* differ at most in a slightly more coriaceous texture to the leaves and less venation. In all other characteristics I have been able to compare, these same specimens agree well with material here considered as *C. montana*.

Coccoloba montana appears to be similar to *C. padiformis* which was described from South America and is represented by recent collections from Panama and Costa Rica. In all specimens seen the apex of the leaf is acute or acuminate, while *C. padiformis* has a rounded or obtuse leaf apex.

México. CHIAPAS: Escuintla, *Matuda 413* (MICH-holotype of *C. escuintlensis*; A, F, GH); Acacoyagua, *Matuda 17410* (F); Esperanza, Escuintla, *Matuda 4143, 4145* (A, F, GH, MICH), *17466, s.n.* (F). **British Honduras.** TOLEDO DISTRICT: at the British Honduras-Guatemala boundary, *Schipp S-687* (F-holotype of *C. schippii*).

Guatemala. ESCUINTLA: Río Guacalate, *Standley 60190, 89302* (F); between Río Jute and Río Pantaléon, *Standley 63464* (F, MICH), *63488* (F); Las Lajas, *Standley 64787* (F). IZABAL: Puerto Barrios, *Standley 25075* (US). QUEZALTE-

NANGO: Colomba, *Skutch 2022* (A, F); Finca "Pireneos" below Santa María de Jesús, *Standley 68207* (F); between Finca "Pirineos" and Patzulín, *Standley 86954* (F), *86964* (MICH); between Santa María de Jesús and Calahuaché, *Steyermark 33677* (F); Calahuaché, *Steyermark 35473* (F); Río Dulce, west of Livingston, *Steyermark 39533* (F-type of *C. steyermarkii*), *39404* (F). RETALHULEU: between Retalhuleu and Nueva Linda, *Standley 87219* (F, US), *87291*, *88516* (F); Ajaxá, east of Santa Cruz Muluá, *Standley 88220*, *88232* (F); vicinity of Retalhuleu, *Standley 88604*, *88807* (F, MICH); between Asintal and Colomba, *Standley 87876* (F). SAN MARCOS: Río Mopá, below Rodeo, *Standley 68770* (F); Finca Vergel, near Rodeo, *Standley 68949*, *68952* (F); Finca El Porvenir, *Steyermark 37601* (F, MICH), *52336* (F). SUCHITEPÉQUEZ: Pueblo Nuevo, *Standley 66936* (F).

El Salvador. AHUACHAPÁN: Sierra de Apaneca, region of Finca Colima, *Standley 20061* (US-holotype of *C. montana*; GH). LA LIBERTAD: near Comasagua between Finca Germania and Finca San Antonio, *Carlson 238* (F).

Coccoloba nicaraguensis Standley & L. Williams, Ceiba 3: 198. 1952.

This species is based on material which is inadequate for an accurate analysis. All the specimens available to me were collected in the mountains at an altitude of 1050–1350 m. west of Jinotega, Department of Jinotega, Nicaragua. The four numbers cited in the original description are *Standley 9768*, *10194*, *10233* and *10409*, the last of which is the holotype in the herbarium of the Chicago Natural History Museum. A fifth number, *Standley 10318*, was also referred to this species by the original authors by annotation, but was not cited in their paper. The type, *Standley 10409*, and one other, *Standley 9768*, bear young developing leaves which have turned black on drying. Another collection, *Standley 10233*, bears both mature leaves as well as young blackish leaves comparable to the type. The other sheets are of mature branches. Only the type sheet bears flowers and this specimen has four immature inflorescences. On the basis of the sterile specimens with mature foliage, the material would be referred unhesitatingly to *Coccoloba diversifolia*, for it is strictly comparable to material described by Lundell as *C. lancifolia* and later referred by Standley and Steyermark to *C. laurifolia*, a species which is here called *C. diversifolia*. However, as indicated in the original description, the young inflorescence axis is minutely puberulent when seen under a microscope. In this characteristic the species is similar to *C. cozumelensis*. *Steyermark 45669*, from Cerro Chinajá, Department of Alta Verapaz, Guatemala, referred to *C. diversifolia* (*C. laurifolia* Standley & Steyermark), is an accurate match except for a glabrous inflorescence rachis.

Coccoloba novogranatensis Lindau, Bot. Jahrb. 13: 192. 1890.

Coccoloba caribaea Urban, Symb. Ant. 5: 337. 1907.
Coccoloba waittii Johnston, Sargentia 8: 122. 1949.

The typification of this species has been discussed in an earlier paper where the lectotype was designated as *Triana 978* (P), Bogotá, Colombia (Jour. Arnold Arb. 40: 85–87. 1959). For over sixty years no collections have been assigned to *Coccoloba novogranatensis*. This is a wide-ranging species found at lower elevations and along the seacoast. The sole exception is *R. S. Williams 945*, a collection of very young material from an altitude of 2800 feet in Panama. Additional material from this area may prove this to be *C. obovata*, for in both species the leaves are attached above the base of the ocrea. In *C. novogranatensis* the leaf blades are broadest above the middle, while those of *C. obovata* are broadest below the middle. Leaves of adventitious shoots are nearly indistinguishable. The species are clearly distinct, however, in the stages with mature flowers or fruit. The Steyermark collection from Guatemala, also sterile, is referred here, again with some question.

Johnston does not make any specific comparison in describing *Coccoloba waittii*, noting only that "it is a well-marked species." Although all the specimens I have seen from Panama are from the Pacific side of the Isthmus, *C. novogranatensis* is to be expected to be on the Atlantic coast, as well.

This species is known from the Lesser Antilles, Trinidad, Venezuela, Colombia and Peru, in addition to the specimens cited below from Guatemala and Panama.

Guatemala. PETÉN: Between Cerro Ceibal and Ceibal, *Steyermark 46178* (F). **Panamá.** HERRERA: Pesé, *Allen 802* (F, GH, MO, NY). PANAMÁ: Perlas Islands, Pedro Gonzalez, *Allen 2602* (MO); San José Island, *Erlandson 377* (GH), *550* (GH, NY), *216* (GH); *Harlow 41* (GH); *Johnston 213* (GH, MO), *230* (GH-type of *C. waittii;* MO), *975*, *1306* (GH). DARIÉN: Cana, *Williams 945* (NY, US).

Coccoloba obovata HBK. Nov. Gen. **2**: 176. 1817.

Coccoloba coriacea Willdenow ex Lindau, Bot. Jahrb. **13**: 194. 1890, not Sagra.
Coccoloba goudotiana Weddell, Ann. Sci. Nat. Bot. III. **13**: 260. 1849.
Coccoloba riparia Lundell, Contr. Univ. Mich. Herb. **6**: 11. 1951.

Coccoloba obovata HBK. was based on a Humboldt specimen collected in flower in June, 1805, at Honda in Colombia. Although the specimen in the Willdenow Herbarium has been considered authentic, I wish to designate a sheet in the herbarium at Paris as the lectotype since the latter sheet is more complete, in better condition and bears a label with more adequate data than does the specimen in Berlin.

The name *Coccoloba coriacea*, attributed to Willdenow by Lindau (not *C. coriacea* Sagra), was not published by Willdenow but occurs on the label of the lectotype as the first two words of a long polynomial written in one line. On the sheet which Lindau saw in the Willdenow herbarium the label is smaller and the name "*Coccoloba coriacea*" appears as one complete line, the two words being underlined. It is unfortunate that Lindau chose to pay any attention to this binomial which has no standing.

Lundell described *Coccoloba riparia* from Panama but did not discuss the species or indicate affinities or differences. *Coccoloba riparia* as represented by the type specimen is clearly the same as *C. obovata*.

The majority of the specimens cited below from Central America had been identified either as *Coccoloba marginata* or *C. leptostachya*. I consider the former species to be the same as *C. nitida* and *C. guianensis* from Trinidad and northeastern South America. The latter species, *C. leptostachya*, is referred to the synonymy of *C. barbadensis*.

Coccoloba obovata is known from Costa Rica, Panama and Colombia. The type is *Humboldt s.n.* from Honda, province of Tolima, Colombia. The type of *Coccoloba goudotiana* is *Goudot s.n.* from San Luis in Colombia.

Costa Rica. Peninsula Osa near Puerto Jimenez, *Brenes 12218* (F); *Cufodontis 91* (F); San Rafael de San Ramón, *Brenes 22020* (F, NY); Santo Domingo de Golfo Dulce, *Tonduz 7122* (F, GH, US), *9934* (BR, LE, M).

Panamá. CANAL ZONE: Barro Colorado Island, *Aviles 998* (F), *Salvoza 984* (A), *Shattuck 1063* (F), *Starry 298* (F); F. L. Island, *Bangham 593* (A, F); Salamanca Hydrographic Station, *Dodge, Steyermark & Allen 16983* (BR, DS, G, K, MO), *16983a* (BR, K, MICH, MO); *Woodson, Allen & Seibert 1572* (A, F, MO); northwestern part of Canal Zone, *Johnston 1519* (MO); between Tumba Vieja & Salamanca, *Steyermark & Allen 16758* (BR, MO). CHIRIQUÍ: Cerro Galera Chorcha, Gualaca, *Allen 5020* (A, MO); San Félix, *Allen 3655* (A, BR, MO); between San Félix and Cerro Flor, *Allen 1917* (F, GH, MO); Progreso, *Cooper & Slater 270* (US); San Bartolomé, *Woodson & Schery 947* (F, MO); between Río Chiriquí and Remedios, *Woodson, Allen & Seibert 1182* (A, F, MO). COCLÉ: El Valle, *Allen 2229* (MICH-holotype of *C. riparia*).

Coccoloba padiformis Meisner, DC. Prodr. **14**: 166. 1856.

Coccoloba roseiflora Standley & L. Williams in Allen, Preliminary Index to the Trees of the Golfito-Palmar area, 37. 1952; Rain Forests of Golfo Dulce, 177. 1956.

Coccoloba padiformis Meisner is very similar to *C. densifrons* Martius and perhaps is not distinct. At the present time the distinguishing characteristics of *C. densifrons* are the larger leaves, broadest above the middle, and the longer inflorescence rachis. Lindau did not include *C. densifrons* in his key; hence it is difficult to determine his basis of separation.

Coccoloba candolleana Meisner is likewise similar, if not identical, and further material is needed for study before drawing the final limits of any of these species. Certainly the specimens of "*Goudot 4*" cited by Lindau in extending the range of *C. candolleana* from Bahia, Brazil, to Colombia are better referred to *C. padiformis*. The type of *C. candolleana*, *Blanchet 1818*, has a nearly orbicular and umbonate leaf blade. If this is true of the species and not just a growth form, *C. candolleana* can be maintained as a distinct species.

Coccoloba roseiflora, credited to Standley and L. Williams by Allen in the latter's book, "The Rain Forests of Golfo Dulce" is not validly published, since it lacks a description in Latin. The holotype in the herbarium of the Escuela Agricola Panamericana at Tegucigalpa cannot be sent on loan, but I have seen duplicates of the two collections cited by Allen and on the basis of these, refer the species to *C. padiformis*. *Allen 5964* consists of branches with young leaves indicating a completely deciduous plant. Mature foliage of this species is represented by *Allen 5944* and the Tonduz collection from the same area of Costa Rica.

The species is currently known from Costa Rica, Panama, Venezuela and Colombia. The type is *Moritz 377*, collected near Caracas in Venezuela.

Costa Rica. PUNTARENAS: Palmar Norte de Osa, *Allen 5944* (F-isotype of *C. roseiflora*), *5964* (F); Santo Domingo de Golfo Dulce, *Tonduz 7119* (A, F, GH), *7120* (A, F, GH).

Panamá. CANAL ZONE: South of Fort Sherman, *Johnston 1737, 1814* (MO); Quebrada Ancha, *Steyermark & Allen 17101* (MICH, MO); Río Indio de Gatun, *Pittier 2785* (GH).

Coccoloba parimensis Bentham in Hooker, Lond. Jour. Bot. **4**: 626. 1845.

Coccoloba parimensis var. *schomburgkii* Meisner, Fl. Bras. **5**(1): 35. 1855.
Coccoloba excelsa var. *glabra* Lindau, Bot. Jahrb. **13**: 171. 1890.
Coccoloba bracteolosa Meisner, Fl. Bras. **5**(1): 30. 1855.
Coccoloba paraensis Meisner, Fl. Bras., **5**(1): 38. 1855.

The habit of this plant has accounted in part for the confusion surrounding its description in botanical literature. With regard to the collections studied here, the specimens have been described as a liana, a slender climber, a small tree, a tree, or a tree with scrambling branches. As for the varying leaf aspects which have been described, many of which are cited below, there is no question in my mind that they can be associated with the growth habits of the plant. Other species in northern South America also show the habit of a woody, tree-like plant with scrambling branches. The branches are often so thin and tenuous as to be liana-like in character. Collections made from older plants or those growing in isolated situations show a tree-like habit. Collections from the ends of branches or from plants growing in thickets are likely to be considered liana-like.

Most of the specimens I have seen are in fruiting condition. One specimen, *Maxon & Harvey 6700* from Panama, is in flower and has been cited by Lundell as *Coccoloba bracteolosa* Meisn. (Contr. Univ. Mich. Herb. **6**: 9. 1941). The type specimen of *C. bracteolosa* was a staminate flowering specimen and all specimens I have seen referred to this species have likewise been in flowering condition. The same is true for *C. parimensis*. *Coccoloba paraensis*, however, was based on fruiting material and only fruiting material has been referred to this species since.

The numerous specimens from Barro Colorado island were all collected near the laboratory and are either sterile or in fruit. Nevertheless, the series is elaborate and complete, showing the variation in leaf shape, size and texture between the flowering material called *Coccoloba bracteolosa* and the fruiting material called *C. paraensis*. The thin-textured leaves associated with the flowering condition indicate a tendency towards deciduousness in this species. The mature foliage associated with the fruiting specimens is coriaceous and the leaf blades are umbonate or bullate.

Although this evidence is convincing from the specimens on hand, *Cocco-*

loba bracteolosa was based on specimens from Bahia and Alagoas on the east coast of Brazil. It is possible that further collections from that area will show that *C. bracteolosa* is better assigned to the synonymy of *C. ochreolata.* The latter species is distinctive in the shape of the fruit.

Coccoloba parimensis was based on a Schomburgk collection, without number, from Rio Parime. Lindau assigned this species to the synonymy of *C. excelsa.* I cannot agree completely with this conclusion and am recognizing these as distinct species to call attention to the problem. Field study and mass collections from one plant are needed. For the present, *C. excelsa* is distinct in being more pubescent on the lower leaf surface and on the inflorescence axis. *Coccoloba excelsa* also appears to have larger hairs which break off and leave clear hair bases or black-colored hair bases, either of which frequently appear as punctations. *Coccoloba parimensis* leaves, in contrast, are only puberulent with minute hairs. When Lindau assigned *C. parimensis* to the synonymy of *C. excelsa* he recognized a glabrous state which he called *C. excelsa* var. *glabra.* Lindau also recognized *C. paraensis* and distinguished between this species and *C. excelsa* on a key character of pubescence being present in *C. excelsa* and absent in *C. paraensis.* Lindau's *C. excelsa* var. *glabra,* therefore, becomes an anomaly in his key.

Meisner divided Bentham's *Coccoloba parimensis,* recognizing two varieties. *Coccoloba parimensis* var. *schomburgkii* contained the type and is assigned here to *C. parimensis.* Meisner's second variety, *C. parimensis* var. *hostmanni,* is better referred to *C. excelsa.*

Coccoloba paraensis Meisner was based on an unnumbered Martius specimen from Iquapèmirim in the Province of Pará and a Spruce collection, also without number, from Barra in the province of Rio Negro. The latter collection has been distributed with labels written "Coccoloba /2/" and printed "In vicinibus Barra, Prov. Rio Negro, coll. R. Spruce, Dec.–Mart. 1850–51." The Spruce specimens appear in many herbaria and all are unidentified. No type was designated by Meisner but the Field Museum has distributed photographs of the Martius collection from the Munich herbarium and indicated this as the lectotype.

I have seen material of this species from Brazil, British Guiana, Colombia, Peru and Panama.

Panamá. CANAL ZONE: Barro Colorado Island, *Aviles 15* (F), *L.H. & E.Z. Bailey 219* (F), *654* (GH), *Bangham 447* (A, F), *Salvoza 904* (A), *Shattuck 1123* (F), *Standley 41099* (A), *Wetmore & Woodworth 859* (A). PANAMÁ: Juan Díaz region, near Tapia river, *Maxon & Harvey 6700* (F).

Coccoloba pubescens Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

This is a West Indian species which I have seen, studied in the field, collected many times and discussed in a previous paper (Jour. Arnold Arb. **38**: 229–231. 1957). Lindau described the species (Bot. Jahrb. **13**: 202. 1890), citing, in addition to West Indian collections, a Schiede specimen from "herb. Petrop." credited to Mexico without specific location and a specimen from "Guyana batava" which Meisner also cited. I have not seen *Kegel 1339* which Meisner cited from Dutch Guiana, nor was it present in the Prodromus Herbarium at Geneva.

Coccoloba pubescens was also credited to the Mexican flora by Standley in his "Trees and Shrubs of Mexico" (page 245), although he uses a later homonym, *C. grandifolia* Jacq., for the species. No recent collections are cited by Standley and none is available to me. This species is conspicuous wherever it occurs and it is difficult to believe that it would be overlooked or not be collected in a flora where sterile material has been the basis of many species.

I have on loan three sheets credited to Schiede from Mexico and identified as *Coccoloba pubescens*. Two of these sheets, one from the Berlin herbarium and one from Paris, were not cited by Lindau and do not bear his annotation label. These sheets bear a number "60" in the same script as the generic name, although the specific name and the collector and locality of "Mexico" are in a different hand and possibly may be different from each other. The sheet from the herbarium at Leningrad bears Lindau's annotation label, as well as a label indicating that the specimen was from Fischer's herbarium and was collected at "la Cuesta grande de Chiconquraos." There is no indication of the collector (i.e., Schiede), and "Mexico" has been added in a different script.

Schiede's travels in Mexico have been described in Linnaea, volumes four and five, in 1829 and 1830. There are several references to *Coccoloba*. One is referred to as a seacoast plant known as "uva" and this is probably *C. uvifera*. The other two refer to plants collected between Río de Tecoluta and Río de Nantla and at Cambre del Obispo. Neither of these locations fits the data cited above for *Schiede 60*. Lindau refers to three unnumbered Schiede collections, but all are cited by him as having come from "Mexico" without further locality.

All three specimens called "*C. pubescens*" consist of a single leaf and a short piece of branch with a terminal bud. The leaves are large (30 × 28 cm. and 38 × 32 cm.) and the branch stout (10 mm. diameter), suggesting an adventitious shoot or one of vigorous growth. The leaves are suggestive of *Coccoloba pubescens* and the pubescence distribution and hair type can be matched in recent West Indian collections. However, the terminal bud is not that of the West Indian *C. pubescens* but is that of the Mexican *C. liebmannii* Lindau. Only one collection of *C. liebmannii* (*Ferris 6061* from the vicinity of Manzanillo, Colima, Mexico) is available showing the large leaves of vigorous and adventitious shoots. In the three examples of *Ferris 6061* cited elsewhere in this paper, the specimen consists of a fertile branch in fruit with small leaves (average 9 × 3.5 cm.) and a single detached larger leaf (23 × 13 cm). No stem section is available for these larger leaves. The pubescence is similar to that of the Schiede specimens; the terminal bud is the same, though the leaves are smaller.

The Fischer herbarium, particularly in reference to *Coccoloba* specimens, is primarily of fragments from cultivated plants; adventitious shoots and associated leaves are common. It seems likely that the Schiede specimen cited by Lindau is from a plant cultivated in a greenhouse and that the country of origin given on the label is faulty. However, if the data with the specimen are correct, it is probable that this specimen should be identified as *C. liebmannii* and the record of *C. pubescens* be removed from the Mexican flora. Additional field study of *C. liebmannii* is needed to determine variation in size and shape of the leaves and the terminal buds of vigorous and adventitious shoots.

Coccoloba reflexiflora Standley, Publ. Field Mus. Bot. **4:** 203. 1929.

Coccoloba colonensis Lundell, Contr. Univ. Mich. Herb. **6:** 9. 1941.

This species is readily distinguished by the basically obovate-oblong leaves, broadest above the middle, which are borne on pale grayish petioles which, in turn, are borne above the bases of the ocreae. The margin of the leaf is invariably revolute and the upper surface is darker than the lower surface upon drying.

The inflorescence is rarely longer than the leaves and the staminate flowers appear to be reflexed, a character on which Standley based the specific name. However, the fruiting pedicels are at right angles to the inflorescence axis and are 1–1.5 mm. long, exceeding the ocreolae. The fruits are smaller than those of other Central American species and the perianth lobes are imbricate, not coronate, over the obtuse apex of the achene.

Coccoloba colonensis was based by Lundell on sterile material. He suggested an affinity with *C. lundellii*, which I have concluded is a hybrid of *C. uvifera* and an unknown parent, possibly *C. reflexiflora*. The type of *C. colonensis* is from an adventitious shoot. In the characteristics of the ocreae and the point of attachment of the petiole, as well as in the color and venation of the leaf blade, the specimen is clearly identical with comparable vegetable adventitious shoots of *C. reflexiflora*.

México. CAMPECHE: Villahermosa, *Lundell 1139* (F, MICH). YUCATÁN: Chichén Itzá, *Steere 1600* (F, MICH). **Guatemala.** PETÉN: Between Uaxactun & San Clemente, *Bartlett 12815* (F, MICH); Carmelita, *Egler 42–244* (F). **British Honduras.** BELIZE DISTRICT: Northern River, *Gentle 990* (A, F, LE, MICH); Maskall, *Gentle 1223* (A, F, GH, MICH), *1274* (A, DS, F, GH, MICH), *O'Neill 8557* (A, F, MICH); Sibun Road, southwest of Belize, *O'Neill 8570* (*Mich*). COROCAL DISTRICT: San Antonio, *Schipp S-614* (F, GH). ORANGE WALK DISTRICT: Honey Camp, *Lundell 488* (A, F), *Meyer 45* (F); Hillbank, *Winzerling I-17* (Y). STANN CREEK DISTRICT: Silk Grass Creek Reserve, *Gentle 2959* (A, MICH). TOLEDO DISTRICT: Monkey River, *Gentle 4150* (A, MICH). District unspecified: Tower Hill, *Karling 15* (F-holotype; US); Manatee Lagoon, *Peck 92* (GH). **Honduras.** COLÓN: Guarunta, Wispernini Camp, *C. & W. von Hagen* (NY-isotype of *C. colonensis*).

Coccoloba spicata Lundell, Bull. Torrey Club **66:** 594. 1939.

"*Coccoloba coronata* Jacquin?," Millspaugh, Publ. Field Mus. Bot. **1:** 294. 1896.

Lundell compares this species with *Coccoloba mayana* Lundell which I have placed in synonymy with *C. barbadensis* Jacq. The specimens cited below, with one exception, are those also cited by Lundell in the original publication.

Coccoloba spicata was based on staminate flowering material. Only one fruiting collection is known. The species appears distinct in the sessile flowers and densely flowered inflorescence. In fruit the pedicels are scarcely developed and, if present, are less than one-fourth the length of the ocreolae. In contrast to *C. barbadensis*, the apex of the fruit is obtuse to rounded and not at all coronate. The perianth lobes are orbicular and represent the upper third of the fruiting perianth. In sterile condition it is almost impossible to distinguish *C. spicata* from *C. barbadensis*.

México. QUINTANA ROO: Coba, *Lundell 7813* (A, F, MICH). YUCATÁN: Chichén Itzá, *Bequaert 103* (A, F); Valladolid, *Flores 1935* (F); Kancabdzonot, *Gaumer & sons 23894* (A, F); Izabal, *Gaumer 819* (F, GH); Location unspecified, *Gaumer 23976* (F, GH, MICH), *Steggerda 1B* (F); Chichén Itzá, Sacred Cenote, *C.A. & A.A. Lundell 7325* (MICH-holotype; A, F). **British Honduras.** COROZAL DISTRICT: Santa Rita, *Lundell 4951* (A, F, GH, MICH). ORANGE WALK DISTRICT: Honey Camp, *Lundell 560* (DS, F, GH).

Coccoloba standleyana Allen, The Rain Forests of Golfo Dulce 177, 409. 1956.

The holotype of this species, *Allen 6645*, is in the herbarium of the Escuela Agricola Panamericana, Tegucigalpa, Honduras. Since the school does not send specimens on loan, I have been unable to study the material; duplicates are not available in other institutions.

Coccoloba standleyana is based on sterile material collected in the Esquinas forests of Costa Rica, at an elevation of 200 feet. Allen suggests that the species is "probably related to *C. hirsuta* Standl. and *C. belizensis* Standl. but amply distinct in the much smaller ocreae and other characters." I regard *C. hirsuta* as the same as *C. belizensis* and I suspect that *Coccoloba standleyana* will ultimately be assigned to the synonymy of *C. belizensis*.

Coccoloba swartzii Meisner, DC. Prodr. **14:** 159. 1856.

Coccoloba corozalensis Lundell, Bull. Torrey Club **66:** 588. 1939.
Coccoloba gentlei Lundell, Bull. Torrey Club **66:** 591. 1939.

Coccoloba swartzii has not been recognized previously in the flora of Central America, although it is a common element in the vegetation of the West Indies, occurring from Cuba and Jamaica to Curaçao and Aruba and having a great variation in leaf size and shape on all the islands of the Lesser Antilles. The collections cited can be compared favorably with many other collections from the West Indies, especially those populations occurring in the Virgin Islands, the Leeward Islands and the French islands of Guadeloupe and Martinique.

I am not satisfied that the Central American specimens have characteristics of sufficient value to create even a geographical variety. Only the slightly more tenuous inflorescence axis, with its fewer flowers, appears to differ from the West Indian representatives of the species.

The type of *Coccoloba gentlei* Lundell is *Percy Gentle 56*. The meager material appears to be from a vigorous shoot, perhaps even an adventitious shoot. If considered as the latter, the leaves are comparable to collections I have made on St. Kitts and Montserrat (*R.A. & E.S. Howard 11882, 11867, 11938*). In describing the species Lundell put undue emphasis on the branched inflorescence which in reality is a spike with one anomalous branch developing from the base. This is not an unusual condition either in the genus, or in the West Indian specimens of *C. swartzii*. Standley and Steyermark (Fieldiana Bot. **24**: 108. 1946) place this species in a section of their key with other species having much-branched panicles.

Coccoloba corozalensis Lundell is clearly the same as *C. swartzii*.

British Honduras. BELIZE DISTRICT: Belize-Sibun Road, *Gentle 56* (MICH-holotype of *C. gentlei*); Pine Ridge, Maskall, *Gentle 1113* (A, F, GH, MICH). COROZAL DISTRICT: Xiabe, *Lundell 4908* (MICH-type of *C. corozalensis*; A, GH). ORANGE WALK DISTRICT: Honey Camp, *Lundell 347* (DS, F). TOLEDO DISTRICT: Monkey Ridge, *Gentle 3651, 3656* (A, MICH). District unspecified: Cornhouse Creek, *Bartlett 11281* (MICH, NY); Mullins River at Stann Creek Road, *Gentle 3359, 3368* (A, MICH). **Honduras.** Point Triumfo, Puerto Sierra, *Wilson 33* (NY).

Coccoloba tuerckheimii Donnell Smith, Bot. Gaz. **37**: 213. 1904.

Coccoloba guatemalensis hort. ex Lindau, Bot. Jahrb. **13**: 226. 1890.
Coccoloba latifolia Goyena, Flora Nicarag. **2**: 707. 1911, not Lam.

According to the collectors' labels, several botanists have believed *Coccoloba tuerckheimii* to be similar to, if not identical with, *C. latifolia* Lamarck from Trinidad and northern South America, although John Donnell Smith made no comparison of these two species in his original description. In a footnote to his monograph of the genus, Lindau assigned cultivated material carrying the unpublished horticultural name *Coccoloba guatemalensis* to *C. latifolia*. I have seen this material which has been attributed to Guatemala and believe it is more correctly referred to the present species than to *C. latifolia*.

Coccoloba latifolia is similar to *C. tuerckheimii* in having stout, generally hollow stems, petioles borne slightly above the base of the ocrea, and a paniculate inflorescence. The leaf base is generally rounded or cordate, while the blades are bullate between the veins. In contrast, *C. tuerckheimii* has solid stems with leaf blades tapering to a cuneate base and appearing to be flat. The fruits of *C. tuerckheimii* appear to be larger and more stalked than those of *C. latifolia*.

Guatemala. ALTA VERAPAZ: Finca Santa Inés, *Record & Kuylen G-92* (Y); Tucurú, *Standley 70724* (F); between Campur and Socoyó, *Standley 91708* (F); Cubilgüitz, *Steyermark 44674* (F), *Tuerckheim 8493* (F-isotype; GH); Cerro, Chinaja, *Steyermark 45568* (F). IZABAL: Río Dulce, Livingston, *Steyermark 39552* (F).

Honduras. ATLÁNTIDA: Lancetilla Valley near Tela, *Standley 55812* (A, F);

La Ceiba, *Yuncker, Koepper & Wagner 8603* (F, GH, MICH); Tiquitapa, *Howard, Briggs, et al. 560* (A). YORO: Progreso, *Hottle 92* (F); Subirana, *C. & W. von Hagen 1058* (F). **Nicaragua.** CHONTALES: La Libertad, *Standley 9064* (F). **Costa Rica.** ALAJUELA: San Carlos, Suere, *A. Smith H-1694* (F, MICH). **Panamá.** BOCAS DEL TORO: Changuinola Valley, Island of Potrero, *Dunlap 181* (F, Y). COLÓN: Dos Bocas, Río Fato Valley, *Pittier 4197* (F). **Cultivated.** *Kalbreyer s.n.* as *C. guatemalensis* (B).

Coccoloba umbilicata Sessé & Mociño, Fl. Mex. ed. 2. 96. 1894.

No specimens are cited in the original description in which the species is attributed to Mexico. I have seen the Madrid specimens on loan to the Field Museum, and the sheets labelled "*C. umbilicata*" are all to be referred to *Coccoloba pyrifolia* Desf., a species limited to Puerto Rico.

Coccoloba uvifera Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

Polygonum uvifera Linnaeus, Sp. Pl. 365. 1753.

A common strand plant known to all botanical collectors and, as a consequence, one which is poorly represented in herbaria. Presumably the species has a wider distribution in Mexico and Central America than is indicated by the collections cited below.

México. CAMPECHE: Lerma, *Seler 4019* (A, F); Champotón, *Steere 1968* (F, MICH). SINALOA: Mazatlán, *J. Gonzalez Ortega 7203* (BRUX). TAMAULIPAS: Moron, *LeSueur 103* (F); Tampico, *Palmer 477* (F). YUCATÁN: Chichancanab, *Gaumer 1897* (F); Sisal, *Gaumer 23235* (F); Cozumel Island, *Goldman 673* (F) *Millspaugh 1590* (F); Progreso, *Goldman 603* (F); *C.L. & A.A. Lundell 8060* (MICH); Location unspecified, *Gaumer 638* (F), *Millspaugh 6* (F). **Guatemala:** IZABAL: Bay of Santo Tomás, *Steyermark 39248* (F, MICH). **British Honduras.** BELIZE DISTRICT: Turneffe Island, *Egler 42–42* (F); Belize, *Gentle 27* (A, F, MICH). COROZAL DISTRICT: Corozal, *Lundell 4927* (F, MICH). STANN CREEK DISTRICT: Stann Creek, *Gentle 3119* (MICH), *3120* (MICH), *3131* (A, MICH), *3123* (MICH). District unspecified: All Pines, *Schipp 796* (A, F, MICH). **El Salvador.** LA LIBERTAD: La Libertad, *M.C. Carlson 575* (F). SAN SALVADOR: San Salvador, *Calderón 2624* (F). **Honduras.** ATLÁNTIDA: Tela, *Chickering 51* (MICH), *Standley 53056* (A, F), *Yuncker 4655* (A, F, MICH); Ceiba, *Yuncker, Koepper & Wagner 8235* (F, MICH). COMAYAGUA: Comayagua, *Standley & Chacón 5486* (F). Department unspecified: Puerto Sierra, *P. Wilson 23* (F). SWAN ISLANDS: *Nelson 22* (GH). **Nicaragua.** ZELAYA: Bahia de Bluefields, Río Escondito, *A. Molina 1281* (F). **Costa Rica.** ALAJUELA: San Roque de Barbe, *León 10* (F). LIMÓN: Limón, Costa de Portete, *Quirós 508* (F); Talamanca, Puerto Viejo, *Tonduz 9423* (BRUX). PUNTARENAS: Los Loros and Tivives, *Brenes 22661* (F). **Panamá.** BOCAS DEL TORO: Almirante, *G. Proctor Cooper 558* (F, Y); Changuinola Valley, *Cooper & Slater 82* (Y); Chiriquí Lagoon, *Von Wedel 2826* (MO). Province unspecified: Isthmus of Chagres, *Fendler 287* (LE, MO).

Coccoloba venosa Linnaeus, Syst. Nat. ed. 10. 1007. 1759.

Campderia floribunda Bentham, Bot. Sulphur 159. *tab. 52.* 1846.
Campderia mexicana Meisner, DC. Prodr. **14:** 171. 1856.
Coccoloba alagoensis Weddell var. *major* Meisner, DC. Prodr. **14:** 163: 1856.

Coccoloba floribunda Lindau, Bot. Jahrb. **13**: 217. 1890.
Coccoloba molinae Standley & L. Williams, Ceiba **3**: 198. 1952.

The synonymy given for *Coccoloba venosa* is new, *C. floribunda* and *C. molinae* and *Campderia mexicana* being reduced here for the first time. An examination of the type specimens alone would make this decision a questionable one, except for *C. molinae* which is clearly the typical West Indian expression of *C. venosa.* Standley and Williams described *C. molinae* in 1952 but were incorrect in believing that their new species was unlike any material then known from southern Central America. In his Flora Nicaragüense (**2**: 707. 1911), M. Ramírez Goyena recognized *Coccoloba nivea* from Nicaragua and gave the same common name reported for *C. molinae. Coccoloba nivea* Jacq. is a synonym of *Coccoloba venosa* L. The specimens which Standley and Williams cite for *C. molinae* are obviously variable, since two phases of coriaceous leaves are shown even in the two specimens of the type number which I have seen. *Coccoloba molinae* is undoubtedly the same as *C. venosa* L.

Coccoloba floribunda described by Bentham was based on material collected on the voyage of the Sulphur. The type came from Tiger Island in the Gulf of Fonseca, Honduras. *Campderia mexicana* was based on *Andrieux 115*, a specimen from Tehuantepec, Oaxaca, Mexico, and since there is no difference between these, Lindau placed *Campderia mexicana* in synonymy. Recent collections from the same area are also cited.

Coccoloba floribunda as defined by Lindau and as generally recognized in current floras is strikingly different from *C. venosa* as generally recognized in the West Indies. In drier areas the leaves are thick and almost rigidly coriaceous. The leaf apex is obtuse, rounded or even truncate and the base slightly narrowed but rounded or obtuse. Bentham described the leaf base as emarginate to slightly peltate, although the type specimen and the illustration fail to show the latter condition. The leaves are much smaller and the inflorescence generally shorter and thicker than *C. venosa.* At greater altitudes and in wetter areas, according to the data on the specimens studied, the differences are less obvious between *C. floribunda* and *C. venosa.* The leaves become thinner, longer, the apex pointed, the inflorescence axis longer and more tenuous in comparison.

A full range of variation between the extremes has been found in the specimens cited below to indicate a variable population over the geographic range of the species. I have been unable to find any stable characteristics which would allow the segregation of the smaller, coriaceous-leaved form as a geographic variety. Lindau separated *C. floribunda* from *C. venosa* (his *C. excoriata*) in a key to the species (Bot. Jahrb. **13**: 130. 1890) by placing *C. floribunda* in a group in which the leaves are more or less pubescent below or at least barbellate in the vein axils, while *C. venosa* reportedly had glabrous leaves. Comparable pubescence along the midrib and in the axils of the veins is found in the West Indian specimens, so Lindau's distinction does not hold.

Additional study of this species in the field is needed to establish leaf shape, size and texture variations on single plants in Central America, especially since none of the collections I have seen represents adventitious or fast-growing shoots. In their treatment of *Coccoloba floribunda* for the Flora of Guatemala (Fieldiana Bot. **24**: 113. 1946), Standley and Steyermark described the species as "a densely branched shrub or tree, sometimes 9 meters high, with a broad spreading crown, the low trunk often gnarled and twisted, sometimes a meter in diameter." This description fits well many of the plants seen in the Antilles. Variations in leaf texture from membranaceous and chartaceous to coriaceous have also been encountered in *C. venosa* in the Lesser Antilles, although a reduction in leaf size or an adjustment of shape comparable to that found in many of the specimens cited has not been encountered.

Among the specimens cited is *Standley 74249* from Guatemala, represented by two sheets from two different locations.

Coccoloba venosa is under cultivation in Cuba and has been reported from Jamaica in old literature, but no specimens referable to the island have been seen. It is common in Hispaniola, Puerto Rico and the Virgin Islands south through the Lesser Antilles to Trinidad. I have also seen two collections from Venezuela.

México. Chiapas: Belem, Mapastepec, *Matuda 16741* (F, GH); Tapachula, *Fisher 35437* (F, NY); Huixtle, *Matuda 16795* (F); Las Garzas, Acapetagua, *Matuda 2683* (A, F, MICH); Mojarra, Tonala, *Matuda 17125* (F). Colima: Manzanillo, *Ferris 6057* (DS), *6245* (A, DS). Guerrero: Acapulco, *MacDaniels 199* (F, MICH). Jalisco: Mazatlán, *Liebmann s.n.* (B). Oaxaca: Salina Cruz, *Deam 121* (GH, MICH), *L. I. Williams 9708* (F, MICH); Tehuantepec, *Zuccarini s.n.* (M). Province unspecified: *Haenke 1608* (F); *Sessé & Mociño 5432, 5435* (F).

Guatemala. Chiquimula: Quebrada Shusho above Chiquimula, *Standley 74249* (F). Guatemala: Location unspecified, *Aguilar 550* (F). Jutiapa: Jutiapa, *Standley 75193* (F, MICH). Retalhuleu: Champerico, *Bernoulli & Cario 2663* (LE), *Standley 66507* (A, F), *87547* (F, MICH). Santa Rosa: between Chiquimulilla & El Ahumado, *Standley 79541* (F). Zacapa: Zacapa, *Standley 74249* (F); *74379* (F, MICH); Río Motagua west of Teculután, *Steyermark 29195, 42167* (F). Department unspecified: Location unspecified, *Friedrichsthal s.n.* (MICH-type of *C. alagoensis* var. *major*; F).

El Salvador. La Libertad: La Libertad, *Standley 23231* (GH, US), *Calderón 2399* (F). La Unión: La Unión, *Grant 722* (A, F), *Standley 20644* (GH). San Miguel: Laguna de Olomega, *Standley 21015* (GH); San Miguel, *Standley 21133* (GH). San Salvador: Hacienda Santo Tomás, *Carlson 1124* (F). Santa Ana: Metapán, *Standley & Padilla 3297* (F). Sonsonate: Acajutla, *Calderón 1662* (GH, US); Izalco, *Standley 21861* (GH, US). Department unspecified: location unspecified, *Choussy 2054* (US).

Honduras. Valle: San Lorenzo, *Rodriguez 3299* (F); Isla Tigre, near Amapala, *Standley 20728* (GH, US); El Tigre volcano above Amapala, *West 3534* (GH); Jícaro Galán, *Williams & Molina 15002* (F); Nacaome, *Williams & Molina 16721* (F).

Nicaragua. *Chinandega*: Corinto, *Standley 11545* (F). Chontales: Juigalpa, *Standley 9220* (F). Granada: Granada, *Baker 203* (DS, GH), *Lévy 1352* (F). Managua: Managua, *Garnier 320* (W); Sierras de Managua, *Grant 1097* (A, F).

ZELAYA: Río Grande, *Molina 2291* (F, GH); Toumarin, Río Grande, *Molina 2436* (F-isotype; GH); El Recreo on Río Mico, *Standley 19600* (F). Department unspecified: Asseradores Island, *Baker 81* (DS, GH); Location unspecified, *Lévy 1103* (B), *Wright s.n.* (GH, NY).

Costa Rica. GUANACASTE: Libano, *Standley & Valerio 44900* (F). NICOYA: Nicoya, *Tonduz 13779* (F, GH, MICH). PUNTARENAS: Los Loros, *Brenes 22470* (F); between Los Loros & Tivives, *Brenes 22680* (F); Caldera, *Echeverria 4155* (F); Isla de Chira, *Orozco 233* (F); *Valerio 1466* (F).

THE POLLEN OF EPHEDRA

Margaret Wolfe Steeves and Elso S. Barghoorn

The origin of the Gnetales and their relationship to other fossil and living gymnosperms is a problem which is nearly as baffling as that of the origin of the flowering plants; and indeed the two problems have often been linked. On the study of the Gnetales, paleontology has contributed very little because of the extreme paucity of fossil remains (Pearson, 1929). Consequently any early fossil material of this group, and particularly of the most primitive member, *Ephedra*, may be regarded with great interest by students of plant evolution. The first reference to fossil remains of this gnetalian genus is found in *Die im Bernstein befindlichen organischen Reste der Vorwelt*, a description of the Oligocene Baltic Amber flora (Berendt and Göppert, 1845). In their study, twigs bearing ovuliferous structures were designated *Ephedrites johnianus*. A translation of their Latin description is as follows:

> Stem jointed, joints cylindrical with longitudinal striations ending in an annular sheath.
>
> Aments subglobose, single, composed of imbricated bracts, and elevated on the apex of thickened peduncles. The peduncles are verticillate, in the axis of the sheath and non-articulate.

As a result of Menge's subsequent discovery of a preserved male strobilus from the same flora and further study of Göppert and Menge's material, the close similarity between the fossil remains and modern *Ephedra* became apparent. For this reason the genus was redescribed as *Ephedra* (Göppert, 1853; Göppert and Menge, 1883).

Later workers have described *Ephedra* fragments from the Miocene of Germany and Switzerland (Unger, 1851, 1870), and the Miocene of France (Saporta, 1889, cited by Wodehouse, 1934) but there has been some dispute concerning the validity of these identifications. Heer (1855), in publishing a report of *Ephedrites sotzkianus* Unger in his *Flora Tertiaria Helvetiae*, conceded that there was a superficial similarity between these articulate, striated, fossil stems and those of *Casuarina*, an isolated, Australian genus of angiosperms. However, Schimper (1890) saw no similarity with the genus *Casuarina* but questioned all previous reports of the genus from the Tertiary on the grounds that they could belong to poorly preserved specimens of either *Equisetum* or the conifer *Callitris*.

As a result of this confusion it was not until the application of pollen analysis to older sediments that remains of *Ephedra* were uncontestably demonstrated in the Tertiary. Furthermore, with the discovery of *Ephedra* pollen by Wodehouse from the Green River Formation (1933), the past geographic distribution of the genus was broadened to include North America. Likewise, its geologic record was extended back to the Eocene.

Although Tertiary and Pleistocene records in the Western Hemisphere have become more complete with the discoveries of megascopic remains of *Ephedra* from the Florissant beds of Colorado (Wodehouse, 1934), the Pleistocene of California (Axelrod, 1937), the Pleistocene of Nevada and Arizona (Laudermilk and Munz, 1934, 1938), micropaleontological evidence has been surprisingly rare both in Europe and the United States. Thiergart (1940) reported the presence of fossil *Ephedra* pollen grains from Tertiary beds in Germany, Cookson (1956) has recorded them from Australian Tertiary sediments, and, as a result of recent pollen studies, it has been shown that *Ephedra* persisted as a late- and postglacial desert steppe plant in protected areas in Europe (Christensen, 1949, cited by Iversen, 1954; Lang, 1951; Iversen, 1954; Welten, 1957) as well as in South America (Auer, 1933) and the United States (Anderson, 1954).

In view of the facts that *Ephedra* possesses a high degree of structural specialization, and also that early Tertiary *Ephedra* exhibits pollen structures essentially comparable with that of modern species it is apparent that the genus or its close ancestral type had an extended pre-Tertiary history. An extension of this pre-Tertiary history has been found during an analysis of a series of cores from the Cretaceous Raritan and Magothy formations from east-central Long Island, New York. In these sediments a number of intact, as well as fragmented, pollen grains assignable to *Ephedra* were observed. This discovery extends the known fossil record of the genus in North America back to the lower Upper Cretaceous period.

The first part of this paper will deal with a description of the fossil grains found on Long Island; in the second part the results of a detailed survey of the pollen morphology of the living members of the genus will be presented with a view to interpreting the fossil forms and their phylogenetic significance.

FOSSIL EPHEDRA FROM CRETACEOUS SEDIMENTS OF LONG ISLAND

In the process of exploratory sub-surface geologic studies at the Brookhaven National Laboratory, two deep well cores were recovered from two borings approximately one mile apart. The cores extended from the surface Pleistocene drift through the Cretaceous and into the underlying bedrock. The cores were recovered nearly intact and represent an unusually complete section of the Cretaceous formations underlying eastern Long Island. One of us had the opportunity to sample both of these cores throughout, and this study comprises one aspect of an intensive micropaleontological study still in progress.[1]

The cores, designated Well No. 1 (S 6409) and Well No. 2 (S 6434) were drilled to a depth of 1,568 feet and 1,294 feet, respectively. In both

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[1] Samples of the cores were made available in May 1950 by the Ground Waters Division of the U. S. Geological Survey and were transmitted through the courtesy of the Paleontology and Stratigraphy Branch of the Geologic Division of the U. S. Geological Survey.

cores, which were drilled through the Magothy and Raritan formations, the sediments recovered were all non-marine, Coastal Plain deposits, comprising variegated and lignitic clays, white, fine-grained and coarse arkosic sands, and gravels. Occasional lignite beds were dispersed throughout the section. The entire sequence rested on crystalline igneous rocks of presumed pre-Cambrian age.

The Magothy formation is regarded as of Upper Cretaceous age and has been correlated with the Austin chalk of the Gulf Coast region. Although it rests unconformably on the Raritan, rarely is the Magothy clearly differentiated from it. According to Spangler and Peterson (1950), the two formations are comparatively easy to differentiate in the field but insufficient contacts of the two have been found to map them satisfactorily. Data available from well logs are usually too uncritical and incomplete for stratigraphic purposes. The Raritan formation of New Jersey was considered by Spangler and Peterson (1950) as equivalent to those non-marine sediments in Delaware, Maryland and Virginia referred to as "Raritan," Patapsco, Arundel and Patuxent. This series, they believe, should be considered as a single unit and comprises both Upper and Lower Cretaceous beds. Furthermore, the beds called "Raritan" in Maryland-Delaware are only part of the sediments called Raritan in New Jersey. However, they point out that the contact of the Upper and Lower Cretaceous occurring within the Raritan formation in New Jersey has not been recognized in outcrop and sub-surface sediments have not been studied. This interpretation has been refuted by Dorf (1952) who, after reviewing the faunal and floral evidence, reaffirmed the assignment of the Raritan formation to the early Upper Cretaceous. Hence, in his view, the Potomac beds (Arundel, Patapsco and Patuxent) are pre-Raritan and assignable to the Lower Cretaceous. One of the purposes of this study was to examine the possibility of separating the Raritan from the Magothy on the basis of evidence from plant microfossils. Such a separation might render stratigraphic correlation possible in other parts of the Coastal Plain where the two formations are at present unsatisfactorily separable.

Small samples (1–2 gms.) taken at intervals along the length of both cores were prepared according to techniques modified from Erdtman (1943), Faegri and Iversen (1950). The material was first demineralized by a treatment of cold 50% HF for 24–48 hours, then boiled in 10% KOH in a water bath for six minutes, washed, and dehydrated with glacial acetic acid. The remaining cellulose was removed by acetylation for 1½ minutes at 100° C. By this sequence of chemical treatments such constituents as quartz and clay minerals, lignin and cellulose are removed and the cutinized and suberized pollen grains and spores are concentrated.

In our material, evidence for the existence of a species of *Ephedra* was provided by the presence of ridged pollen grains found at the 603–613 foot level of Well No. 2. To these grains, which could be related to modern forms of *Ephedra*, the designation "Type A" was given.[2]

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[2] This terminology is based on a study of modern *Ephedra* and will be clarified in the second part of this paper.

A total of eight intact grains of Type A and a number of fragments of similar type were found. A list of the intact fossil grains and their measurements is shown in TABLE I.

The Type A grains are prolate, their shape class index[3] varies from 1.5 to 1.9, the average being 1.7. The polar axis measures 47–53 μ, the average being 49 μ; the equatorial diameter varies from 26–33 μ, the average being 29 μ.

TABLE I. **A list of the fossil grains and their measurements.**

Ephedra	LOCATION	SIZE	NUMBER OF RIDGES	S.C.I.*
A 1	45–85.5 (S1)	47 × 29 μ	5	1.6
A 2	45–85.5 (S1)	49 × 26 μ	6	1.9
A 3	39.8–88 (S3)	53 × 33 μ	6	1.6
A 4	27.5–88 (S2)	47 × 30 μ	6	1.5
A 5	41–97 (S2)	dia. 32 μ	6	
A 6	37.5–103(S1)	50 × 27 μ	6	1.8
A 7	40–87.5 (S1)	53 × 29 μ	6	1.9
A 8	42–95.5 (S1)	47 × 30 μ	6	1.5
Average		49 × 29 μ	6	1.7

* Shape class index.

Characteristic features of these pollen grains are the narrow, undulating ridges which extend meridionally from pole to pole. These ridges fuse at the poles so that there are actually three continuous, intersecting ridges circumscribing the grain.

The exine is double and intectate. It consists of a thick endexine and a highly variable ektexine. In thickness the endexine is constant, averaging between 0.5 and 1 μ over the entire surface of the grain. However, the ektexine fluctuates considerably in thickness, averaging 0.5–1 μ along the region between the ridges and 3–4 μ at the central peak of the ridge at the equator. Furthermore, ridge height increases poleward to 4–5 μ as a result of the fusion of the ridges.

In surface view, the highly undulate wave-like pattern of the ridge is evident. The wave height measures 2–3 μ and the wave length averages 2–4 μ. In the majority of cases the ridges are continuous. However, in a few cases the ridges are composed of short, individual, angular undulations which overlap one another but are not fused. In width, the ridges average between 0.8 μ and 1.5 μ at the equator becoming thinner at the poles. With high magnification two slender, hyaline lines, averaging less than half a micron in width can be seen to run along the surface of each ridge bordering its edge. A central strip 0.2 μ wide, which remains dark, separates these two undulate and highly refractive borders. With changing focal levels a reversal of the light–dark relationship of the central strip and

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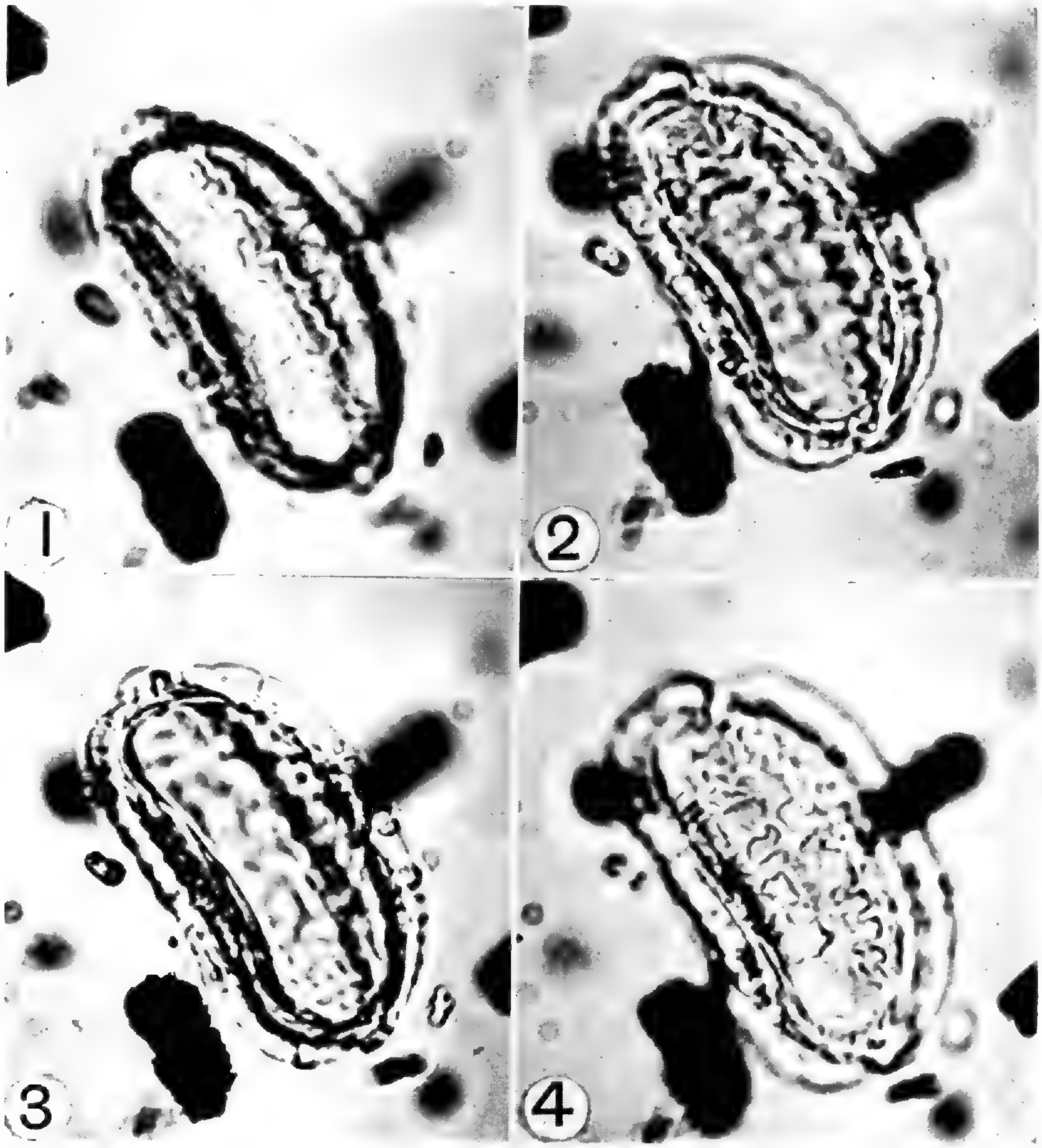
[3] Shape class index is the ratio of the long axis to the short axis (Erdtman, 1943).

the bordering lines is produced, so that the central strip appears as a single hyaline line.

In optical section, the ridges appear to be composed of individual baculate projections which extend out from the grain at right angles to the endexine. However, these are not true baculae, which are defined by Faegri and Iversen (1950) as "radial projections with the height of the element greater than the greatest diameter of projection and the upper end of the element not thicker than the base." Rather, the projections represent profile views of the ridge which is seen optically sectioned at various angles as a consequence of its highly irregular form.



TEXT-FIGURE I. *Ephedra stapfii* Steeves & Barghoorn, n. sp. 1, High focus view of the undulating ridge. 2, Same grain at mid-focus, showing the outline of the distinct, thick endexine. 3, A view slightly beyond mid-focus showing the thickness as well as the baculate appearance of the ektexine in optical section. 4, High focus view of the reticulate sculpturing found on the surface of the exine between the ridge crests on the opposite side of the grain. (All × 1000.)

The grains as a whole appear slightly angular in polar aspect with the ridges forming the angles. In this view the ridges themselves appear rounded and slightly constricted at their bases.

The surface sculpturing of the grain is rugulate-reticulate with muri 0.8–1 μ wide and 0.5 μ high extending out from the ridge crest down the ridge flanks enclosing lumina 2–4 μ in diameter.

Ephedra stapfii, n. sp. TEXT-FIGURE I.

DIAGNOSIS: Grains prolate, the polar axis varying from 47 to 53 μ, averaging 49 μ; equatorial diameter varying from 26 to 33 μ, averaging 29 μ. Ridges 5 or 6, highly undulate, extending from pole to pole. Shape class index varying from 1.5 to 1.9, averaging 1.7.

LOCALITY: Brookhaven, Long Island, New York; U.S.G.S. Well No. 2, 603–613-foot level.

GEOLOGIC OCCURRENCE: Raritan formation, lower Upper Cretaceous.

MATERIAL: Eight intact pollen grains and a number of fragments.

HOLOTYPE: No. 56011, Palaeobotanical Collections, Harvard University.

POLLEN MORPHOLOGY OF MODERN SPECIES OF EPHEDRA

Stimulated by the discovery of ephedroid pollen of considerable geologic age, an intensive study was made of the pollen of existing species of *Ephedra* with a view to determining the possible phylogenetic significance of the fossils.

Modern *Ephedra* pollen was first described extensively by Wodehouse (1935), who recognized basic differences within the genus based on his work with *E. equisetina* and *E. foliata*. In his description of *E. equisetina* he states that the pollen is characterized by having "high few ridges 5–8 with their crests blade like and arching from end to end of the grain, and in each of the grooves between the ridges is a hyaline line which follows a serpentine course its full length." A description of *E. foliata* notes that "when the ridges are more numerous, 11 to 15, they are not so high and the hyaline lines in the grooves are absent or only represented by a faint streak." His descriptions of these two species represent a few of the many variations in form that characterize pollen of the genus. Although the grains are all similar in their possession of ridges, they differ in size, in shape, in number of furrows and ridges and in exine structure. Recently, Welten (1957) studied extensively the species of the Mediterranean and western Asian regions in order to identify pollen of *Ephedra* from northern and central European late- and postglacial sediments.

Although the taxonomic treatment of the genus is somewhat unsatisfactory, forty-three of the currently recognized forty-eight species of *Ephedra* were examined in the present study. A list of the species, as well as their geographic source, is given in TABLE II. In the course of the work it became apparent that the pollen of *Ephedra* falls into certain major morphological categories. These we have arbitrarily designated A, B, C, and D. The characteristics of the four designated pollen types will be considered in detail as illustrated by descriptions of individual species. It would be of much interest to examine the relationship of these divisions, based on pollen morphology with those based on other organs and parts of the plant. Although such information is not available on a wide range of species it would add to the phylogenetic significance of the fossil forms.

POLLEN TYPE A

The grains are perprolate to subprolate in shape, their shape class index varying from 1.1 to 2.6 but generally averaging 1.8. The grains are sculptured by an average of 5 to 9 heavy, hyaline, ektexinous ridges which extend meridionally from pole to pole. The least amount of variation is observed in *Ephedra sinica* where the ridge number ranges between 4 and 6 and averages 5.8. The greatest number is found in *E. pachyclada* and *E. funera.* In the former species the ridge number varies from 5 to 12 and averages 7.9, in the latter it ranges from 6 to 13 and averages 8.3. (See Chart II which is based on an average of 50 grains per species.)

In the polar view the grains are polygonal with the alternating ridges and deep concave furrows forming an angular outline. A narrow and serpentine colpus [4] is situated at the base of each furrow. In most cases the colpi are highly undulate. The undulation of the colpus may be either rounded or highly angular and the frequency of undulation may vary, as well as the degree. The colpus may divide forming lateral branches which extend up the ridge where they may occasionally divide again. In this manner the ektexine forms a reticulate pattern, such as that found in *E. distachya.* In a few cases, as in *E. clokeyi*, the colpus scarcely divides. Also, the width of the colpus may vary, as well as the depth to which it cuts into the ektexine.

The ridge itself may be relatively smooth or highly verrucate. The term "verrucate" in the manner in which it is used here may be open to question but it is chosen for the sake of simplicity. The true "verruca" has been defined as a sculpturing element in which "the greatest diameter of the radial projection is greater than the height of the element" (Faegri and Iversen, 1950). In *Ephedra* pollen, however, the ridge crest appears verrucate in optical section because of the cutting of the ektexine by the branching colpi which extend up the ridge. In all species possessing Type A pollen, except *E. sinica*, the ridges are triangular in shape in the polar aspect with bases which vary in width from 0.5 to 18 μ and central axes which range in height from 3 to 8 μ. As was recognized by Welten (1957), the ridge in this view is composed of an inner, central, hyaline core and a thin,

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[4] Colpus (pl. colpi), germinating furrow, the area on the grain forming or surrounding the normal place of emergence of the pollen tube, with a length-breadth ratio higher than 2. The ektexine is reduced, even absent (Faegri and Iversen, 1950; Ingwersen, 1954). Although the terms furrow and colpus may be used interchangeably, in this case a distinction between the two will be made. The term "furrow" will be used to refer to the region between the ridges; the term "colpus" will be used to describe the thin, longitudinal, serpentine grooves located in the middle of the furrow area and formed by the absence of or the thinning of the ektexine.

TABLE II. **Species of Ephedra examined in this study.***

SPECIES	SOURCE	COLLECTION
Ephedra alata Dcne.	Algeria	*Bornmüller* (A)
E. altissima Desf. var. *mauritanica* Stapf	Morocco	*Balls 2487* (A)
E. americana Humb. & Bonpl. ex. Willd.	Bolivia	*Cardenas 3422* (GH)
E. andina Poepp. & Endl.	Chile	*Joffuel 2751* (GH)
E. antisyphilitica Berland	W. Texas	*E. Palmer 1292* (GH)
E. aspera Engelm. ex. S. Wats.	New Mexico	*Wright 1851* (GH)
E. bracteata Miers	Chile	*Jegons* (GH)
E. breana Phil.	Prov. Antofagasta, Chile	*Johnston 3613* (GH)
E. californica S. Wats.	San Diego Co., California	*Epling* (GH)
E. chilensis Miers	Valparaiso, Chile	*Goodspeed 4592* (GH)
E. clokeyi Cutler	Washington Co., Utah	*Gould 1526* (GH)
E. coryi Reed var. *viscida* Cutler	Rock Point, Arizona	*Cutler 2768* (GH)
E. distachya L.	Germany	*Flora Germanica Exsiccatae 7513* (GH)
E. equisetina Bge.	Turkestan	*Korshinsky, Herb. Inst. Bot. Ac. Sc. USSR 6384* (A)
E. foliata Boiss. & Kotschy ex. Boiss.	Punjab, India	*Parker 3304* (A)
E. foliata Boiss. var. *ciliata* (C.A.Mey.) Stapf		*Aitchison 537* (GH)
E. fragilis Desf.	Prov. Almeria, Spain	*Reverchon 611* (A)
E. fragilis Desf. var. *campylopoda* (C.A. Mey.) Stapf	Palaestine	*Bornmüller 1746* (A)
E. frustillata Miers	Rio Negro, Argentina	*Parodi 11858* (GH)
E. funera Cov. & Mort.	California	*Hitchcock 329* (GH)
E. gerardiana Wall.	Kashmir	*G. L. Webster 5830*
E. gracilis Phil.	Prov. Atacama, Chile	*Johnston 6208* (GH)
E. graeca C. A. Mey.	Morocco	*Baumier* (GH)
E. helvetica C. A. Mey.	Switzerland	*Reliquiae Mailleanae 7046* (GH)
E. intermedia Schrenk & C. A. Mey. var. *schrenkii* Stapf	Teheran	*Bornmüller* (A) det. *Florin*
E. major Host var. *procera* Aschers. & Graebn.	Talas Ala-Tau branch of the Tien-Shan Mountains in N. W. Kirghiz USSR.	*Herb. Hort.* (A) *Bot. Univ. Asiae Mediae*

* Pollen obtained from herbarium specimens in the herbarium of the Arnold Arboretum (A) and the Gray Herbarium (GH). The dried herbarium pollen grains were acetylized for one and one-half minutes in boiling water, washed in three changes of distilled water and mounted in glycerine jelly.

Species	Source	Collection
E. major Host var. *villarsii* Stapf	Amasya, Turkey	*Bornmüller 3544* (A)
E. monostachya L.	Saknain-Nor, Tibet	—— (A)
E. multiflora Phil. ex. Stapf	Argentina	*Johnston 6286* (GH)
E. nana Dusen	Patagonia	*Donat* 42 (GH)
E. nevadensis S. Wats.	New Mexico	*Tower* (GH)
E. ochreata Miers	Argentina	*Fisher 15* (GH)
E. pachyclada Boiss.	Afghanistan	*Aitchison 1122* (GH)
E. pedunculata Engelm. ex. S. Wats.	Mexico	*Stewart 2265* (GH)
E. peninsularis I. M. Johnston	Mexico	*Anthony 281* (GH)
E. regeliana Florin	Skardu, Baltistan	*G. L. Webster 5950*
E. rupestris Benth.	Bolivia	—— (GH)
E. sinica Stapf	Prov. Suiyuam, China	*Licewtak 13523* (A)
E. strobilacea Bge.	Turkmenistan, USSR	*Herb. Inst. Bot. Ac. Sc. USSR* (A)
E. triandra Tul.	Bolivia	*Fiebrig 2151* (GH)
E. trifurca Torr.	New Mexico	*Hortman 642* (GH)
E. torreyana S. Wats.	Rocky Mt. Region, Uinta Co., Utah	*Rollins 1719* (GH)
E. tweediana Fisch. & C. A. Mey.	Uruguay	—— *5683* (GH)
E. wraithiana I. M. Johnston	Chile	*Johnston 4705* (GH)
E. viridis Cov.	Mt. Pinos, Kunto, California	*Howell 3824* (GH)
E. vulgaris C. A. Mey.	Magnesia, Greece	*Aitchison 40* (GH)

outer, non-hyaline layer. The ridge peak is not pointed, but rounded, and averages 1.5 to 4 μ in width. The ridges tend to decrease slightly in height at the poles and the verrucae gradually disappear.

The exine is always double and may measure up to a maximum of 8 μ in thickness. It is composed of a relatively thin endexine which extends continuously and evenly around the grain, varying in thickness from 0.8 to 2 μ, and an ektexine which averages 1 to 2.5 μ in thickness in the furrow region and 3 to 6 μ along the central axis of the ridge. The ektexine is double. One component, the inner, hyaline layer forms the triangularly shaped central core of the ridge. This layer extends completely around the grain becoming thinnest at the colpi and accounts for the hyaline appearance of the colpi at some levels of focus. The thinner, outer layer is continuous or discontinuous, depending upon the depth of the colpi.

The group as a whole ranges in size along the polar axis from 51 μ, the average in *E. vulgaris*, to 69 μ, the average in *E. funera*, with considerable overlap between species. To a certain extent a distinction between species with large pollen and species with small pollen in the Type A group can be

CHART I

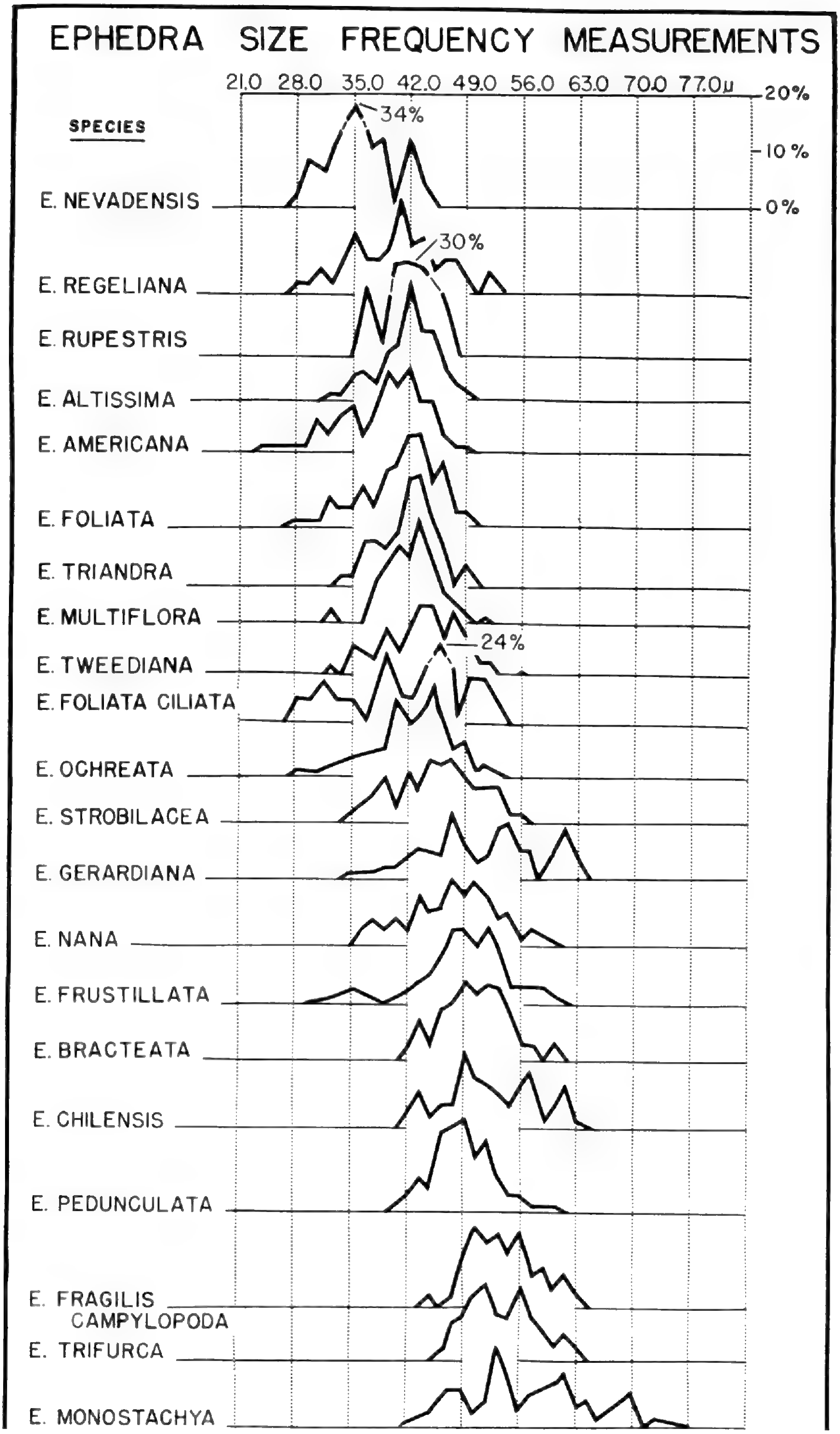
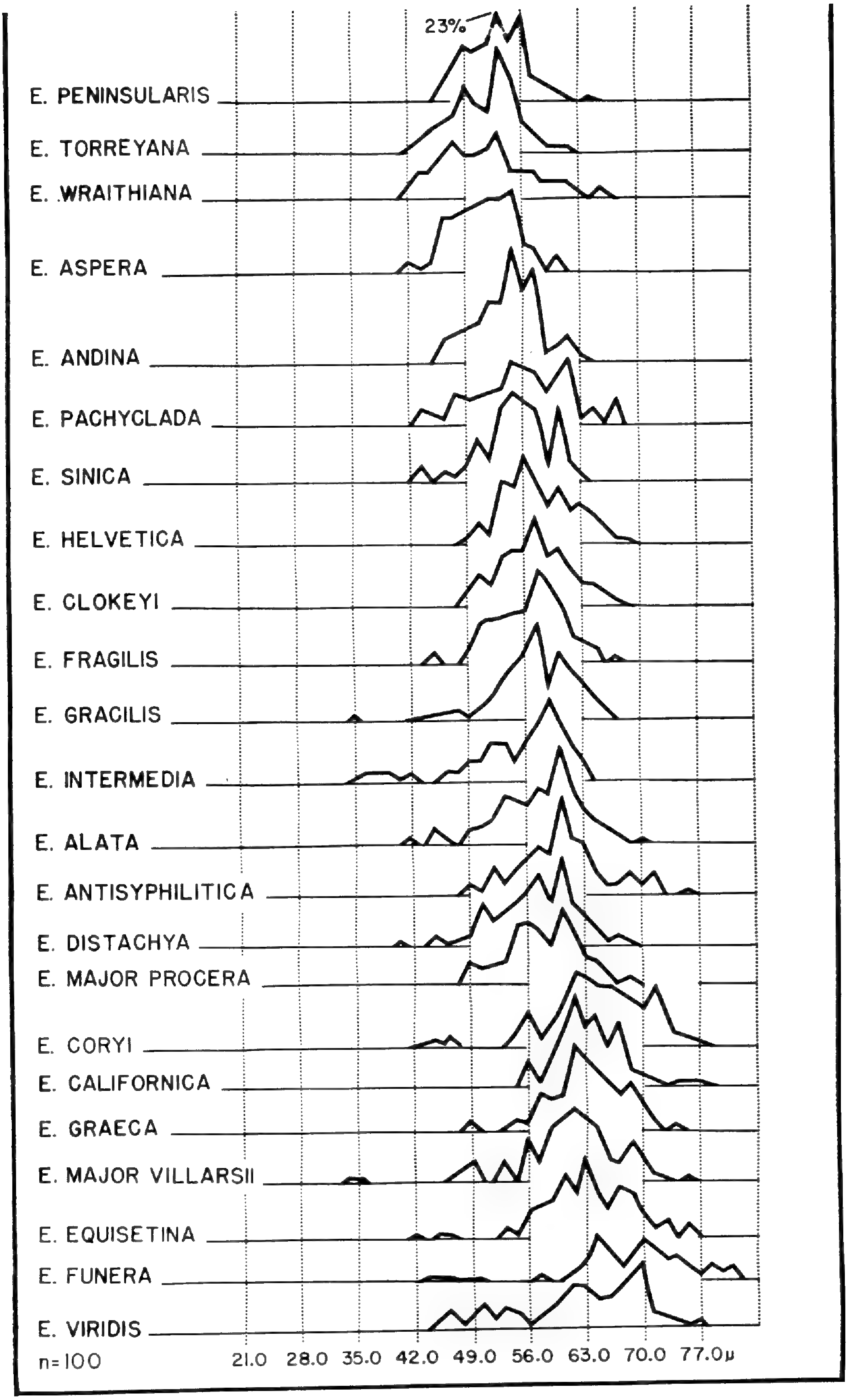

EPHEDRA SIZE FREQUENCY MEASUREMENTS
21.0 28.0 35.0 42.0 49.0 56.0 63.0 70.0 77.0µ
20%
10 %
0%
SPECIES
34%
30%
24%
E. NEVADENSIS
E. REGELIANA
E. RUPESTRIS
E. ALTISSIMA
E. AMERICANA
E. FOLIATA
E. TRIANDRA
E. MULTIFLORA
E. TWEEDIANA
E. FOLIATA CILIATA
E. OCHREATA
E. STROBILACEA
E. GERARDIANA
E. NANA
E. FRUSTILLATA
E. BRACTEATA
E. CHILENSIS
E. PEDUNCULATA
E. FRAGILIS CAMPYLOPODA
E. TRIFURCA
E. MONOSTACHYA

CHART I (*Continued*)



made, although the variability in size within the species limits the taxonomic usefulness of this character (CHART I).

DESCRIPTION OF SPECIES OF TYPE A

Ephedra distachya L. PLATE I, *fig. 3*; PLATE II, *figs. 1, 2.*

Polar axis 56 μ (40–66.5 μ); equatorial diameter 30.5 μ (24–36 μ). Ridges 6.4 (4–9). Shape class index 1.8 (1.4–2.1); prolate.

Viewed in the equatorial plane, the grains are prolate, their shape class index averaging 1.8 and lying between 1.4 and 2.1, whereas in their polar aspect they are polygonal. The furrows are deep, with concave sides and narrow, serpentine colpi situated at their bases. The grains could be termed polycolpate, possessing 4–9 undulating colpi which extend between the poles. The undulations are acutely angular and occur every 2–6 μ. The colpi average 0.8 μ in width and are formed by a complete absence of ektexine in that region. The colpate condition (according to Wodehouse, 1935) permits harmomegathic contraction and expansion along the equatorial axis of the grain where the exine is thinnest or absent. The colpi are bordered by a verrucate ridge 5–6 μ high, the verrucae measuring 2–4 μ in length and 2–3 μ in width. In optical section the individual verrucae appear semicircular in shape with slightly flattened edges. The colpi merge but do not fuse at the poles, terminating just previous to it; the ridges fuse at the poles. At the equator the ridges average 5–7.5 μ in width at the base and 2.5–3 μ at the crest. Their height ranges from 5–6 μ at the equator to 1.5 μ at the poles.

The ektexine is variable in thickness, measuring 3–4 μ along the ridge peak at the equator, decreasing toward the poles where it is 1.5–2 μ, as well as toward the colpi where it is probably absent. The endexine is thinner than the ektexine, measuring 1 μ or less and is continuous. The structure of the exine is intectate. In surface view within the furrow a coarse, reticulate sculpturing of the ektexine is visible. However, this is an inverted reticulum in the sense that the exine is not divided into lumina by the presence of walls or muri but rather by thin, narrow indentations derived from short, lateral branches of the main, longitudinal colpus. This branching occurs only at the angles formed by the undulations of the colpus (Faegri and Iversen, 1950, use the term fossulate to describe an exine dissected in this manner). These lateral branches are set off 2.5–6.5 μ apart along the course of the main colpus, and may dichotomize again and continue up the ridge to the crest, deeply cutting the thick exine into angular, closely set verrucae.

Ephedra clokeyi Cutler

Polar axis 56 μ (47–68 μ); equatorial diameter 31 μ (27–41 μ). Ridges 7.2 (6–9). Shape class index 1.6 (1.4–2.1); prolate.

Similar to the *Ephedra distachya* type but differing in the possession of a markedly smoother exine, the ridge flanks of this species are not cut by branching, lateral colpi, which in the other species of the A type extend from the main colpus up the ridge to its crest. The ridge crest, however, is slightly crenulate. Moreover, the ridge is highly irregular with undulations measuring 8–12 μ in length and 2.5–3 μ in height. At the equator the ridges average 7 μ in width at the base and 2 μ at the crest; the colpi are narrow, straight or only slightly undulate and average 0.3 μ in depth.

Thickness of the ektexine at the ridge crest at the equator 2.5–3 μ, at the poles 2 μ, in the furrow area 0.8–1 μ; thickness of the endexine 1 μ.

Ephedra coryi Reed var. **viscida** Cutler

Polar axis 63 μ (43.5–76.5 μ); equatorial diameter 31 μ (28–42 μ). Ridges 6.9 (4–9). Shape class index 2.0 (1.5–2.6); prolate–perprolate.

Although similar to those of *Ephedra distachya* in general structure, the grains differ in the possession of a thicker exine and in the shallowness of the lateral branches of the colpi. The thickness of the ektexine varies from 4.5–6 μ at the center of the ridge at the equator and decreases to 3 μ at the poles; in the region of the furrow it measures 0.8–1 μ. The endexine averages 1.6 μ in thickness. Unlike those found in *E. distachya* the verrucae are semicircular in optical section, widely spaced and project well above the surface of the grain, averaging 4–6 μ in length. Often the ridge crest itself is undulant.

The colpi average 0.5 μ in width and follow a very slightly angular path to the poles. Lateral branching occurs every 4–6 μ; secondary branching seldom occurs. The depth to which these secondary branches cut into the ektexine along the ridge crest averages 0.5 μ. At the equator the ridges average 10–11 μ in width at the base and 2–3 μ at the crest.

Ephedra equisetina Bunge

Polar axis 56 μ (39–66.5 μ); equatorial diameter 30.5 μ (23–36 μ). Ridges 5.9 (4–8). Shape class index 1.9 (1.4–2.1); prolate.

The grains, more delicate than the preceding species, have thin exines composed of ektexines measuring 1.5 μ at the ridge crests at the equator and endexines averaging 0.8–1 μ in thickness. At the poles and in the furrow region the thickness of the ektexine diminishes to 1 μ. The colpi are narrow, shallow and angular in their undulations. Lateral branching is sporadic. When present, the branches are long and widely spaced, occurring every 6–7 μ; secondary branching is absent. At the equator the ridges average 10 μ in width at the base and 1.4–1.8 μ at the crest. In optical section the ektexine along the ridge crest is verrucate with the verrucae low and semicircular in outline. They average 3.5–5 μ in length.

Ephedra funera Cov. & Mort. PLATE II, *fig. 5.*

Polar axis 69 μ (43–81.8 μ); equatorial diameter 40 μ (36–45 μ). Ridges 8.3 (6–13). Shape class index 1.7 (1.5–1.9); prolate.

This species differs from the preceding in possessing pollen of larger size with smooth, non-verrucate ridges. However, in optical section the ridge crest may appear slightly irregular in outline. At the equator the ridges measure 8–10 μ in width at the base and 2.4–2.8 μ in width at the crest.

Although the colpi are straight, occasional angular undulations may occur. There is no evidence of lateral branching.

Thickness of ektexine at the ridge crest at the equator 2–3 μ, at the poles 1.5 μ, in the furrow region 1 μ; thickness of endexine 1.4 μ.

Ephedra gerardiana Wall.

Polar axis 52 μ (35–63 μ); equatorial diameter 25 μ (21–27 μ). Ridges 9.0 (8–11). Shape class index 2.0 (1.5–2.6); prolate–perprolate.

The grains are characterized by straight, wide-crested ridges which are slightly irregular in texture. In polar view they are triangular in shape, extending 2–3 μ in height, and measuring 5–8 μ in width along the base and 1.5 μ at the crest. The ridges may undulate at the equator, the undulations ceasing near the poles. The colpi may be straight or very slightly undulant with the undulations angular and set close together. Lateral branching may or may not occur. When it does occur the branches are extremely short and shallow; consequently the furrow area is psilate, although there is a slight evidence of verrucate sculpturing along the ridge crest.

Thickness of ektexine at the ridge crest at the equator 2–3 μ, at the poles 1.5 μ, in the furrow region 1 μ; thickness of endexine 0.8 μ.

Ephedra graeca C. A. Mey.

Polar axis 62 μ (49–72 μ); equatorial diameter 31 μ (25.5–34.5 μ). Ridges 6.5 (5–9). Shape class index 1.8 (1.6–2.6); prolate.

The exine is thicker than in *Ephedra distachya*, measuring 5 μ at the ridge axis at the equator and 2–3 μ at the poles. It decreases in thickness to 0.7–1 μ in the furrow region and appears to be absent over the colpi. The endexine is continuous and averages 0.8–1.5 μ in thickness. The colpi are narrow, averaging 0.8 μ in width, angular and undulate to the poles, branching every 5–7 μ. Secondary branching is lacking but the sides of the ridge are highly dissected by long, primary, lateral colpi. The verrucae along the ridge crest are not as prominent as in *E. coryi* nor as numerous as in *E. distachya*. In optical section their surface appears flat or only slightly rounded. They vary in length from 5 to 7 μ. The average width of the ridges at the equator varies from 10 μ at the base to 3.5 μ at the crest.

Ephedra helvetica C. A. Mey.

Polar axis 57 μ (43–67 μ); equatorial diameter 27 μ (21–33 μ). Ridges 6.9 (5–9). Shape class index 2.0 (1.6–2.5); prolate–perprolate.

The grains are coarser in appearance than those of *Ephedra distachya* and are so similar in structure to *E. graeca* that pollen of these species cannot be distinguished. The ektexine averages 4–5 μ in thickness at the ridge crest at the equator and 2 μ at the poles. It decreases to 1 μ in the furrow region. The endexine measures 1–1.5 μ. Individual verrucae average 7–8 μ in length.

Ephedra intermedia Schrenk & C. A. Mey.

Polar axis 54 μ (34–65 μ); equatorial diameter 25.5 μ (20–31 μ). Ridges 7.8 (6–10). Shape class index 1.9 (1.2–2.2); prolate–perprolate.

Although the verrucate ridge is composed of series of smaller, angular verrucae, set close together, measuring 2–3 μ in length, the grains appear coarser than those of *E. distachya* as a result of the thicker exine. At the equator the ridges average 6–7 μ in width at the ridge base and 3.5–4 μ at the apex; the width of the furrow area ranges between 5–5.5 μ. In optical section the ridge surface appears almost smooth because of the shallowness of the dissecting grooves. The colpi are thin, shallow and slightly angular in their undulation. Secondary branching does not occur.

Thickness of the ektexine at the ridge crest at the equator 4–5 μ, at the poles 2 μ, in the furrow region 1 μ; thickness of the endexine 1.5–1.8 μ.

Ephedra major Host var. **procera** Aschers. & Graebn.

Polar axis 56 μ (37–68 μ); equatorial diameter 23 μ (20–27 μ). Ridges 6.3 (5–8). Shape class index 2.3 (1.9–2.6); prolate–perprolate.

The ridge surface is verrucate. In optical section the verrucae are distinctly visible, slightly rounded and average 5–6 μ in length. At the equator the ridges average 8–10 μ in width at the base and 3 μ in width at the crest. The furrow region measures 5–8 μ in width. The colpi are thin, averaging 0.5 μ in width, extremely faint and slightly rounded in their undulations. Long, primary branches of the main colpi occur every 2–6 μ.

Thickness of the ektexine at the ridge crest at the equator 4 μ, at the poles 2 μ, in the furrow region 1 μ; thickness of the endexine 0.5–0.8 μ.

Ephedra major Host var. **villarsii** Stapf

Polar axis 59 μ (33–74 μ); equatorial diameter 27 μ (20–33 μ). Ridges 6.5 (5–8). Shape class index 1.9 (1.6–2.6); prolate.

These grains are similar to those of *E. equisetina* and *E. monostachya* in the possession of a characteristically thin exine which is composed of an ektexine measuring 0.8–1.4 μ in thickness along the ridge crest and an endexine averaging 0.5–0.8 μ. The thickness of the ektexine in the furrow region decreases to 0.5–0.8 μ. The colpi are narrow and shallow measuring 0.5 μ in depth, and slightly undulate to the poles. Sporadic lateral branching may occur. In some cases these may be cut off every 5.5–7 μ along the course of the main colpi. However, they seldom continue up the ridge surface to its crest. The delicacy of the grain is due to the absence of reticulation or to the extremely faint reticulation on the ridges. The ridges are slightly verrucate along the crest, with verrucae semicircular in outline. These average 2.8–3.5 μ in length and are low, ranging in height from 0.8 to 1 μ. At the equator the width of the ridges at the base is 9 μ and at the crest is 1 μ.

Ephedra monostachya L.

Polar axis 56 μ (42–75 μ); equatorial diameter 32 μ (22–39 μ). Ridges 7.3 (6–9). Shape class index 1.6 (1.3–1.8); prolate.

As in the case of *E. equisetina*, the grains are characterized by thin exines, with ektexines measuring 1.5–2 μ along the ridge crest and endexines measuring 0.5–0.8 μ in thickness. The ridges are delicate, and irregularly verrucate with the length of the individual verrucae varying from 4–8 μ. In optical section the verrucae average 1–1.4 μ in height along the ridge crest and the majority are gently domed along their protruding surface. Colpi are shallow, averaging 0.8 μ in depth, and slightly undulate with only occasional branching.

Ephedra pachyclada Boiss.

Polar axis 55 μ (43–68 μ); equatorial diameter 30 μ (27–36 μ). Ridges 7.9 (5–12). Shape class index 1.7 (1.1–1.9); prolate.

The grain is featured by an endexine which may be as thick as the ektexine. The colpi are narrow, shallow and acutely angular in surface view. Short, lateral branches occur every 2–3 μ at the apices of the angles. Secondary branching seldom occurs. As a result of the shallowness of the lateral branches of the colpus the verrucae are indistinct. They average 2–3 μ in length. In optical section their surfaces are slightly rounded. At the equator the ridges average 5.5–8 μ in width at the base and 3 μ in width at the crest.

Thickness of the ektexine at the ridge crest at the equator 2–3 μ, at the poles 1.5 μ, in the furrow region 1 μ; thickness of the endexine 1.6–2 μ.

Ephedra sinica Stapf PLATE I, *fig. 2*; PLATE III, *figs. 3–6*; PLATE IV, *figs. 5, 6.*

Polar axis 54 μ (42–62 μ); equatorial diameter 28 μ (25–31 μ). Ridges 5.8 (4–6). Shape class index 1.6 (1.4–1.8); prolate.

This species possesses the most highly ornamented pollen grains to be found in the genus. They are sculptured by four to six steep, undulating ridges which project sharply above the rounded contours of the grain. The ridge undulations are slightly rounded to angular and the wave of the undulation measures between 3 and 5 μ in length and 3 and 4 μ in height. Furthermore, small ektexinous ridges, or muri, 0.8–1 μ wide, extend out from the crest of the ridge into the inter-ridge area in a rugulate-reticulate sculpturing pattern enclosing lumina 2–4 μ in diameter.

Viewed in the equatorial plane, the grain is prolate to ellipsoidal, whereas in polar aspect the outline is polygonal with the ridges situated at the angles of bulging, convex sides. Also in polar view, it may be seen that the ridges are rounded, with an average diameter of 1.5 μ, a height of 4–5 μ and are slightly constricted at their bases.

Occasionally, evidence of a thin, slightly branched colpus at the base of the ridge can be seen. However, when present the colpus is indistinct.

The exine is double. The ektexine, at the center of the ridge at the equator varies from 4 to 5 μ in thickness, decreasing slightly toward the poles. In polar view, the ektexine abruptly thins, at the base of the ridge, ceasing altogether at the colpi. The endexine is 2–3 μ thick. In profile view, the ektexine appears to be composed of baculae 4 μ high and 2 μ wide. These are merely the optical sections of the undulating ridge.

Ephedra viridis Cov. PLATE IV, *figs. 1, 2.*

Polar axis 61 μ (44–77 μ); equatorial diameter 34 μ (30–39 μ). Ridges 7.1 (5–9). Shape class index 1.7 (1.5–1.9); prolate.

The grains are characterized by straight, thin-crested, smooth ridges. The main, longitudinal colpi are distinct, narrow and acutely angular. Short lateral branches occur every 2–3 μ and an occasional secondary branch may be found. In optical section, verrucae are evident but they are faint because of the shallowness of the lateral colpi and their surface outline is flattened. At the equator the ridges average 10–14 μ in width at the base and 3.5 μ at the crest.

Thickness of the ektexine at the ridge crest at the equator 3 μ, at the poles 2 μ, in the furrow region 1 μ; thickness of the endexine 1.5 μ.

Ephedra vulgaris C. A. Mey.

Polar axis 51 μ (49–57 μ); equatorial diameter 28 μ (25–31 μ). Ridges 7. Shape class index 1.7 (1.5–1.9); prolate.

The ridges are smooth, measuring at the equator 3 μ in width at the crest and 7–10 μ at the base. The colpi are thin grooves which branch occasionally but, as in the case of *Ephedra funera*, the lateral branches do not continue far up the ridge.

Thickness of the ektexine at the ridge crest at the equator 2–3 μ, at the poles 0.7 μ, in the furrow region 1 μ; thickness of the endexine 1 μ.

POLLEN TYPE B

This type is approximately of the same size as Type A. The majority of grains are basically polycolpate, although the colpus is often indistinct, and all are sculptured by ektexinous ridges extending meridionally across the grain merging with those from the opposite side.

However, the grains differ significantly from the preceding type in furrow and ridge characteristics. In Type B the ektexine is thickened irregularly to form extremely narrow, undulating, psilate ridges. When viewed in the equatorial plane the narrow ridges appear as highly refractive, smooth, serpentine lines extending the length of the grain. In some cases as in *Ephedra californica*, the undulations continue to the poles; in others, as *E. altissima*, the height of the ridge as well as the degree of undulation decreases at the poles.

The number of ridges in Type B is generally more numerous than in Type A, ranging, on the average, from 10 to 13. The least amount of variation in our material occurs in *E. californica* where the number of ridges ranges from 10 to 14; the greatest amount of variability was observed in *E. pedunculata* where the ridge number ranges from 9 to 17 (CHART II). The high degree of variability within some species results

CHART II

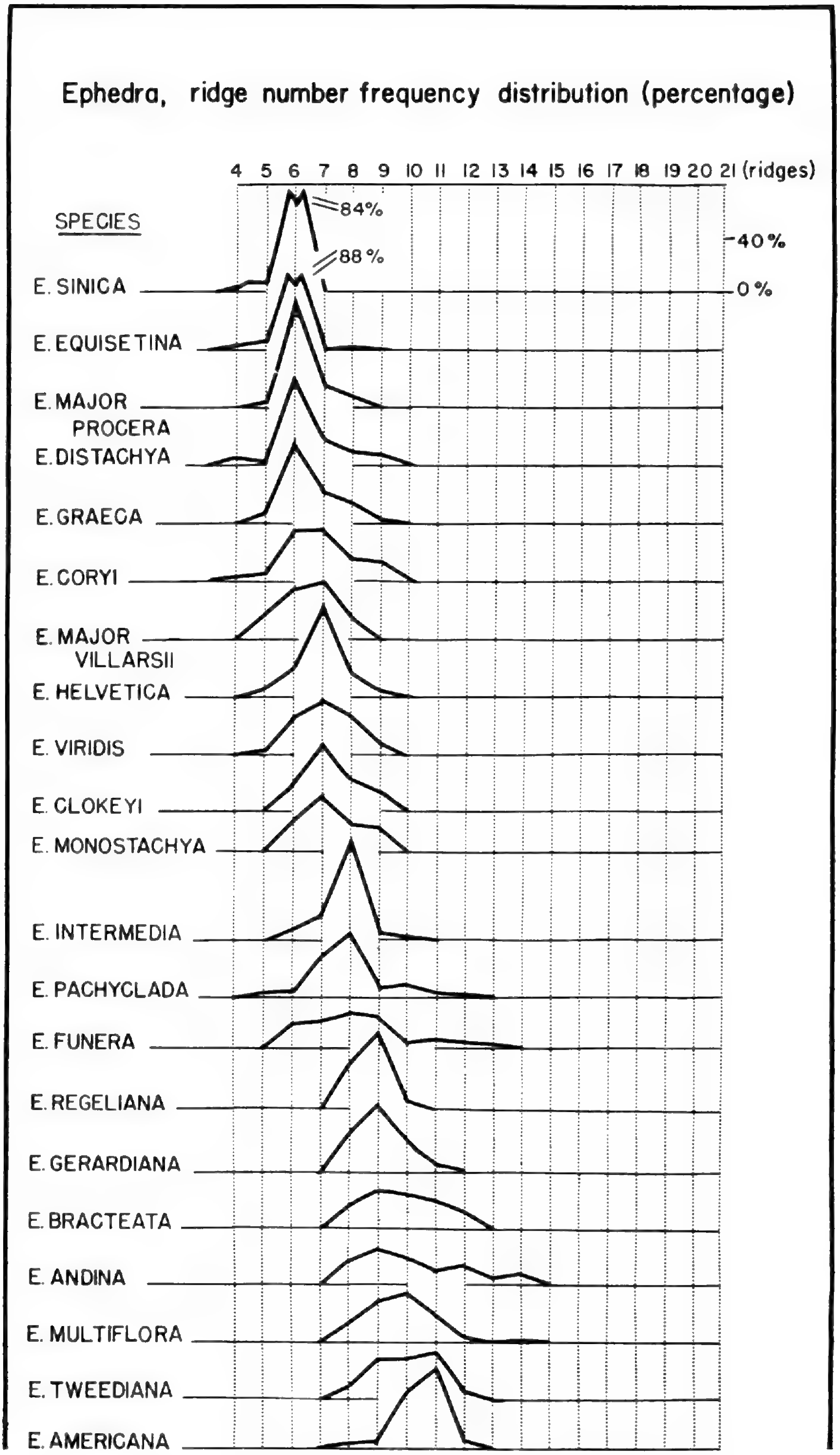
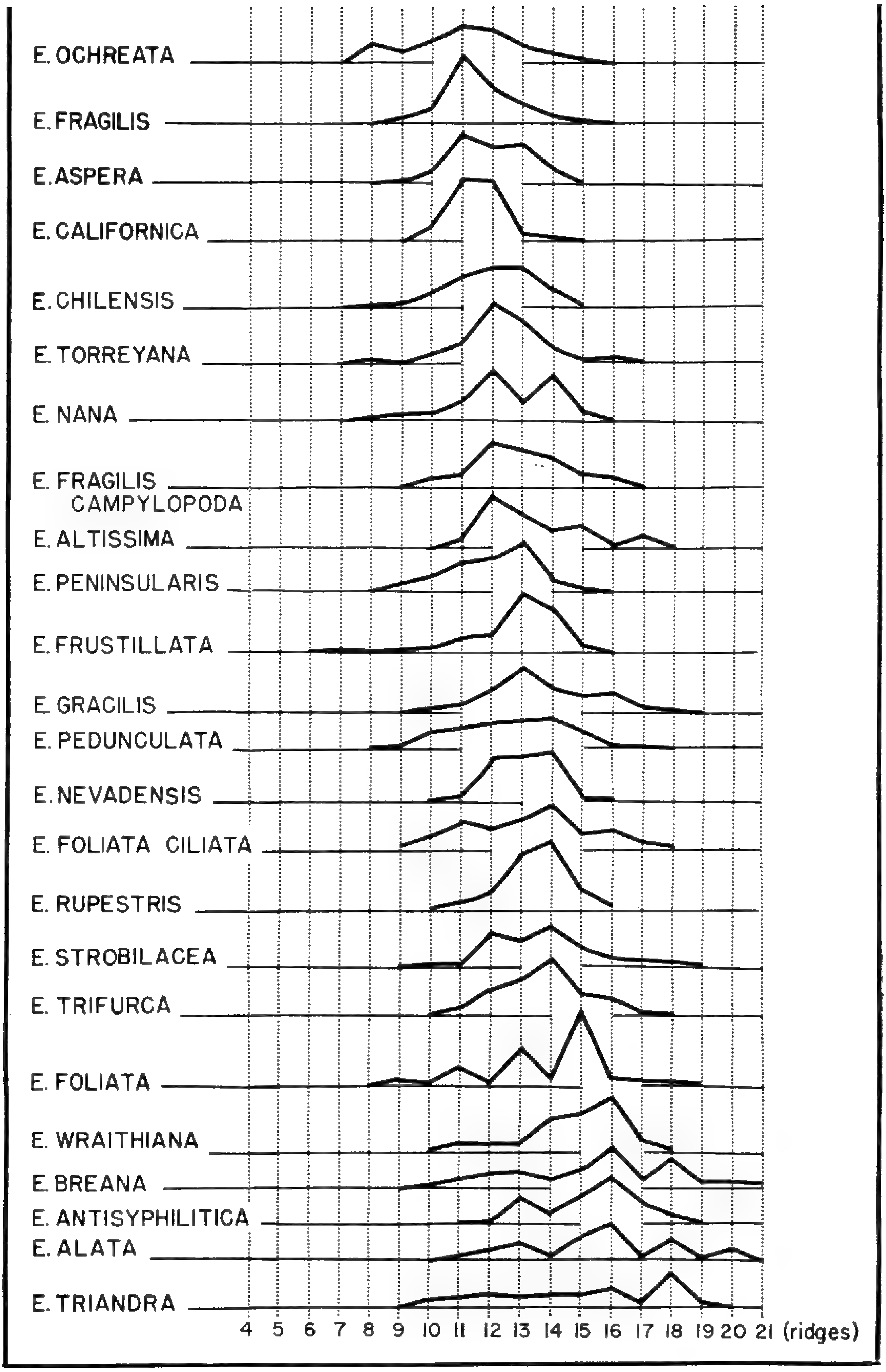

Ephedra, ridge number frequency distribution (percentage)
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21 (ridges)
84%
88%
40%
0%
SPECIES
E. SINICA
E. EQUISETINA
E. MAJOR PROCERA
E. DISTACHYA
E. GRAECA
E. CORYI
E. MAJOR VILLARSII
E. HELVETICA
E. VIRIDIS
E. CLOKEYI
E. MONOSTACHYA
E. INTERMEDIA
E. PACHYCLADA
E. FUNERA
E. REGELIANA
E. GERARDIANA
E. BRACTEATA
E. ANDINA
E. MULTIFLORA
E. TWEEDIANA
E. AMERICANA

CHART II (*Continued*)



in a few individual cases of overlapping values with respect to ridge number in Types A and B. This somewhat lessens the value of but does not preclude the use of this characteristic, in conjunction with others, as a means of separating the two groups. The high amount of intraspecific variation does, however, prevent the use of this characteristic alone in separating species within each group, or in distinguishing between groups.

The exine is distinctly double and is composed of a thin, continuous endexine and an ektexine which may be continuous or discontinuous. The ektexine is laid down in the form of ridges which in polar view are triangular in outline. In this aspect the highly refractive component of the ridge comprises the central core of the triangle which, according to Welton (1957), varies in shape depending upon species. This, in turn, is covered by the non-hyaline layer. Both of these different layers form the ektexinous ridge. In this respect the structure of the ridge is similar to that found in Type A as well as in Type C. The width of the base of the triangle may vary from 2 to 4 μ, decreasing at the top to a narrow peak of 0.5 to 1 μ; the height of the ridge may range from 2 to 3.5 μ. The ridges are not as massive as in the Type A group. Consequently, the grains appear more delicate, an appearance enhanced by the lack of verrucae along the ridge and the absence of reticulate sculpturing in the furrows.

In a few species colpi are absent.[5] When colpi are present they are located at the base of the furrow, extending unbranched their full length. Moreover, the distinctness of the colpi varies between species, depending upon whether the colpus is the result of a complete absence or merely a thinning of the ektexine. In *E. chilensis* the colpi are only occasionally discernible, whereas in *E. tweediana* well defined colpi can be observed.

DESCRIPTIONS OF SPECIES OF TYPE B

Ephedra altissima Desf.

Polar axis 40 μ (30–49 μ); equatorial diameter 23 μ (21–27 μ). Ridges 13.3 (11–17). Shape class index 1.6 (1.4–1.8); prolate.

The ridges undulate slightly in the equatorial region of the grain, gradually ceasing near the poles. In polar view the ridges measure 5–6 μ in width at the base and decrease to a peak 1–1.5 μ wide. The thickness or height of the ektexinous ridges averages 2–3 μ at the equator. The ridge undulations are variable in extent and may average 4–8 μ in length and 2–3 μ in width. A faint, unbranched, straight colpus is present at the base of each ridge.

Thickness of the ektexine in the furrow region 0.8 μ; thickness of the endexine 1 μ. At the poles the ektexine often projects 5–6 μ beyond the endexine.

Ephedra antisyphilitica Berland.

Polar axis 59 μ (42–59 μ); equatorial diameter 43 μ (33–49 μ). Ridges 15.3 (12–18). Shape class index 1.4 (1.2–1.8); prolate.

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[5] For our definition of colpus as applied to *Ephedra* pollen see footnote 4.

This species possesses the largest pollen grains in the group. These may be further characterized by the presence of an extremely tenuous ektexine which easily becomes dissociated from the endexine. The ektexine may become free at one pole only, at both poles, or irregularly around the entire grain. The ektexine is irregularly thickened forming ridges which measure 2.5 μ in height at the equator. In the polar aspect they are triangular in shape and at the equator average 2.5–5 μ in width at the base and 0.7 μ at the crest. The ridges may be either highly undulate, slightly undulate or, in a few cases, almost straight. A slightly undulate, faint, unbranched colpus is present between each ridge. The thickness of the ektexine decreases to 0.5 μ in the furrow region. The endexine averages 1 μ in thickness.

Ephedra californica S. Wats. PLATE I, *fig. 5*; PLATE III, *figs. 1, 2.*

Polar axis 63 μ (53–77 μ); equatorial diameter 32 μ (21–40 μ). Ridges 11.5 (10–14). Shape class index 2.0 (1.5–2.5); prolate–perprolate.

The grains are characterized by ridges 6–7 μ apart that zigzag meridionally the length of the grain. In polar view, the ridges appear triangular with a base measuring 3–4 μ in width, decreasing to a thin crest of 0.5–1 μ. The serpentine ridge undulates sharply throughout its length. The ektexine is 2.4–3.2 μ thick at maximum at the equator, decreasing to 0.5–1 μ in the furrows. The endexine measures 1–1.6 μ. Slightly undulant colpi may be present. The type of undulation varies from tightly angular to widely spaced and semicircular. Occasional primary branches of the main colpi are evident.

Ephedra chilensis Miers PLATE IV, *fig. 3.*

Polar axis 52 μ (35–68 μ); equatorial diameter 30 μ (27–31 μ). Ridges 11.9 (8–14). Shape class index: 1.6 (1.3–1.8); prolate.

Among the Type B species, these grains are distinctive in the greater thickness of their exine. The ektexine averages 2–3 μ along the ridge crest; the endexine measures 1.5–2.8 μ. A thin, serpentine, straight colpus may be visible in each furrow. The ridges are undulant to a varying degree. At the equator they average 5–6 μ in width at the base and 0.5 μ at the crest.

Thickness of the ektexine at the furrow region 1–1.4 μ. As in some of the preceding grains, the ektexine at the poles may project as much as 5 μ beyond the endexine.

Ephedra fragilis Desf. var. **campylopoda** (C. A. Mey.) Stapf

Polar axis 56 μ (44–66 μ); equatorial diameter 30 μ (22.5–36 μ). Ridges 12.9 (10–16). Shape class index 1.8 (1.2–2.4); prolate–perprolate.

Although larger than most members of this group, the pollen grains of this species are smaller than those of *Ephedra californica* or *E. antisyphilitica.* The ridges are narrow at the crest, varying from 1–1.5 μ; wide at the base, the width averaging 2–3 μ; and measure 0.8–1 μ in height at the equator. The ridge crest is acutely undulate with undulations averaging

2.5–5 μ in length and 2.5 μ in width. However, the degree of undulation tends to diminish toward the poles. Indistinct, thread-like, straight colpi are present.

There is a strong tendency for the endexine and the ektexine to separate resulting in the shedding of the ektexine by the grain. This separation is evident at the poles where the ektexine becomes detached and projects out 3–5 μ beyond the endexine to form rectangular enclosures between the two exine layers.

Thickness of the ektexine at the ridge crest at the poles 0.5 μ, in the furrow region 0.5 μ; thickness of the endexine 0.5 μ.

Ephedra multiflora Phil. ex Stapf

Polar axis 41.5 μ (31.5–51 μ); equatorial diameter 24 μ (20–30 μ). Ridges 9.8 (8–14). Shape class index: 1.6 (1.1–2.0); prolate.

The grains are similar to those of *Ephedra tweediana* in their small size, and resemble *E. fragilis* var. *campylopoda* in a tendency to shed their ektexine. The ektexine is 2–3 μ thick at the ridge crest at the equator, often ballooning out 5–6 μ beyond the endexine at the poles. The ridges are featured by a few minor undulations measuring 6–7 μ in length and 3–3.5 μ in width. At the equator the ridges average 7 μ in width at the base and less than 1 μ at the crest. Distinct but thin, straight, unbranched colpi are present.

Thickness of the ektexine in the furrow region 0.8 μ; thickness of the endexine 0.8–1.2 μ.

Ephedra nevadensis S. Wats. PLATE IV, *fig. 7.*

Polar axis 35 μ (31.5–45 μ); equatorial diameter 22 μ (18–27 μ). Ridges 13.0 (11–15). Shape class index 1.6 (1.4–1.9); prolate.

Characteristic features of these grains are the closely undulate colpi which extend along the center of the furrows. The undulations are angular and occur every 2–2.5 μ.

The ridge crests are extremely thin and vary from straight to closely undulate with waves which range in length from 2–2.5 μ and in width from 1.4–1.8 μ. At the equator the ridges measure 3.5–5 μ in width at the base and 0.3–0.5 μ at the crest.

Thickness of the ektexine at the ridge crest at the equator 2.8 μ, at the poles 1.5 μ; thickness of the endexine 0.8 μ. The ridges project out a distance of 2.8 μ beyond the endexine at the poles.

Ephedra pedunculata Engelm. ex S. Wats.

Polar axis 48 μ (40–60 μ); equatorial diameter 29 μ (25–39 μ). Ridges 12.6 (9–17). Shape class index 1.6 (1.4–1.8); prolate.

The ektexine is thicker than the endexine, measuring 2.8 μ at the ridge crest at the equator and 2 μ at the poles. In polar view the ridge measures 3.5–7 μ in width at the base, decreasing to 0.7–0.1 μ at the crest. The colpi are indistinct, thin and slightly undulate. Ridge undulations are irregular in occurrence and measure 4–6 μ in length and 1.5–3.5 μ in width. The thickness of the endexine is 1.6 μ increasing to 2–2.5 μ at the poles.

Ephedra tweediana Fisch. & C. A. Mey.

Polar axis 42 μ (21–55 μ); equatorial diameter 25 μ (24–28 μ). Ridges 10 (8–12). Shape class index 1.7 (1.4–1.9); prolate.

The grains of this species are ornate with highly undulant ridges. At the poles the fused ridges abruptly project forming a circular process at each end of the grain. The ridges are high, projecting 5 μ at the equator. Their basal width at the equator varies from 4 to 12 μ; the crests average 0.5–1 μ. A distinct, straight colpus is present.

Thickness of the ektexine in the furrow region 2 μ; thickness of the endexine 1.5 μ.

POLLEN TYPE C

Although similar to Type B in many respects, the ridge structure in Type C is prevailingly different. The ridges are somewhat higher than in Type B, and usually straight. In some cases, however, there is a tendency for slight undulation in the ridge crest. Although in their most characteristic form the two types are readily separable, there is a tendency in some species for pollen grains to exhibit features of both the B and C types. Hence the Type B and Type C categories are not consistently separable as other than varying degrees of morphological expression. It might be argued that the two types should be merged as one, but in our opinion there is a preponderance of one or the other within a given species, and hence the concept has morphological validity. As will be shown later there is no difficulty in distinguishing the A types from the D types, nor is there in distinguishing the C from the D nor the A from the C types. In this respect we are dealing with a continuous spectrum of structural variation on which arbitrary limits are imposed.

DESCRIPTIONS OF SPECIES OF TYPE C

Ephedra americana Humb. & Bonpl. ex Willd. PLATE II, *figs. 6, 7.*

Polar axis 38 μ (27–49 μ); equatorial diameter 25 μ (21–30 μ). Ridges 10.5 (8–12). Shape class index 1.6 (1.2–1.8); prolate.

A conspicuous feature of these grains is the outbulging of the ektexine which may exceed 6 μ on one or both sides, or circumferentially around the complete grain freeing the two layers of the exine.

In those cases in which the ektexine is attached to the endexine, it measures 2–2.5 μ in thickness at the equator and slightly thicker (3 μ) at the poles. The average thickness of the endexine is 2 μ. With separation of the exine layers the whole grain expands. However, the furrowed ektexine is more flexible than the continuous endexine and expands to a greater degree, resulting in an ektexine "shell" measuring approximately 40 × 30 μ and an endexine "shell" whose average dimensions are 30 × 20 μ.

This disproportionate increase in diameter of the two wall layers of the grain effects a decrease in thickness of the ektexine and endexine proportionately. The average thickness of the ektexine in the mature grain is from 1 to 1.2 μ; whereas the thickness of the endexine remains slightly under 2 μ. Because of the variable nature of the ektexine, the outline of the grain in both polar and equatorial views is highly irregular, but the endexine appears regular in outline and prolate in shape. The ridge crests are narrow, averaging 1 μ in width at the equator and are spaced 4–5 μ apart. At the base of each furrow is a distinct, thread-like, unbranched colpus.

Ephedra andina Poepp. & Endl. PLATE IV, *fig. 4.*

Polar axis 53 μ (42–63 μ); equatorial diameter 27 μ (24–30 μ). Ridges 10.3 (8–14). Shape class index 1.8 (1.7–2.1); prolate.

These grains possess the characteristic, psilate ridges of Type C. At the equator they may measure as much as 4 μ in height. The base of the ridge averages 5 μ in width at the equator, and 0.5–0.8 μ at the crest. The majority of ridges are straight. A narrow, slightly undulating, unbranched colpus is visible at the base of each furrow. The ektexine is thicker than the endexine and averages 3 μ along the ridge crest, thinning to 1 μ in the furrow. The endexine averages between 2 μ and 2.5 μ in thickness. There is a slight projection of the ektexine at the poles.

Ephedra aspera Engelm. ex S. Wats. PLATE I, *fig. 1*; PLATE IV, *fig. 8.*

Polar axis 50 μ (42–59 μ); equatorial diameter 25 μ (22–27 μ). Ridges 11.9 (9–14). Shape class index 1.8 (1.5–2.2); prolate.

The ridges are thin and slight, rising 1.6–2.5 μ above the endexine at the equator, decreasing to 1 μ at the poles. At the equator they measure 4–5 μ in width at the base and 1 μ at the ridge crest. A conspicuous feature of the grains is the projection of the ektexine 3–4 μ beyond the endexine forming small, handle-like structures at both poles. A narrow, slightly undulating colpus is present at the base of each furrow.

Thickness of the ektexine in the furrow region 0.5 μ; thickness of the endexine 1.6 μ.

Ephedra bracteata Miers

Polar axis 50 μ (42–60 μ); equatorial diameter 29 μ (25–33 μ). Ridges 9.8 (8–12). Shape class index 1.6 (1.5–1.7); prolate.

In contrast to the thin, smooth condition of the ridges in *Ephedra aspera*, the ridges in *E. bracteata* are heavy, wide and slightly irregular in surface view. At the equator they measure 5–7 μ in width at the base and 2 μ in width at the ridge crest. The bases of the ridges are cut by an irregular, highly undulate colpus which occasionally branches.

Thickness of the ektexine at the ridge crest at the equator 3–3.5 μ, at the poles 2 μ, in the furrow region 1 μ; thickness of the endexine 3 μ.

Ephedra foliata Boiss. & Kotschy ex. Boiss.

Polar axis 44 μ (30–53 μ); equatorial diameter 28 μ (22–30 μ). Ridges 13.9 (9–18). Shape class index 1.6 (1.4–2.0); prolate.

The grains are featured by narrow, straight ridges, measuring 4–7 μ in width at the base at the equator and 0.5–1 μ at the crest. They extend 1.8–2.5 μ in height at the equator decreasing to 1.4 μ at the poles. The majority of the ridges are straight but a few undulating ones are present. A narrow, straight colpus is present at the base of each furrow.

Thickness of the ektexine in the furrow region 0.5 μ; thickness of the endexine 2 μ.

Ephedra foliata Boiss. var. **ciliata** (C. A. Mey.) Stapf

Polar axis 47 μ (44–54 μ); equatorial diameter 29 μ (25–36 μ). Ridges 13.2 (10–17). Shape class index 1.5 (1.1–1.7); prolate.

The ridges are narrow and straight, measuring 3.5 μ in height at the equator, decreasing to 2 μ at the poles. At the equator they average 3.5–4 μ in width at the base and 0.5 μ at the crest. Thin, thread-like colpi are present at the base of each furrow.

Thickness of the endexine 1.4 μ.

Ephedra fragilis Desf.

Polar axis 53 μ (44–63 μ); equatorial diameter 33 μ (28–51 μ). Ridges 11.5 (9–15). Shape class index 1.5 (1.3–1.7); prolate.

The grain appears almost spherical in equatorial view with projecting, ektexinous ridges at the poles. The ridges measure 1–1.5 μ in height at the equator and project a distance of 3–4 μ beyond the polar limits of the endexine.

With high magnification, the crest of the ridges exhibits tight undulations; under low power there is little evidence of this condition and the ridge crests appear straight. The ridge crests are thin, averaging 0.5 μ at the equator; the bases of the ridges are wider, averaging 5 μ at the equator and decreasing to 1.4 μ at the poles. A thin but distinct, slightly undulating colpus is present in each furrow.

Thickness of the ektexine in the furrow region 0.8 μ; thickness of the endexine 2 μ.

Ephedra frustillata Miers

Polar axis 48 μ (30–60 μ); equatorial diameter 30 μ (28–36 μ). Ridges 12.7 (7–15). Shape class index 1.5 (1.2–1.7); prolate.

These differ from some of the preceding grains in the larger size and in the absence of any tendency toward separation of the exine layers. In company with *Ephedra regeliana* and *E. ochreata* they possess a thin exine which measures 1.5 μ along the ridge crest at the equator, a thin endexine of 0.8 μ, and narrow, straight ridges.

Thickness of the ektexine at the ridge crest at the poles 1 μ, in the furrow region 0.5 μ.

Ephedra nana Dusen

Polar axis 46 μ (35–60 μ); equatorial diameter 27 μ (24–30 μ). Ridges 12.4 (8–15). Shape class index 1.6 (1.4–2.0); prolate.

The grains possess ridges of the Type C structure which are bordered at their bases by thin, tightly undulate or straight colpi. The ridges average 3.5–5 μ in width at the equator at the base and 0.5 μ at the crest.

Thickness of the ektexine along the ridge crest at the equator 2 μ, at the poles 0.7–1 μ; thickness of the endexine 1.5 μ. The ektexine projects 2.5–3 μ beyond the endexine at the poles.

Ephedra ochreata Miers

Polar axis 41 μ (27– 51 μ); equatorial diameter 22 μ (18–30 μ). Ridges 11.0 (8–15). Shape class index 1.7 (1.6–2.0); prolate.

The exine is thin, the ektexine measuring 0.8–1.4 μ in thickness along the ridge crest; the endexine as thick as the ektexine or slightly more so varying between 1 and 1.5 μ. In the furrow region the thickness of the ektexine decreases to 0.5 μ. A slight increase in thickness of the ektexine may or may not occur at the poles. At the equator the width of the ridges at the base averages 3.5–6 μ; that of the ridge crest is 0.7 μ. A tightly undulate to straight colpus is present at the base of each ridge. In optical section the ridge crest is minutely irregular in outline.

Sculpturing of the ektexine: slightly scabrate.

Ephedra peninsularis I. M. Johnston

Polar axis 52 μ (38–63 μ); equatorial diameter 30 μ (30–31 μ). Ridges 11.9 (9–15). Shape class index 1.6 (1.5–1.8); prolate.

The ridges are completely straight, averaging at the equator 5–8.5 μ in width at the base and 1–2 μ at the crest. Each furrow contains a distinct, thin, straight colpus. Although the surface of the ridge is psilate, the overall appearance of the grain is one of massiveness as a result of the thick exine.

Thickness of the ektexine at the ridge crest at the equator 3–4 μ, at the poles 4 μ, in the furrow region 1 μ; thickness of the endexine 1.6 μ.

Ephedra regeliana Florin

Polar axis 38 μ (28–51 μ); equatorial diameter 19 μ (16–21 μ). Ridges 8.7 (8–10). Shape class index 1.9 (1.6–2.0); prolate.

Distinctive because of size, this species, together with *E. americana*, possesses the smallest pollen grains of the group. However, the grains differ from those of *E. americana* in the possession of an ektexine which adheres closely to the endexine. The ridges are straight to slightly undulate, and measure 1–2 μ in height at the equator decreasing to 0.5–1 μ at the poles. At the equator they average 5–7 μ in width at the base and 1–1.2 μ at the crest. A slightly undulate colpus is present in each furrow.

Thickness of the ektexine in the furrow region 0.5 μ; thickness of the endexine 0.5 μ.

Ephedra torreyana S. Wats.

Polar axis 51 μ (38–61 μ); equatorial diameter 27 μ (25–30 μ). Ridges 12.3 (8–16). Shape class index 1.8 (1.5–2.0); prolate.

The exine is thin, composed of an ektexine measuring 1.6 μ in thickness along the ridge crest, and an endexine equally as thick as the ektexine, 1.6 μ. There is some tendency for the ektexine to project 2–3 μ beyond the polar limits of the grain. The ridges are straight and at the equator measure 0.8 μ in width at the crest and 4 μ through the base. Thin, unbranched straight or slightly undulant colpi are visible.

Ephedra wraithiana I. M. Johnston

Polar axis 50 μ (38–65 μ); equatorial diameter 26 μ (24–28 μ). Ridges 14.8 (11–17). Shape class index 1.6 (1.4–2.1); prolate.

The grains are similar in structure to the preceding species. They possess characteristic Type C ridges measuring 4.5–5 μ in width at the base at the equator, and 1 μ at the crest. Each furrow is featured by a thin, straight colpus. In optical section the ridges appear slightly irregular in outline.

POLLEN TYPE D

The grains of Type D are characterized by wide, low, gently rounded, ektexinous ridges which measure 2–3 μ in height and 3.5–9 μ in width. In polar view the ridges appear semicircular in outline, in contrast to the triangular outline of the ridges in the three preceding groups. The furrows which abruptly flank the ridges at their bases are narrow (1–3.5 μ), unbranched and straight. They are the result of extreme thinning of the ektexine. No colpi are present.

Within this group occurs the species which possesses the greatest number of ridges, *E. alata* (Chart II). Moreover, the average number for the group as a whole is greater than in Types B and C. Pollen grains of the D type are quite distinctive and readily separable from the other pollen types. However, within some species, possessing predominantly Type D grains, occasional grains of the B and C types occur. None of the seven species possessing D type grains shows the least tendency toward the A type.

DESCRIPTION OF SPECIES OF TYPE D

Ephedra alata Dcne.

Polar axis 57 μ (42–70 μ); equatorial diameter 35 μ (30–39 μ). Ridges 15.6 (11–20). Shape class index 1.6 (1.4–1.8); prolate.

These grains are characterized by large size as well as by a granulate texture of the ektexine ridges. The ridges are sculptured by minute granules approximately 0.5 μ in diameter scattered irregularly over the surface. They may be found in distinct clumps or widely separated. When the granules are widely spaced, there is some indication that the intervening space is slightly pitted. The width of the ridges at the base varies from 4–7 μ at the equator to 2–3.5 μ at the poles, while the furrows measure 1–2 μ in width continuously along their complete length to their abrupt termination near the poles. The furrows are somewhat irregular in shape, and in surface view the ektexine of the furrow appears slightly granulate. The degree of sculpturing in the floor of the furrows is much less than on the ridges; the granules are smaller and less numerous.

In most cases the endexine is thicker than the ektexine, and may measure as much as 2.5 μ in thickness. The ektexine measures 1–1.5 μ at the center of the ridges at the equator but may project as much as 4 μ beyond the polar limits of the grain.

Ephedra breana Phil. PLATE IV, *fig. 9.*

Polar axis: 44 μ (34–54 μ); equatorial diameter 32 μ (27–39 μ). Ridges: 15.2 (10–16). Shape class index 1.3 (1.1–1.6); prolate.

Similar to *Ephedra rupestris*, these pollen grains are small and very compact in appearance. There is no tendency for the ektexine to project at the poles, although the ektexine is a little thicker there than at the equator. The average width of the ridges at their base at the equator varies between 3.5 μ and 4.5 μ.

Thickness of the ektexine at the ridge crest at the equator 2–3 μ, at the poles 4 μ, in the furrow region 1 μ; thickness of the endexine 0.8–1.4 μ.

Ephedra gracilis Phil.

Polar axis 56 μ (35–65 μ); equatorial diameter 26 μ (24–31 μ). Ridges 13.5 (10–18). Shape class index 1.9 (1.7–2.3); prolate.

The grains possess an average of 13 low ridges which measure 4–7 μ in width at the equator decreasing to 2.5–3 μ at the poles. The furrows are narrow, 1–1.5 μ, and slightly irregular in outline. The exine is composed of a variably thickened ektexine which averages 3–3.5 μ in thickness, the height of the ridges at the equator, decreasing laterally to 1 μ at the furrow, and a continuous endexine which measures 1.5–2 μ in thickness. The ektexine does not project at the poles.

Ephedra rupestris Benth.

Polar axis 39 μ (37–45 μ); equatorial diameter 28 μ (27–31 μ). Ridges 13.5 (11–15). Shape class index 1.4 (1.2–1.6); prolate.

These grains are among the smallest of the type D group. The ektexine measures 2 μ at the central point of the ridge at the equator, but gradually thins laterally in the furrow, and increases poleward to 3.2 μ. The endexine measures 0.8–1.5 μ in thickness. The ektexine adheres closely to the endexine of the grain at the poles and there seems to be no tendency for separation. The basal width of the slightly rounded ridges at the equator is 8–9 μ decreasing to 6–7 μ at the poles. The ridges are separated by extremely straight, narrow, psilate furrows.

Ephedra strobilacea Bunge

Polar axis 44 μ (31–60 μ); equatorial diameter 26 μ (20–31 μ). Ridges 13.7 (10–18). Shape class index 1.6 (1.5–1.7); prolate.

The ridges are thin, averaging 3 μ at the equator. The thickness of the ektexine at the equator varies from 0.8 μ in the furrow region to 1.5–3 μ at the ridge crest. The endexine varies in thickness from 1–1.5 μ. The ektexine projects 4–4.5 μ beyond the endexine at the poles in a manner similar to the preceding species. An indistinct, threadlike, straight furrow is present.

Ephedra triandra Tul.

Polar axis 41 μ (32–49 μ); equatorial diameter 26 μ (24–28 μ). Ridges 15.0 (10–19). Shape class index 1.4 (1.3–1.7); prolate.

The pollen grains closely resemble those of *Ephedra rupestris.* The ridges are low, measuring 1.5 μ in height and 4–5 μ in width at the equator.

Thickness of the ektexine at the ridge crest at the equator 1.5 μ, at the poles 1.5 μ, in the furrow region 0.5 μ; thickness of the endexine 1.5 μ. The ektexine projects 4 μ beyond the polar limits of the endexine.

Ephedra trifurca Torr. PLATE I, *fig. 4;* PLATE II, *figs. 3, 4.*

Polar axis 53 μ (39–63 μ); equatorial diameter 29 μ (28–30 μ). Ridges 13.7 (11–17). Shape class index 1.8 (1.5–2.1); prolate.

These grains possess the thinnest exine in the D type group. The thickness of the two exine layers at the equator averages between 1.8 and 2.4 μ, of which 0.8–1 μ is the thickness of the ektexine and 1–1.4 μ is the thickness of the endexine. However, the thickness of the ektexine increases to 2 μ at the poles. In addition, the ektexine ridges, after following the contour of the grain up to this point, project outward. As is characteristic of the Type D group the grains possess gently rounded, wide ridges 2.8–5 μ in width. These narrow to 2–3 μ at the poles. The ridges are separated by distinct, unbranched furrows which are slightly irregular in outline where they border the steep-sided ridges.

DISCUSSION

The system of pollen classification presented here is based primarily on the number and structure of ektexine ridges, the size and form of the intervening furrows and the presence or absence and structure of the "colpi."[6] On the basis of these features, *Ephedra* grains may be divided into four groups, here designated as Types A, B, C and D. Pollen Types A and D represent the two extremes in the genus while Types B and C tend to be intermediate in ridge number and other characteristics. Furthermore, pollen grains of Type B seem to be more closely related to Type A (as is also true of Type C) than to Type D. Type A pollen grains tend to predominate

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[6] For definition of our use of the term colpus see explanatory footnote 4.

in a taxonomically coherent group of species and there is less variation in ridge number within this group than in the other three. Furthermore, since the *average* ridge number in this group of species does not overlap with the *average* ridge number in other groups, species possessing grains of Type A may often be determined on the basis of ridge number alone. This is not the case for species possessing the other types of pollen because of the extensive variation within each group of species and even within a single species. The three remaining groups of species are separated by the use of other characters of the ridges, such as height, steepness of slope and shape in polar view. To a considerable extent this classification system possesses practical value only in separating species featured predominantly by the A and D pollen types, respectively, and is of more limited value in grouping species under the B and C types. In this respect the concept of pollen types as we have employed it here, is morphological rather than taxonomic.

An effort was made, however, to determine whether any relationship or correlation exists between the different pollen types and the generally accepted taxonomic system. Pearson (1929), in discussing the taxonomy of *Ephedra*, points out that the general habit of the plant is of little value as a systematic character because in most species it is profoundly influenced by environment. As an example he cites *E. distachya* which may occur as a dwarf bush a few inches in height, or may develop into a shrub up to six feet in height. He emphasized that the remarkable degree of uniformity in the vegetative form and anatomical structure of the plant introduces difficulty in the way of separating and grouping the species. The present taxonomic system is one proposed by Stapf (1889) who based his monographic study of the genus on the characteristics of the bracts of the female inflorescence. His study, although extensive, did not include all presently known species of *Ephedra*. A more recent taxonomic revision of the North American species of the genus was presented by Cutler (1939) and some of the South American species were investigated by Hunziker (1949), but no attempt was made to revise the genus as a whole nor to consider the phylogenetic relationships of the American species with those of the old world. The system in use (Stapf, 1889) remains incomplete and there is still great need for a revision of the entire group. Stapf's system is presented here in an effort to determine whether the pollen groups recognized in the present study have any relation to his taxonomic groups within the genus.

Section I. ALATAE. Mature spike dry; bracts more or less indurated along the midrib, otherwise membranous, produced laterally into wing-like expansions.
  1. Tropidolepides.[7] *E. alata* (D); *E. strobilacea* (D).
  2. Habrolepides. *E. trifurca* (D); *E. torreyana* (C); *E. multiflora* (B).

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[7] Designated as tribes by Stapf, these subdivisions of sections are not validly published (Article 5, International Code of Botanical Nomenclature 1956) and should be republished as either subsections or series. They are used here, however, for purposes of comparison.

Section II. ASARCA. Mature female spike dry; bracts slightly hardened, scarcely membranous-winged.

3. Asarca. *E. californica* (B); *E. aspera* (C).

Section III. EPHEDRA (Pseudobaccatae). Mature bracts of female spike often narrowly membranous-margined, at length becoming thick and fleshy.

4. Scandentes. *E. altissima* (B); *E. foliata* (C); *E. fragilis* (C); *E. fragilis* var. *campylopoda* (B).
5. Pachycladae. *E. pachyclada* (A); *E. intermedia* (A).
6. Leptocladae. *E. helvetica* (A); *E. distachya* (A); *E. monostachya* (A); *E. gerardiana* (A); *E. equisetina* (A); *E. sinica* (A); *E. regeliana* (A).
7. Antisyphiliticae. *E. nevadensis* (B); *E. antisyphilitica* (B); *E. americana* (C); *E. gracilis* (D); *E. tweediana* (B); *E. triandra* (D); *E. ochreata* (C).

It is apparent that our pollen classification scheme shows only partial agreement with Stapf's groups. In the case of the "Pachycladae" and "Leptocladae" of Section III the correlation is good, inasmuch as Type A pollen only occurs throughout the group. Moreover Type A pollen is restricted in occurrence to these two groups in the genus. In Section I, the "Habrolepides" possess intermediate (Types B and C) as well as Type D pollen; while Section II (Asarca) has only intermediate pollen (Types B and C); Section III (Ephedra) is characterized by the presence of all four groups. In the "Scandentes" the intermediate pollen types are found; while in the "Antisyphiliticae" both intermediate and Type D pollen are characteristic.

As a further comparison, the pollen types and the species of *Ephedra* in which they occur are arranged below by major geographical areas.

ASIA.

Type A: *E. equisetina, E. gerardiana, E. major* var. *procera, E. monostachya, E. pachyclada, E. sinica.*
Type B: None.
Type C: *E. foliata, E. regeliana.*
Type D: *E. strobilacea.*

MEDITERRANEAN REGION.

Type A: *E. distachya, E. graeca, E. helvetica, E. intermedia, E. major* var. *villarsii, E. vulgaris.*
Type B: *E. altissima, E. fragilis* var. *campylopoda.*
Type C: *E. foliata* var. *ciliata, E. fragilis.*
Type D: *E. alata.*

NORTH AMERICA.

Type A: *E. clokeyi, E. coryi* var. *viscida, E. funera, E. viridis.*
Type B: *E. antisyphilitica, E. californica, E. pedunculata, E. nevadensis.*
Type C: *E. aspera, E. nana, E. torreyana, E. peninsularis.*
Type D: *E. trifurca.*

SOUTH AMERICA.

Type A: None.
Type B: *E. chilensis, E. tweediana, E. multiflora.*
Type C: *E. americana, E. andina, E. bracteata, E. frustillata, E. ochreata, E. wraithiana.*
Type D: *E. breana, E. gracilis, E. rupestris, E. triandra.*

From the above material it will be noted that pollen type A is predominantly Asiatic and Mediterranean in range, with only four of the sixteen species possessing Type A occurring in the western hemisphere and all of these in the United States. In contrast to this, five of the seven species bearing Type D pollen occur in the western hemisphere, four being located in South America and one in the United States. Concerning the remaining two species, one, *E. alata*, is North African, the other, *E. strobilacea*, is Asiatic. Among the intermediate groups B and C seventeen of the twenty-four species are found in the western hemisphere.

Insofar as the authors are aware, the fossil *Ephedra* pollen from Long Island represents the first Cretaceous occurrence known from North America. The grains represent an extreme in one of the four morphological types which we propose as characterizing *Ephedra* pollen. Moreover the grains are morphologically indistinguishable from *Ephedra sinica*, an old world species of the Type A group.

Ephedra today is predominantly a warm desert-steppe plant restricted to both meteorologically and physiologically dry areas. In North America it extends from the southwestern desert areas of the United States eastward to Texas and south to Mexico. In South America it occurs from the drier parts of Ecuador through western Chile into Patagonia. In Europe it extends along the northern Mediterranean coast in Spain and France and extends north and east into Germany and Hungary. It also occurs along the north coast of Africa, and extends eastward through Afghanistan into western China. According to Gams (1952, cited by Iversen, 1954) it is indifferent to temperature but seems to require both climatic and edaphic dryness. For example, the typical localities of *E. distachya* are warm, but the same species is found in isolated, remote localities in Siberia north to the arctic circle and in the alpine zone in Tibet. This extreme adaptability possibly explains the presence of *Ephedra* in North America and Europe during late glacial time. Gams (1927) further states that it occurs in very dry and open pine woods. This is extremely interesting in view of the association of the fossil material from Long Island with abundant pollen assignable to the Coniferales and Cycadales.

Tchigouriaeva (1954) suggests that an ancestral form of *Ephedra* (*Ephedrites*) evolved by the Jurassic. This conclusion is based on the similarity between modern *E. foliata* pollen and Permo-Triassic remains of the Cordaitales. These Permian cordaitalian remains are ridged pollen grains bearing two bladders. By the Lower Triassic a progressive reduction in bladder development had occurred until the bladders were either vestigial or, in a few cases, completely absent. Tchigouriaeva reasoned, therefore, that by the Jurassic, pollen of the modern *Ephedra* type (without bladders) had probably evolved. It should be noted, however, that no such Jurassic remains have thus far been discovered. Pollen having gnetalian affinities, possessing a varying number of ridges and occasionally a furrow, as in *Welwitschia*, has been described from Cretaceous sediments in Nigeria and Venezuela (Kuyl et al., 1955). Tchigouriaeva's hypothesis is rendered more plausible, however, by the discovery of Cretaceous pollen of essentially modern structure as demonstrated in this paper. Doubtless future discoveries will bridge the gap between ancestral forms and true *Ephedra* pollen, and clarify more fully the evolutionary story of *Ephedra* in pre-Cretaceous time.

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DEPARTMENT OF BIOLOGY
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EXPLANATION OF PLATES

PLATE I

FIGS. 1–5. Major morphological types characterizing *Ephedra* pollen grains. FIG. 1. *Ephedra aspera,* Type C. FIG. 2. *Ephedra sinica,* Type A. FIG. 3. *Ephedra distachya,* Type A. FIG. 4. *Ephedra trifurca,* Type D. FIG. 5. *Ephedra californica,* Type B. (All figures × 1200.)

PLATE II

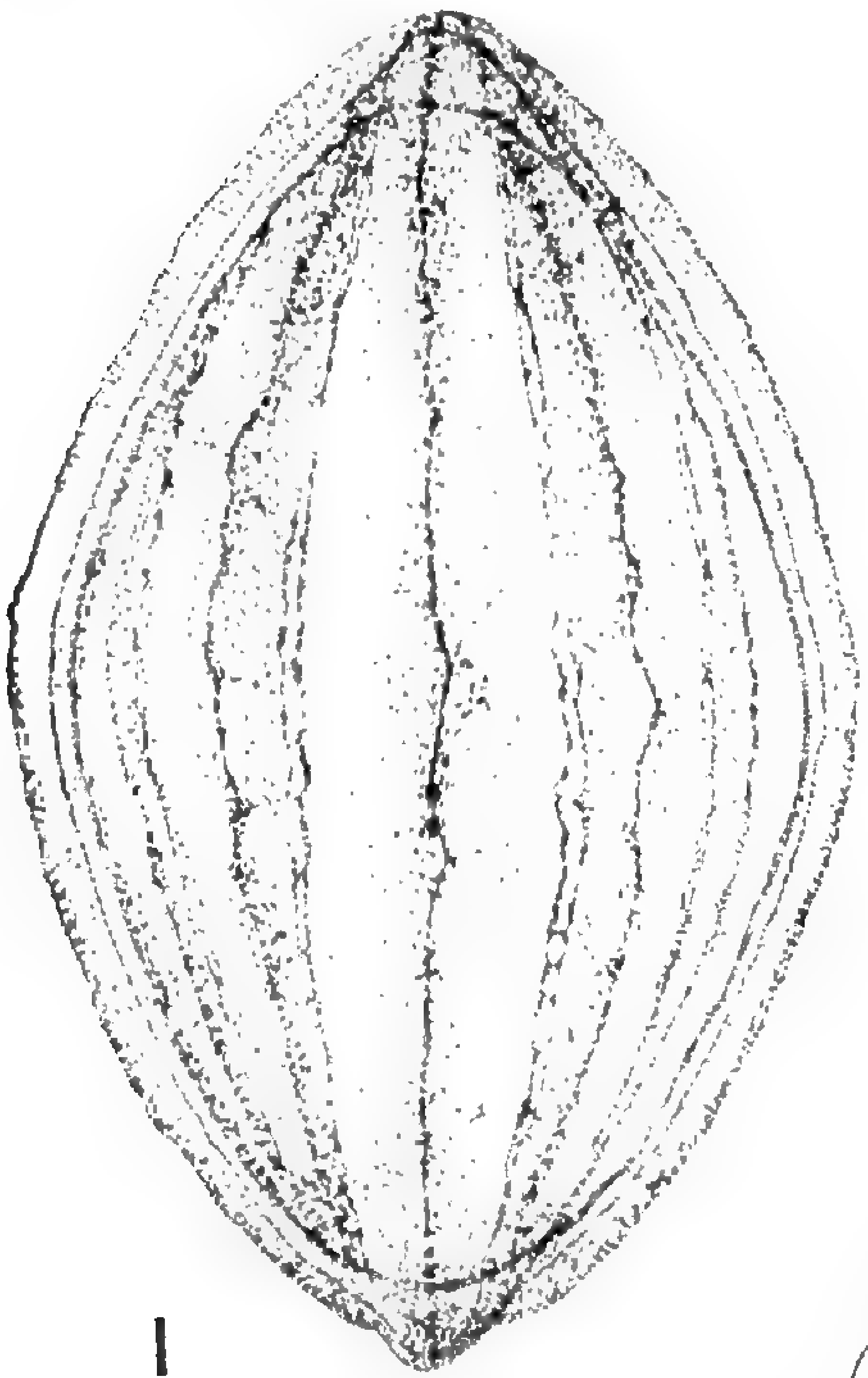
FIG. 1. Modern *Ephedra distachya.* View of the serpentine colpus. Note the primary and secondary branching. FIG. 2. Same grain at mid focus, showing the thickness of the exine in outline. Note also the dissection of the ektexinous ridge crests which are visible in optical section along both edges of the grain. This dissection is caused by branching lateral colpi. FIG. 3. Modern *Ephedra trifurca.* View at high focus of the wide, low, slightly scabrate ridges characteristic of Type D pollen. Note the bright, hyaline furrows. FIG. 4. Same grain at mid focus, showing the thickness of the ektexine. FIG. 5. Modern *Ephedra funera.* High focus view of the straight, slightly verrucate ridges. FIG. 6. Modern *Ephedra americana.* Mid focus view showing the projecting ektexine at the poles. FIG. 7. *E. americana.* A polar view of a similar grain. Note the high but fine, straight ridges and their junction at the poles. (All figures × 1000.)

PLATE III

FIG. 1. *Ephedra californica.* High focus view of the narrow, undulating, hyaline ridges which characterize Type B pollen. FIG. 2. Same grain at mid-focus, showing the outline of the ridges along the edges of the grain. FIG. 3. *Ephedra sinica.* High focus view of the reticulation found along the surface of the exine between the ridge crests. FIG. 4. Same grain at mid-focus, showing the extent of the outline of the endexine. FIG. 5. The undulating ridge along the opposite side of the body is visible. FIG. 6. *E. sinica.* A smaller specimen in which the baculate condition of the ektexine is visible in optical section. (All figures × 1000.)

PLATE IV

FIG. 1. *Ephedra viridis.* High focus view of the angular, undulating colpus. FIG. 2. Same grain at higher focus. Note the smoothness of the ridge crest. FIG. 3. *Ephedra chilensis.* High focus view of the undulant ridge crest. FIG. 4. *Ephedra andina.* Typical Type C pollen grain. FIG. 5. *Ephedra sinica.* Polar view of mid focus showing the structure of the ridge. Note the continuous and evenly distributed endexine, the hyaline central core of each ridge and the thin outer tissue. FIG. 6. Same grain at high focus showing the junction of the ridges at the poles. FIG. 7. *Ephedra nevadensis.* High focus view of the tightly undulant ridge. FIG. 8. *Ephedra aspera.* High focus view of the characteristic straight ridges of Type C pollen grains. FIG. 9. *Ephedra breana.* High focus view of the low, gently domed ridges characteristic of Type D pollen grains. (All figures × 1000.)



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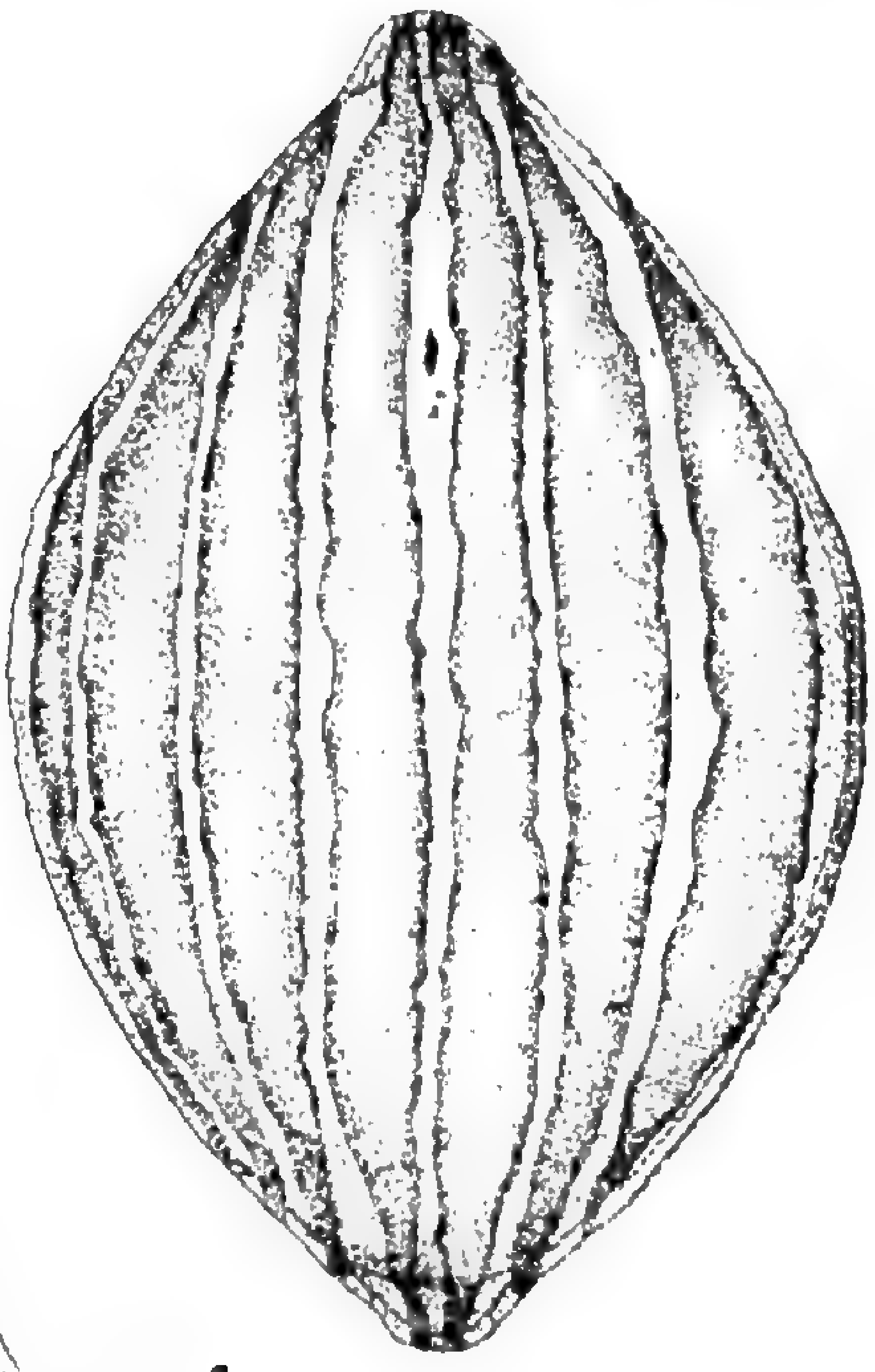

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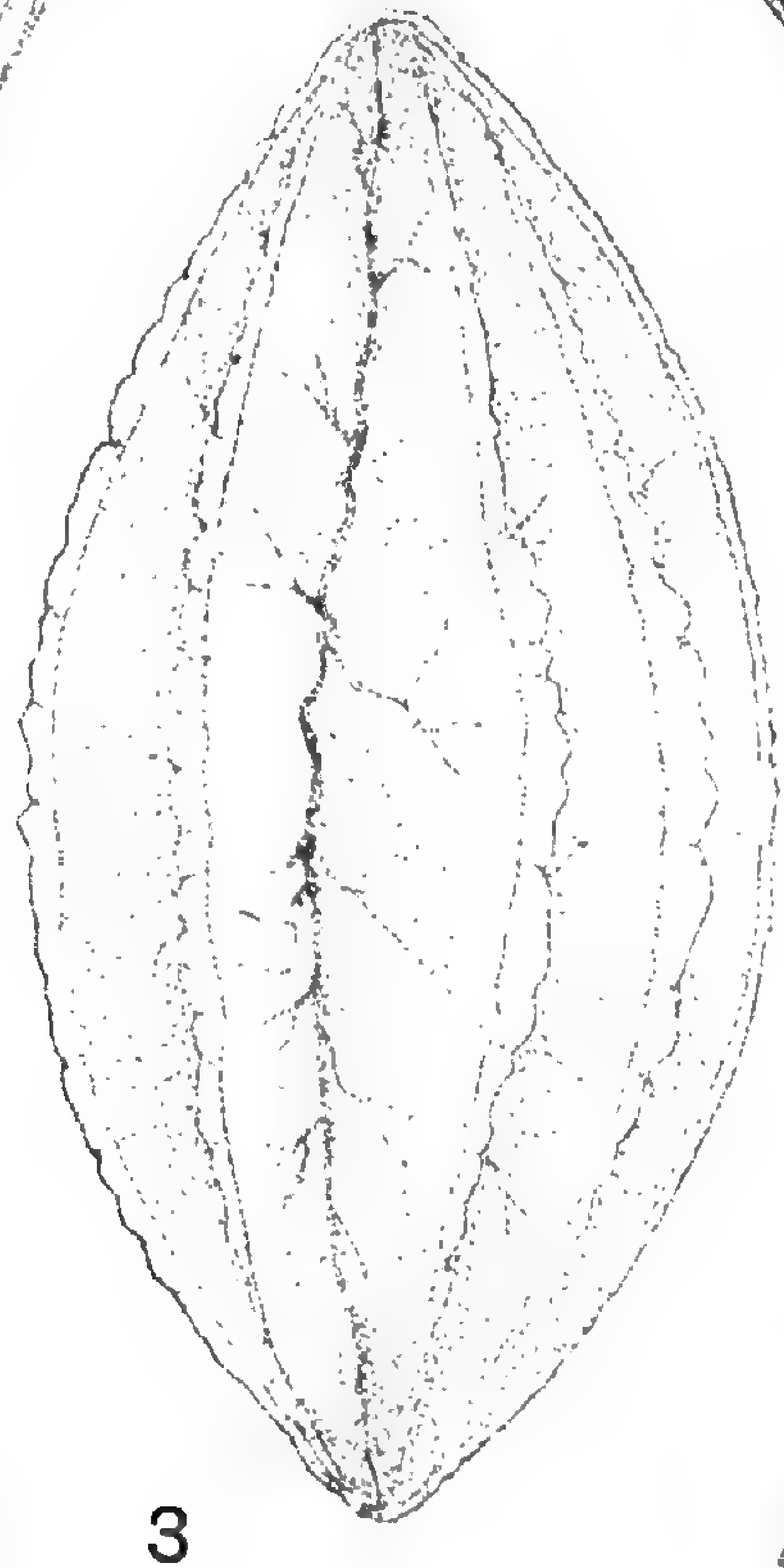

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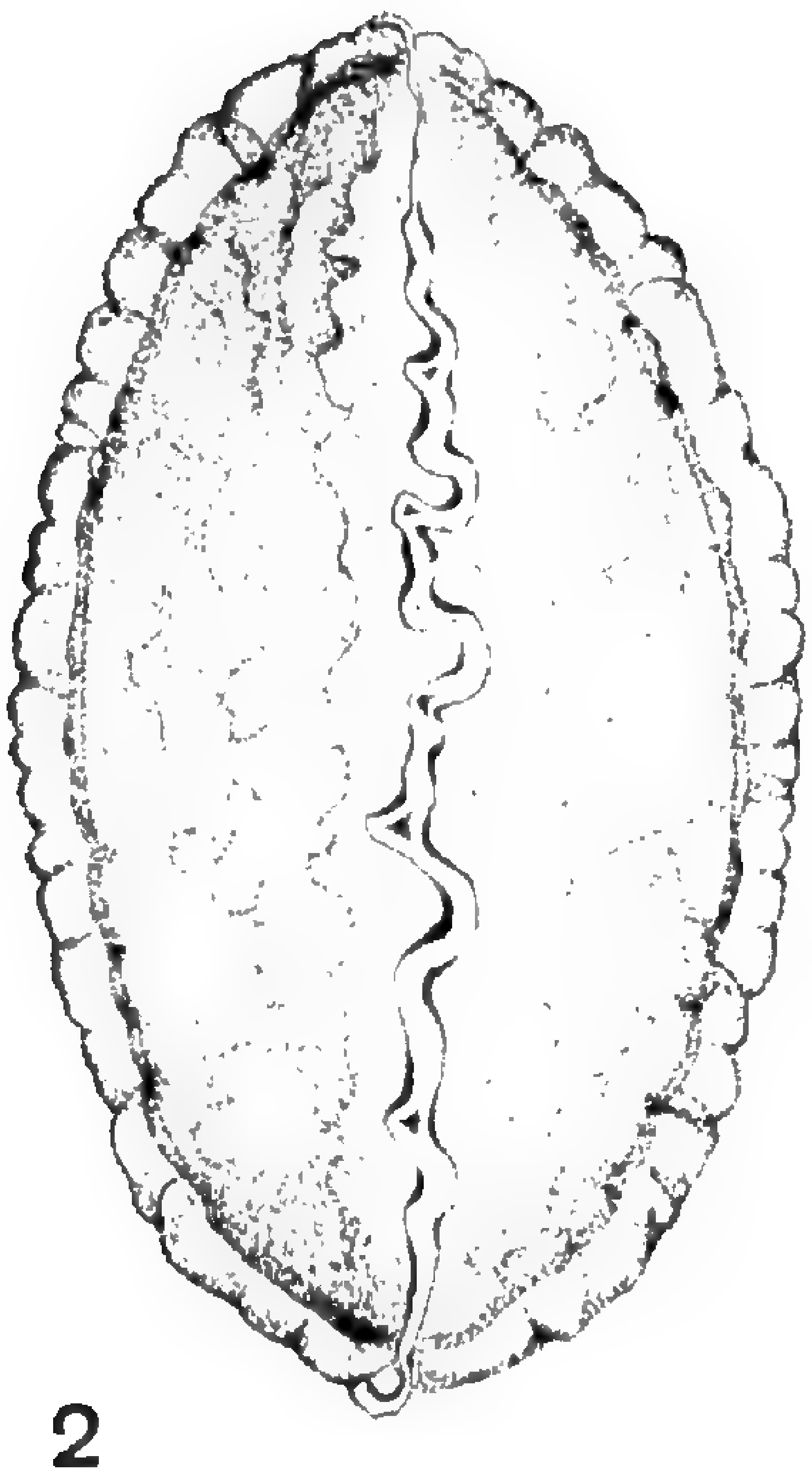

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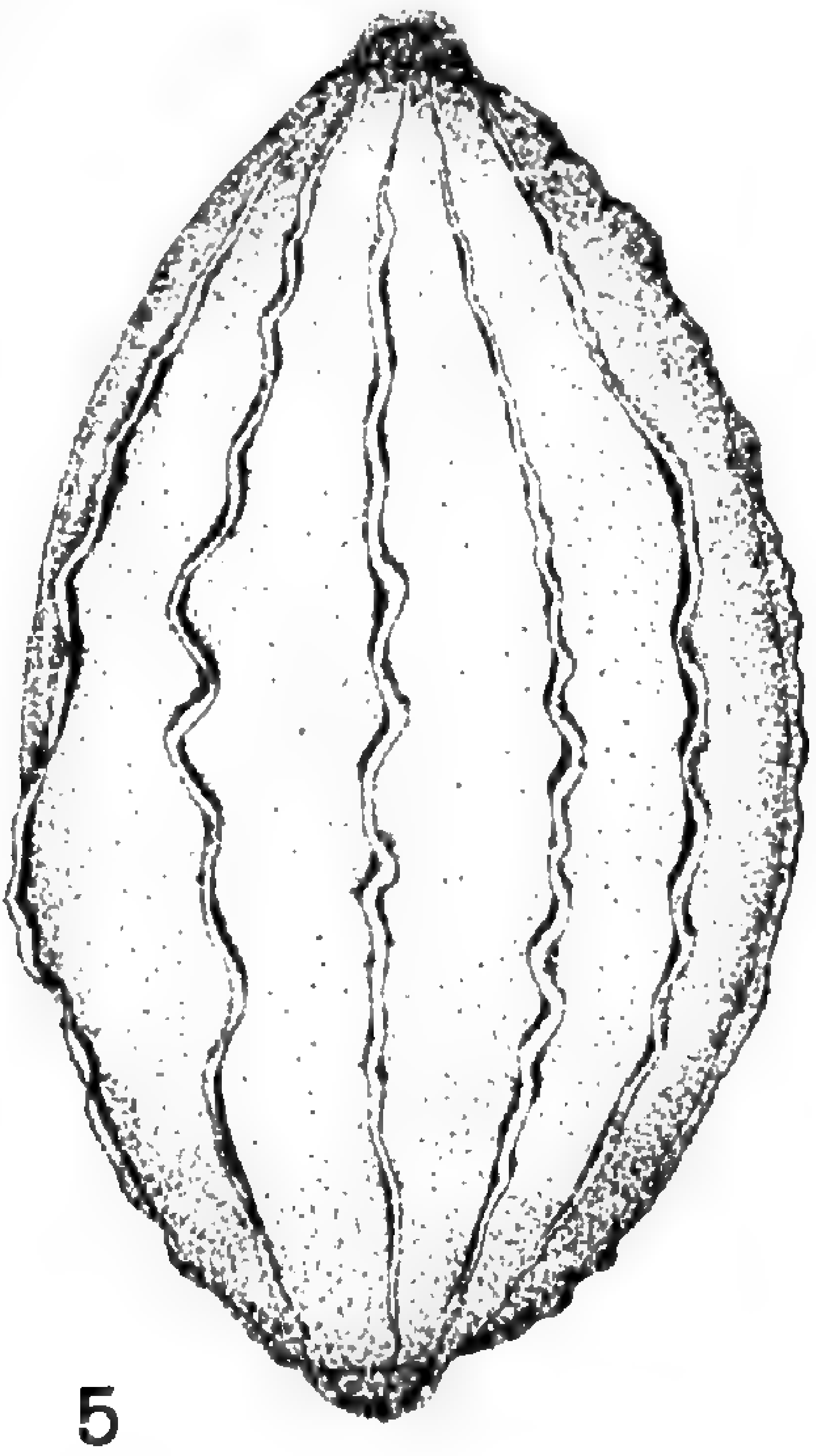

5

STEEVES & BARGHOORN, POLLEN OF EPHEDRA


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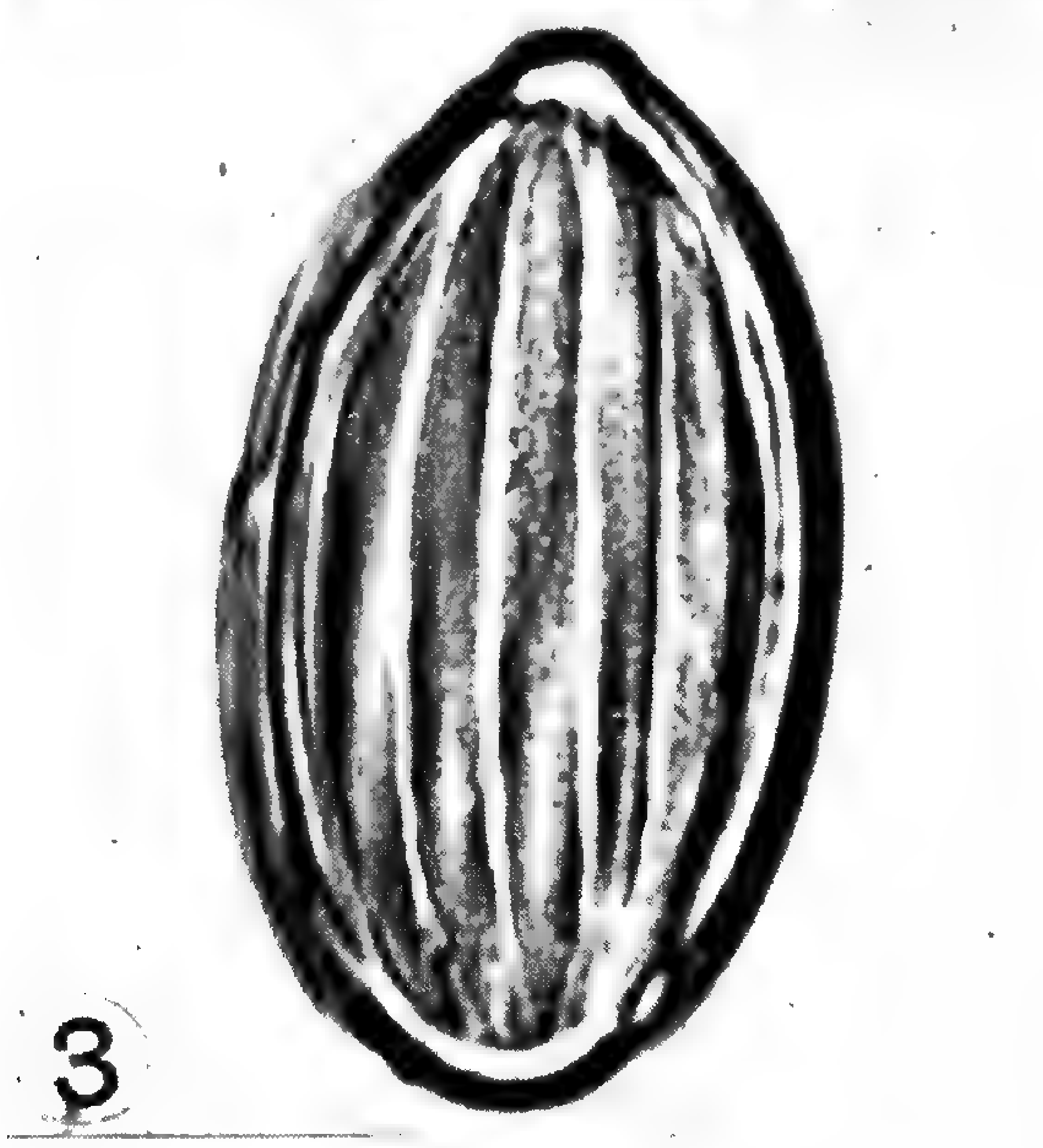
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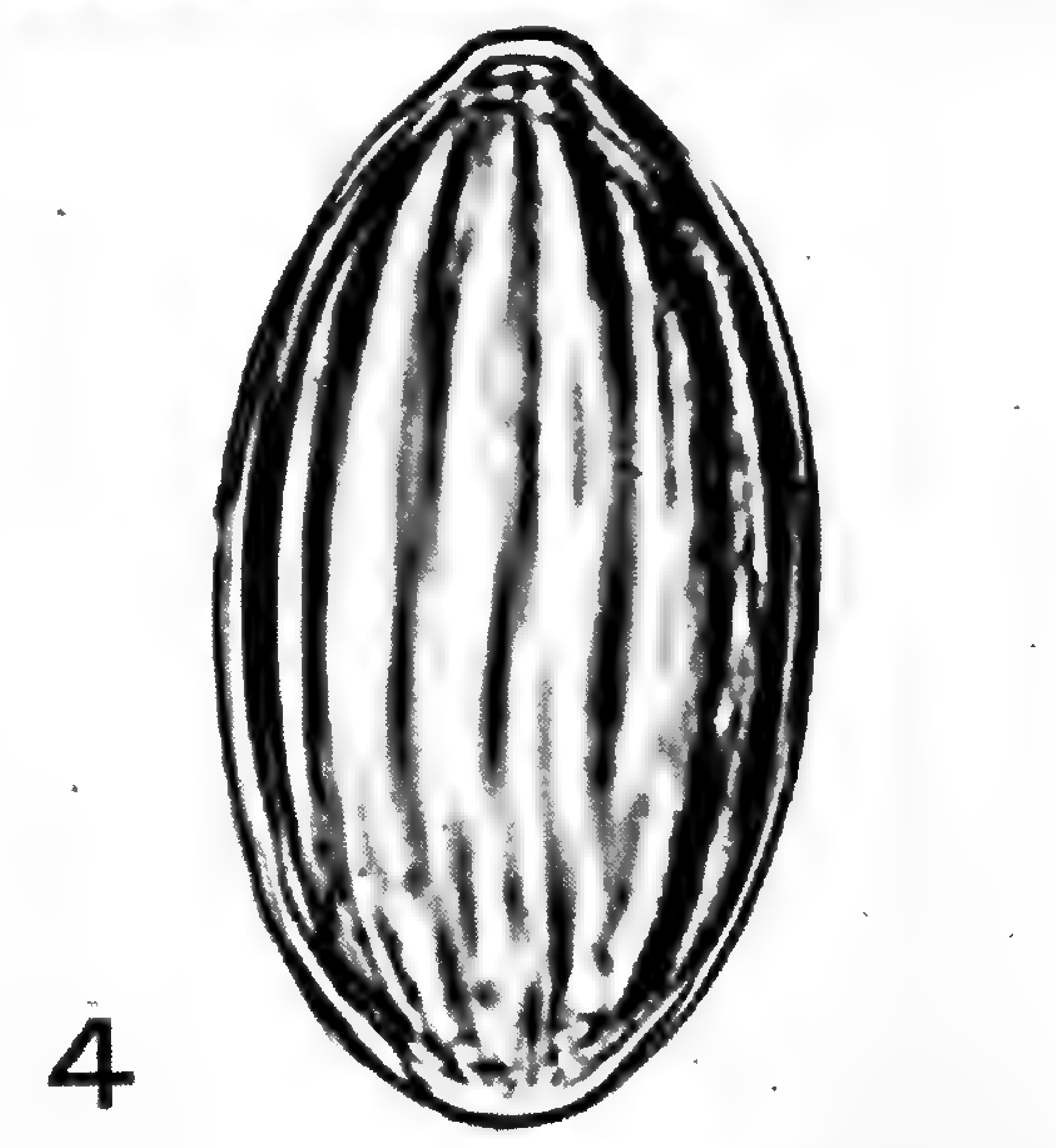
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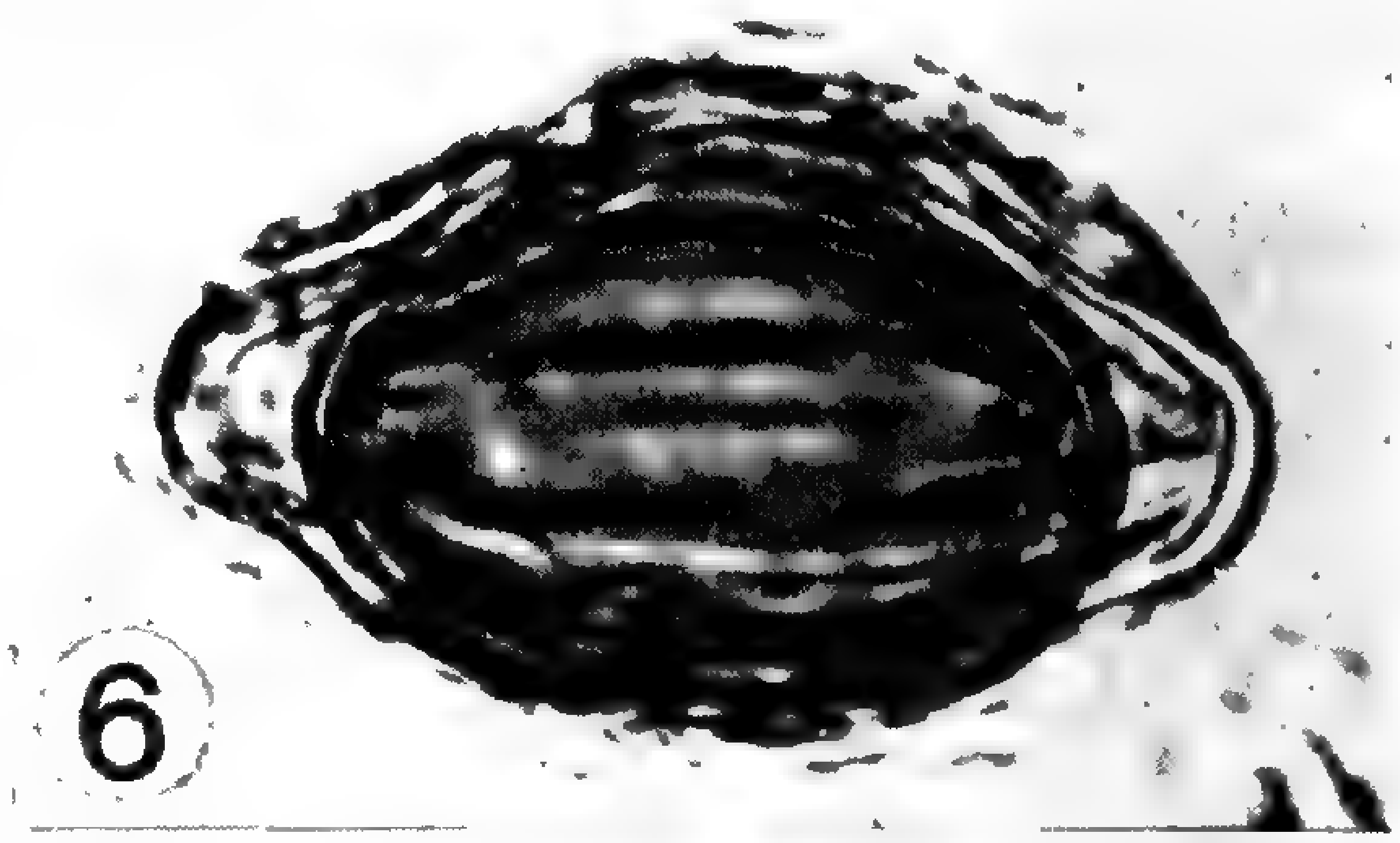
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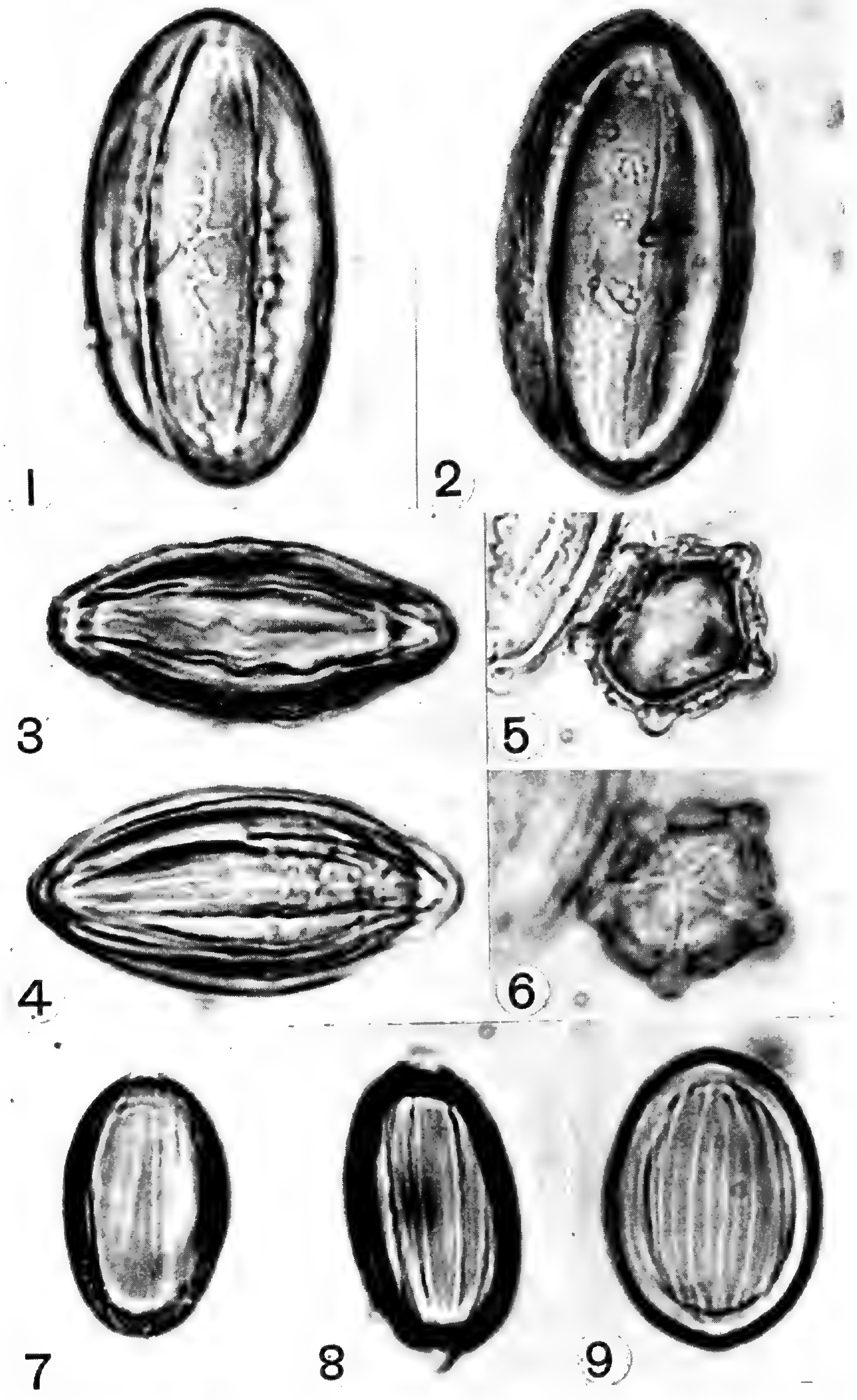
Steeves & Barghoorn, Pollen of Ephedra Plate II

Steeves & Barghoorn, Pollen of Ephedra



Steeves & Barghoorn, Pollen of Ephedra

ANATOMICAL STUDIES OF BARK REGENERATION FOLLOWING SCORING

KYAW SOE

SCORING of the trunks or branches of fruit and ornamental trees to induce earlier and more prolific flowering and fruiting has been practised for thousands of years. This method of checking phloem transport is more temporary in its effect than the ancient procedure of ringing or the more recent bark inversion (Sax, 1954), but it is easily done and is less hazardous than either of these practices. If scoring does not inhibit phloem transport long enough to insure maximum response, it can be repeated. In order to determine the duration of the effect of scoring and the nature of bark regeneration, studies were made with both slow- and rapid-growing trees.

Two types of trees were used, the fast-growing silver maple (*Acer saccharinum*) and a hybrid poplar (ex *Populus deltoides*), and the slow-growing apple, 'Prairie Spy,' and the 'Seckel' pear. The maple and poplar trees were three years old while the pear and apple trees were five to six years old. The trunks and branches were scored by cutting with a knife through the bark to, and often into, the underlying xylem. In the earlier experiments, the cuts were made directly around the trunk or branch, but in the later the cut was made in a diagonal spiral to prevent the breakage of branches. Samples of the cut bark and underlying wood were taken every few days after scoring in order to study the regeneration of the severed bark. After fixing, longitudinal radial sections were cut, stained and mounted.

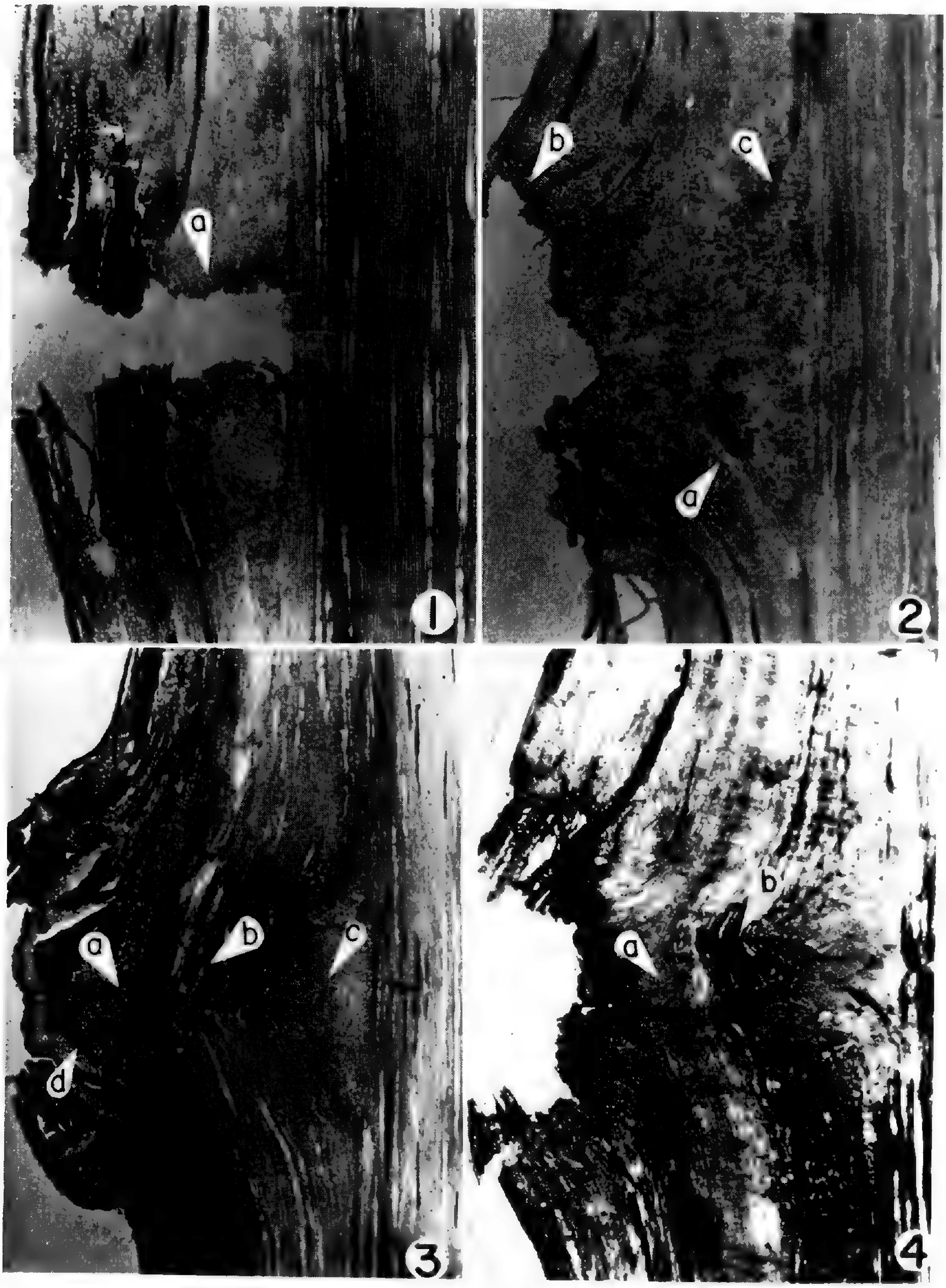
HISTOLOGICAL TECHNIQUE

Samples removed from the trees were treated in two ways. In most of the cases, the samples were cut into 15–20 μ sections on a sliding microtome. The majority of the sections were radial longitudinal sections, but cross sections were cut when necessary. For more detailed studies of the material removed from the trees, it was fixed in formalin acetic alcohol (Johanson, 1940). A modified Zirkle's n-butyl alcohol method for dehydration was employed and the paraffin-tissuemat method of Pratt and Wetmore (1951) was used for embedding the material. Just before microtoming, the embedded material was exposed by cutting off the unnecessary paraffin on the required surface and soaked in 50% alcohol for at least three hours before cutting. To avoid curling and to insure easy handling of the sections a thin sheet of polyethylene was used to cover the top of the material before each section was cut. The flattened sections on the polyethylene sheet were mounted on cleared slides smeared with egg-albumen fixative and flooded with 2% formalin.

Different stain combinations for studying different elements during the development of the new bark were used as follows: (a) 1% safranin counter-stained with 0.5% fast green in 100% ethyl alcohol and clove oil (Johanson, 1949); (b) 1% safranin with 2% analin blue in methyl cellosolve; (c) bismark brown, iodine green, resorcin blue (lacmoid) (Esau, 1948) all diluted 1/5,000 (Esau, 1948).

OBSERVATIONS

Poplar. The three-year-old poplar stem has a thick cortical region and the phellem of the normal bark consists of five to ten years of cork cells. In the phloem, the sieve elements were in patches and were arranged in alternate tangential rows with phloem fibers, each row being of one to eight phloem fibers thick. The cambial zone (vascular) with its immediate derivatives formed a distinct zone. When studied after scoring, it was shown that the ringing reached into the mature xylem two to ten cells (or approximately so) deep. By the third day, the exposed cut surfaces of the wound had dried out, especially the marginal cells in the region of cork, cork cambium, cortex and outer mature phloem cells. Callus formation took place at this stage from two living tissue systems: (a) the living cells of the longitudinal conducting system which includes phloem parenchyma, vascular cambial zone and xylem parenchyma; (b) the horizontal living cells which comprise the vascular rays of the phloem, the vascular cambium, and both immature and mature xylem (Figs. 5, 6). On the sixth day, there was very active callus formation and the two edges of the callus formed on the upper and lower margins of the cut fused (Fig. 2) and bulged out. The outermost cells of the callus were exposed and dried out. Some of the immature xylem elements near the wounds became mature while callus was forming. They became lignified and were characteristically distorted as they were pushed out by the increasing volume of callus below them, especially the active growth of the vascular ray cells (Fig. 2). Just outside of these lately-formed, distorted xylem elements, a series of cells within the callus developed into a distinct cambial zone which formed a bridge over the cut (Fig. 2). This formation of a new cambial zone began at the regions where the callus tissue met the normal undisturbed cambial zone. At the deepest part of the cut, mature xylem cells characteristically show the lumen filled with cells which closely resemble tyloses. The entrance of these cells into the vessels has not been observed, but all indications seem to point to their being tylose in nature, originating from neighboring ray initials or callus cells formed from such ray initials. Practically every mature vessel in the neighborhood of the bottom of the cut is so filled. While some of the xylem elements became distorted as they matured, the mature phloem which was not taking part in the formation of callus was pushed outward. Some phloem tissue entered into the formation of callus. On the ninth day, it was found that the newly formed vascular cambium had produced new xylem elements of a short and distorted nature towards the inside. Also, phloem elements were formed outwards as usual, and these were also distorted and abnormal in their mor-



FIGS. 1–4. Development of callus and new vascular cambium, cork cambium, phloem and xylem at the region of the cut after scoring.

FIG. 1. Radial longitudinal section of poplar stem at the region of the wound, three days after scoring: a, callus formation is initiated on either side of the wound in the region of immature phloem, vascular cambium and immature xylem (× 24). FIG. 2. Radial longitudinal section of poplar stem at the region of the wound, six days after scoring: a, vascular cambium; b, cork cambium; c, some immature vascular elements become mature after being pushed out by the growth of callus tissue (× 21). Note that the callus tissue from both sides of the wound fuses to form a continuous mass. FIG. 3. Radial longitudinal section of poplar stem sixteen days after scoring: a, region of new phloem; b,

phology. Some sieve-tube elements even showed the presence of callose formation. The phloem fibers, instead of showing their normal elongated form, took the form of rounded sclereids. By this time a new cork cambial layer was well established in the callus region outside of the vascular cambium where it joined the normal cork cambium zone on either side, thereby becoming continuous over the wound. From the twelfth day to the sixteenth day, the xylem elements produced gradually assumed their normal characteristics in size and form, while the newly formed phloem elements were still abnormal in their morphology (FIG. 3). However, on the twentieth day the new vascular system, phloem as well as xylem, and periderm formation became perfectly normal.

Maple. In a three-year-old maple stem, the bark is thinner than in the poplar. The observations made on bark regeneration were more or less comparable to those of the poplar. On the third day after scoring, the usual drying of the cells in the exposed area took place in the cork, cork cambium, phloem and even the immature xylem elements. Callus was actively forming by the sixth day; it was comparable to the callus formation of poplar as described. On the ninth day, the two callus masses, one above and one below the wound, fused, and a distinct vascular cambial layer was formed in the callus which united the two edges of the undisturbed vascular cambium. On the twelfth day, the vascular cambial zone was well established and began to produce its derivatives, but no mature vascular elements were found as yet. By the sixteenth day, the mature products of the newly formed vascular cambium became distinct, both xylem and (less distinctly) phloem. Although the earlier-formed xylem elements were short, distorted and irregularly arranged, the later ones became more normal. Newly formed phloem elements were more distorted, irregular in arrangement, and fewer than the newly formed xylem elements. By the twentieth day, the vascular cambium was producing perfectly normal phloem and xylem elements.

Apple. The apple variety we used ('Prairie Spy') had a green bark which was thicker than that of the poplar mentioned above. On the third day after scoring, there was no obvious change, but there was a slight callus formation in the region of immature phloem and xylem along the flanks of the cut. On the sixth day, there was more drying of the exposed edges of the wound and there was a more obvious production of callus which originated in a manner similar to that in the previously mentioned plants. At this time, a layer of living cells which was below the dried cells at the regions of cork cambium, cortex and outer portion of the phloem became active and acted as a new cork cambium. On the ninth day, the callus formation became faster than before and the two edges of

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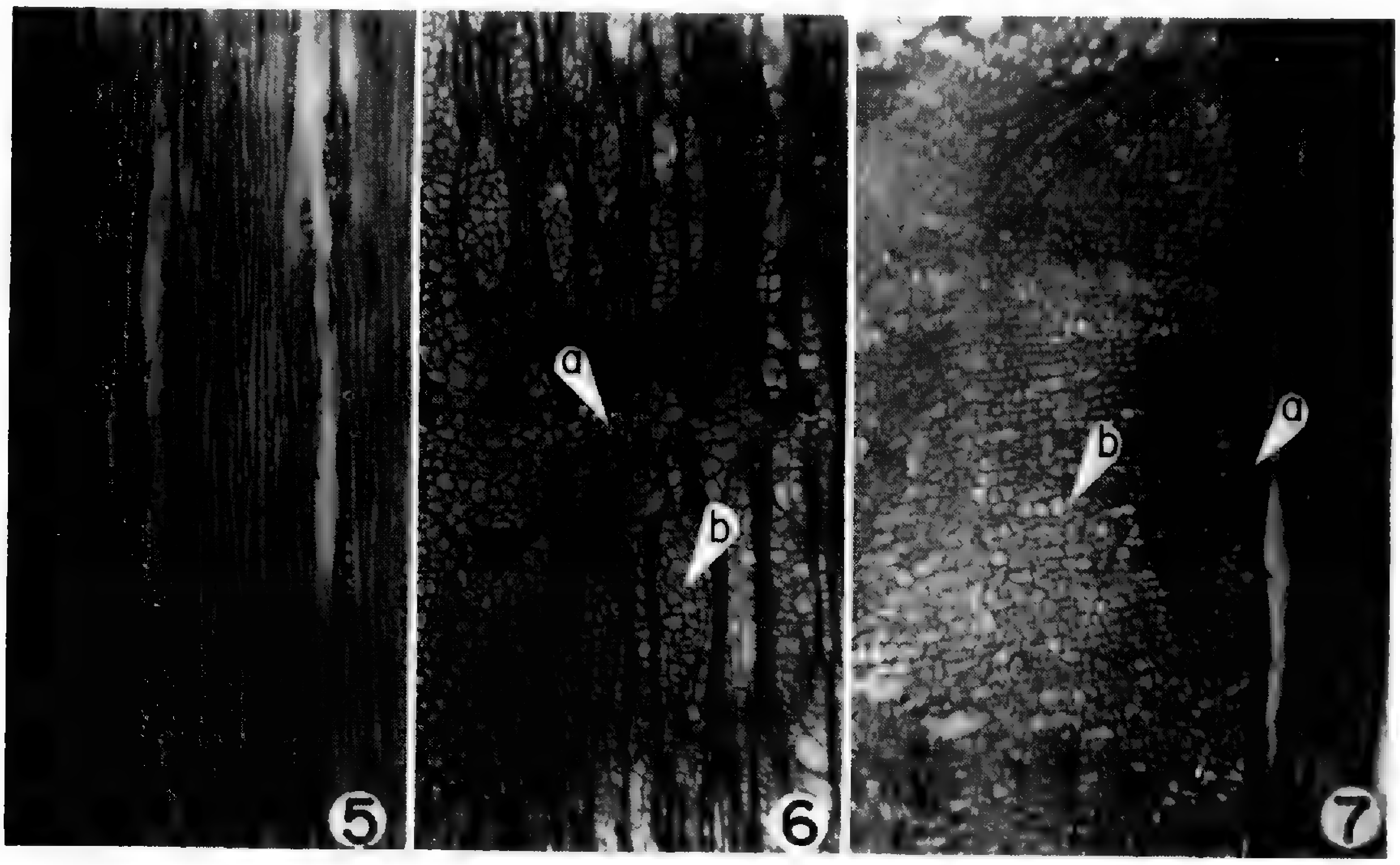
region of newly formed xylem elements; c, callus cushion between the new and old xylem; d, new cork cambium (× 21). FIG. 4. Radial longitudinal section of stem of apple twenty days after scoring, showing resumption of normal vascular and cork cambial activities: a, region of newly formed phloem; b, region of newly formed xylem (× 18). Compare the amount of callus produced in apple (FIG. 4) with poplar (FIG. 3).

callus tissue fused together. There was a definite cambial zone formed which bridged the cut, but no obvious vascular elements were formed as yet. By then the cork cambium had produced four or more layers of derivatives. On the twelfth day, the callus formation did not show any progress and thus the amount of callus formed did not even reach to the level of the epidermis of the axis (FIG. 4). The hidden small amount of callus which developed and differentiated to produce both cork cambium and vascular cambium in no more time than in the abundant callus of poplar and maple, was very deceptive when one examined the wound superficially. But, remarkably, the vascular cambium had already been producing both phloem and xylem composed of short, distorted and irregularly arranged elements, and by the sixteenth day, the production of normal phloem and xylem was resumed. On the twentieth day, the newly formed vascular cambium and cork cambium were perfectly normal and were producing normal derivatives (FIG. 4).



FIGS. 5–7. Callus development from cells of the rays after scoring. FIG. 5. Tangential longitudinal section of poplar showing the characteristic uniseriate rays of a normal plant (× 36). FIG. 6. Tangential longitudinal section of stem of poplar at the region of the wound, showing the multiseriate ray cells which take a major part in the formation of callus: a, the region of the cut made by the knife in scoring; b, multiseriate ray with large component cells (× 36). FIG. 7. Radial longitudinal section of stem of maple showing callus tissue being derived from the ray cells: a, vascular ray cells continuous with their derivative callus cells; b, callus cells which have divided by successive periclinal divisions to form horizontal rows of callus cells (× 36).

Pear. In pear, the nature of bark regeneration was almost the same as the apple. The callus formation began on the sixth day, and it was relatively small in comparison with the poplar and maple. On the twelfth day, the vascular cambium was produced and the new cork cambium was well established. By this time, the vascular cambium was producing short and distorted vascular elements. By the sixteenth day, the production of the normal vascular tissue was resumed and by the twentieth day, both cork cambium and vascular cambium resumed their normal functions perfectly and produced derivatives which were normal in structure, size and arrangement.

DISCUSSION

The present investigation indicates that the amount and the rate of callus production in a wounded area following scoring varies in the different plants studied. The source of callus also varies to some extent. In scoring experiments on trees of poplar, silver maple, pear and apple, callus formation is mainly contributed by living cells of vascular rays (Figs. 5, 6, 7) in the proximity of the cut. There is also some evidence that living longitudinally oriented parenchyma cells of phloem, of xylem and of vascular cambium take part in the formation of callus (Fig. 1). If we look at the literature on the source of callus in the regeneration of new bark, well discussed by Bloch (1941), one finds a diversity of opinions on the origin of callus. Sass (1932) in his study of the formation of callus knots on apple grafts showed that it is produced exclusively by tissues located outside of the xylem cylinder. According to him, any living tissue of the bark, excluding the periderm, may proliferate, and the cambium may produce very little callus. On the other hand, Sharples and Gunnery (1933) showed that in their study of the development of callus in the healing of a surface wound produced by an excision of a strip of bark from the stem of *Hibiscus rosa-sinensis* and *Hevea brasiliensis* (1933), the development of the callus cushion is predominantly from the vascular ray system and the cambium takes no part in its early stage of development. It is clear that Sass in his investigation showed the origin of callus from all the living tissues of the bark except periderm, while Sharples and Gunnery showed that the vascular ray cells are the main source for the origin of callus. The latter are supported by observations made in the present investigation (Figs. 5, 6, 7). Both of them agree that the cambium took very little part in callus formation which is also supported by the present investigation.

In this study it was found that new vascular cambium formation took place on the sixth day in poplar and on the ninth day in maple, pear and apple trees. The new vascular cambium formation is usually independent of the amount and the rate of callus production. It was also found that the activity of the new cork cambium started as soon as the wound callus pad is well developed. The formation of cork cambium was always found ahead of the vascular cambium formation in the plants studied.

In the present investigations, the new xylem elements, followed quickly by the new phloem elements, started appearing soon after the formation of the vascular cambium (that is, about on the ninth day) but they were not abundant and all were abnormal and distorted. In some cases, callose material was seen in and near plates of the sieve-tube elements even on the ninth day. It was only on the twentieth day, or approximately so, that the plants studied showed normal and regular development of xylem and phloem elements. However, as before the scoring, the number of xylem elements produced was naturally more than that of the phloem. It is interesting that the amount of callus formed in poplar and maple was more and appeared earlier than in pear and apple; yet all four produced new phloem and xylem at about the same time. The result of the present investigation on bark regeneration agrees with that of Murneek (1939), in which he states that the branches of apple trees ringed with a wire girdle healed in three to five weeks.

The anatomical studies of spiral ringing in crab apple and branches of other apples showed that the conducting tissue formed by the cambium subsequent to the scoring was changed in orientation so that the long axes of the elements were parallel to the spiral.

CONCLUSION

Following scoring, the new cambium is formed in about a week, but the complete restoration and functioning of the phloem required about three weeks. If done at an appropriate time of year, a single scoring may check phloem transport long enough to induce flowering and fruiting, but, if not, the process can be repeated every two or three weeks to insure earlier flowering and fruiting of ornamental and fruit trees.

The author wishes to thank Dr. Karl Sax for providing the experimental material. Thanks are also due to Dr. R. H. Wetmore for reading the manuscript, and also to Mr. Dean Whittier for his kind help in preparing this paper.

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Department of Biology
Harvard University

THE GENERA OF THE PRIMULALES OF THE SOUTHEASTERN UNITED STATES *

R. B. CHANNELL AND C. E. WOOD, JR.

THE FAMILIES Theophrastaceae, Myrsinaceae and Primulaceae which compose the order Primulales are almost universally agreed to be rather closely related. Both Theophrastaceae and Myrsinaceae are woody tropical groups (with few exceptions), while the Primulaceae are primarily of temperate distribution and are herbaceous, apparently approaching the Myrsinaceae most closely through a few woody species of *Lysimachia*. All three groups are held together, however, by the mostly pentamerous and sympetalous flowers; by the androecium of an outer, antesepalous whorl of staminodia (which may be lacking) and an inner, antepetalous whorl of stamens; by the similar pollen; by the unilocular ovary with free-central placentation; and by the bitegmented ovules.

Although in the Englerian sequence of families the Primulales are placed immediately following the Ericales and Diapensiales, the free-central placentation has led various botanists to associate the Primulales with the Caryophyllales (Centrospermae). Cronquist (Bull. Jard. Bot. Bruxelles **27**: 25, 26. 1957) has pointed out, however, that difficulties attend the derivation of the woody and tropical Myrsinaceae from the predominantly herbaceous Caryophyllales. "A resort to woody members of the Caryophyllales such as some of the Phytolaccaceae, as possible near-ancestors of the Primulales tends to vitiate the significance of the free-central placentation as an indicator of relationship between the Primulales and Caryophyllales, inasmuch as the genera of the Phytolaccaceae with united carpels have axile placentation. If the Primulales are indeed related to the Caryophyllales it must be through a woody common ancestor with axile placentation or even with separate carpels, and the free-central placentation has been independently achieved in both groups. On the basis of present evidence the Guttiferales meet the qualifications of a possible ancestor of the Primulales at least as well as do any of the Caryophyllales."

Although the Plumbaginaceae are sometimes included in the Primulales, several lines of evidence indicate that the apparent similarities to this group are probably parallel developments. The Plumbaginaceae seem to be treated best as a separate order Plumbaginales, related to but distinct from the Caryophyllales, although they have been placed with this group by Friedrich (Studien über die natürliche Verwandtschaft der Plumbaginales und Centrospermae. Phyton Austria **6**: 220–263. 1956).

The familial and generic treatments below follow the general scheme out-

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* Previously published papers in this series include the genera of the woody Ranales (Jour. Arnold Arb. **39**: 296–346. 1958), the Nymphaeaceae and Ceratophyllaceae (**40**: 94–112. 1959), and the Empetraceae and Diapensiaceae (**40**: 161–171. 1959).

lined in the first paper of this series of studies prepared for a biologically oriented generic flora of the southeastern United States. It may be called to attention again, however, that the area is bounded by and includes North Carolina and Tennessee, Arkansas and Louisiana; that the descriptions are based primarily upon the species occurring within this area, with any supplementary material added for clarity being included in brackets; that the abbreviations used for periodicals follow the useful principles of Schwarten and Rickett (Bull. Torrey Bot. Club **76**: 277–300. 1958); and that all references which we have not seen are marked by an asterisk.

This work on the flora of the southeastern United States, which is being conducted as a joint project of the Gray Herbarium and the Arnold Arboretum, has been made possible through the kind support of George R. Cooley and through a grant from the National Science Foundation. The treatments below were prepared originally by the first author in 1957 while he was associated with the Gray Herbarium and the Arnold Arboretum; they have been edited by the second author as a result of the development of a standard format for these studies and have been modified by him through the incorporation of additional material which has been located since that time. In all of this work on the southeastern United States we are greatly indebted to many of our colleagues and friends for their interest and assistance. In connection with the Primulales we are further indebted to George R. Cooley, for temperature data in connection with the effects of the low temperatures in Florida in 1957–1958 (see *Rapanea*), and to Richard A. Eaton, for his assistance in obtaining living specimens of *Hottonia* for illustration. As in the previous papers in this series, the illustrations are the careful work of Dorothy H. Marsh.

THEOPHRASTACEAE (JOEWOOD FAMILY)

Shrubs and trees differing from the Myrsinaceae in the biseriate androecium, the outer (antesepalous) whorl staminodial, and by anatomical features, including the absence of secretory elements and the presence of long strands of sclerenchymatous tissue beneath the leaf epidermis. The presence of broad rays in the wood apparently is correlated with the highly dissected nature of the vascular system of the axis. The relationship of these two families is worthy of further anatomical investigation. The fruit of the Myrsinaceae is a 1–few-seeded drupe, usually small and dark brown or black, while that of the Theophrastaceae is usually a large yellow or orange berry, only rarely a 1-seeded drupe. TYPE GENUS: *Theophrasta* L.

A family of four genera, differing in the form and disposition of the staminodia, and about 60 species distributed in the American tropics and Hawaii. Represented with us by a single indigenous species of *Jacquinia*. *Clavija longifolia* (Jacq.) Mez is sometimes cultivated as an ornamental in the South. Native to Venezuela and Colombia, it is a shrub of *Mahonia*-like habit, attaining a height of 3–5 m. It has large oblong-spatulate to lanceolate, leathery, spinose-toothed leaves and drooping racemes of fragrant, orange or saffron flowers with glandular staminodia.

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1. **Jacquinia** L. Amoen. Acad. **5**: 388. 1760, "*Jaquinia*"; L. Sp. Pl. ed. 2. **1**: 271. 1762, "*Jaquinia*"; Jacq. Select. Stirp. Am. Hist. 53. 1763; L. Gen. Pl. ed. 6. 101. 1764.

Shrubs or small trees with alternate, simple, persistent, exstipulate leaves without resin ducts. Flowers complete, hypogynous, actinomorphic, 5-merous, gamopetalous. Androecium biseriate: fertile stamens 5, epipetalous at the base of the corolla tube in a single whorl opposite the corolla lobes, the anthers extrorse; staminodia 5, alternating, forming the outer series, petaloid, adnate near the base of the corolla lobes. Gynoecium derived from 5 carpels but appearing simple: ovary unilocular with a central free placenta and several anatropous 2-integumented ovules embedded in the mucilaginous matrix filling the ovary cavity; style and stigma 1. Fruit a dry berry. Seeds few, with well developed embryo and copious endosperm. TYPE SPECIES: *Jacquinia ruscifolia* Jacq. (= *J. aculeata* (L.) Mez). (Generic name in honor of Nicolaus Joseph Jacquin, 1727–1817, distinguished Austrian botanist, sent by Emperor Francis I to the West Indies to procure plants for the Imperial Garden at Schoenbrunn, of which he later became director.) — JOEWOOD, CUDJOEWOOD.

A tropical American genus of about 25–30 species, of which a single one, *Jacquinia keyensis* Mez (*J. armillaris* sensu Chapm. non Jacq.), occurs in our area. Our plant is a compact, symmetrical shrub or small tree with a round-topped crown of yellowish green foliage, attaining a height of about 5 meters. It is characteristically a strand species, distributed in our area in dry coastal hammocks of southern peninsular Florida, on calcareous rock of the Everglade Keys and the Florida Keys, and beyond our region in the Bahamas and Hispaniola. The obovate or cuneate-spatulate coriaceous leaves, usually notched at the apex, have entire, revolute margins and are often clustered at the ends of the brittle, sclerose-tomentose twigs. The very fragrant yellowish or straw-colored flowers are produced in racemes at the ends of the twigs, primarily in winter. The fruits are borne on erect or ascending, bracteate pedicels and are pointed with the base of the persistent style.

Jacquinia armillaris Jacq. (*J. Barbasco* Mez), a native of the West Indies, is sometimes cultivated in Florida as an ornamental. Resembling *J. keyensis* in foliage, this species has white flowers with scarious-margined, non-ciliate sepals and red fruits.

REFERENCE:

SARGENT, C. S. *Jacquinia*. Silva N. Am. **5**: 155–158. *pl. 242*. 1893.

MYRSINACEAE (MYRSINE FAMILY)

Shrubs or trees, mostly with alternate, simple, entire, exstipulate, glandular-punctate leaves, in ours persistent. Flowers 4–6-merous, regular, usually hypogynous, complete or polygamo-dioecious, variously disposed, often clustered on scaly spurs or in panicles or cymes. Calyx shorter than the corolla, the sepals imbricate, connate at the base, persistent. Corolla rotate or short-salverform, the lobes united at the base or sometimes distinct. Stamens distinct, in a single whorl adnate to the corolla tube opposite the lobes, the anthers [transversely or] longitudinally dehiscent; staminodia absent. Pistil 1, derived from 4–6 carpels but appearing simple: ovary 1-loculed, bearing few to many semi-anatropous or semi-campylotropous ovules buried in a fleshy-proliferated axile or basally attached free central placenta filling the ovary cavity. Fruit in ours a 1-seeded drupe, usually dark colored, the seed with a cylindrical embryo and copious endosperm. (Including Ardisiaceae.)

A relatively large family of about 32 genera and approximately 1000 species widely distributed in the tropics and subtropics; two indigenous species in our area, representing two of the largest genera, both of subfam. MYRSINOIDEAE Pax, characterized by the superior ovary and the 1-seeded fruits.

The Myrsinaceae and the Theophrastaceae are distinguished from the Primulaceae by their woody habit, the indehiscent 1–few-seeded drupaceous or berry-like fruits and the fleshy or pulpy, sometimes mucilaginous placenta surrounding or embedding the ovules. The Myrsinaceae differ from the Theophrastaceae by the absence of staminodia and by anatomical features enumerated under the latter family.

The pollen grains of the Myrsinaceae are usually 3(–5)-colpor(oid)ate, suboblate to prolate, more or less similar to those of Primulaceae and Theophrastaceae.

The family is of limited economic importance. It is the source of several ornamental shrubs.

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KEY TO THE GENERA OF MYRSINACEAE

Ovules multiseriate (Tribe ARDISIEAE); inflorescences terminal, manifestly paniculate, the pedicels slender, longer than the flowers or fruit; flowers conspicuous, the corolla lobes reflexed; style slender; stigma entire. . . . . 1. *Ardisia*.

Ovules in a single circumferential series (Tribe MYRSINEAE); inflorescences appearing as congested cymes scattered along the twigs on scaly spurs, the pedicels 1–2 mm. in length, shorter than the flower or fruit; flowers inconspicuous, the corolla lobes erect or spreading; style short; stigma lobed. . . . . 2. *Rapanea.*

Tribe ARDISIEAE A. DC.

1. **Ardisia** Swartz, Prodr. Veg. Ind. Occ. 48. 1788, nom. cons.

Shrubs or small trees, the flowers of our species conspicuous, in terminal panicles, the pedicels slender, articulate at the base, the corolla rotate, 5(rarely 4–6)-parted, the lobes convolute in the bud or sometimes one wholly exterior, recurved at anthesis. Stamens distinct, erect, connivent in a column around the style; anthers sagittate at the base, pointed at the apex, dehiscent by slits, the filaments equalling the anthers in length. Style linear, exceeding the anthers; stigma entire. Fruit a drupe, the endocarp longitudinally ribbed, bony. (Including *Icacorea* Aubl. 1775, nom. rejic.) TYPE SPECIES: *Ardisia tinifolia* Swartz. (Name from Greek *ardis*, point, apparently referring to the apiculate-tipped stamens of some species.) — MARLBERRY, MARBLEBERRY, CHERRY.

A large genus of about 250 species, mostly tropical. Represented with us by a single indigenous species of subgenus ARDISIA (subg. *Pickeringia* (Nutt.) Mez). *Ardisia escallonioides* Cham. & Schlecht. (*A. Pickeringia* Nutt., *Icacorea paniculata* (Nutt.) Sudw.) is a common small tree of coastal hammocks of southern Florida, extending northward along about two-thirds of the east coast of the peninsula and about one-half of the west, and occurring inland to some extent in moist hammocks and in the hammocks and pinelands of the Everglade Keys and Florida Keys. Beyond our area it is most abundant in the Bahamas, Cuba and Hispaniola, less frequent in Mexico and Central America. In Florida the marlberry commonly grows in the shade of other trees, the small crown of leaves often elevated to 3 m. or more. The white, purple-streaked, fragrant flowers appear in abundance in paniculate clusters at the ends of the leafy twigs, usually about November. The globose, shining, black fruits, about 7–8 mm. in diameter, mature more or less throughout the year. The long, linear styles are often persistent in fruit.

Ardisia polycephala Wall. (subg. TINUS (Burm.) Mez), native to Burma, has been reported to occur in hammocks and around old homesteads in southern Florida as an escape from cultivation. This species has axillary clusters of white or pinkish flowers with contorted corolla lobes and slender-tipped anthers. The nearly black fruits are about 1 cm. in diameter. Although persisting, this shrub does not appear to spread to any significant extent.

Ardisia crenata Sims (*A. crispa* sensu A. DC. and many others, not *A. crispa* (Thunb.) A. DC.), of subg. CRISPARDISIA Mez, and *A. japonica* (Hornsted) Blume, of subg. BLADHIA (Thunb.) Mez, both natives of eastern Asia, are used rather extensively as horticultural ornamentals for their foliage and showy red berries.

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WALKER, E. H. A revision of the eastern Asiatic Myrsinaceae. Philip. Jour. Sci. **73:** 1–259. 1940. [Correct application of *A. crenata,* 115; *A. japonica,* 134.]

Tribe MYRSINEAE Pax

2. **Rapanea** Aubl. Hist. Pl. Guiane Franç. 1: 121. *pl. 46.* 1775.

Shrubs or small trees, the flowers small, inconspicuous, congested-umbellate, on short, scaly axillary spurs scattered along the twigs, the pedicels short. Corolla spreading or rotate, 5-parted, the tube short. Stamens with ovate-oblong anthers, nearly sessile. Style obsolete, shorter than the stamens; stigma lobed. TYPE SPECIES: *Rapanea guianensis* Aubl. (Name derived from a native name for the plant in French Guiana.)

About 140 species of tropical and subtropical distribution in both hemispheres. *Rapanea guianensis* (*Myrsine Rapanea* Roem. & Schult., *Myrsine floridana* A. DC.) occurs in coastal hammocks of southern peninsular Florida as far north as Volusia County on the east coast and Levy County on the west, in hammock "islands" in the Everglades, on the Everglade Keys and the Florida Keys. It is distributed through tropical America to southern Brazil and Bolivia, being most common in the West Indies, less frequent or rare in Mexico. The flowers and fruits are borne on short spurs along the branches, as in species of *Myrica,* and fruiting specimens bear a very close superficial resemblance to *M. inodora* Bartr., even the foliage being comparable. The globose fruits are dark blue or black in color and at maturity are about 4 mm. in diameter, capped by the persistent sessile stigma. The oblong-obovate leaves, 4–10 cm. long, are mostly clustered at the ends of the branchlets.

The unusually cold winter of 1957–1958 provided various examples of the effects of low temperatures on tropical and subtropical genera. *Rapanea guianensis* which was seen in abundance in April 1958 in Gulf Hammock, near Chassahowitzka, Citrus County, not far from the apparent northern limit of the species on the west coast of Florida, had been killed to the ground by the cold of the winter (temperatures of 15° F. reported locally) but was sending out abundant sprouts from the bases of the plants. Severe winters such as this undoubtedly are one of the primary factors involved in determining the northern limit of this species.

PRIMULACEAE (PRIMROSE FAMILY)

Annual, winter-annual or perennial herbs [or very rarely shrubs] with alternate, opposite or whorled simple leaves and regular, complete, hypogynous or (in *Samolus*) perigynous, 4–8-merous flowers. Stamens as many as the gamopetalous corolla lobes, epipetalous, inserted opposite the lobes on or at the base of the tube, sometimes with as many alternating staminodia, the filaments sometimes connate, the anthers introrse, longitudinally dehiscent. Pistil 1, compound (as indicated by the valves of the ovary); ovary 1-locular with a free-central placenta arising from the base and bearing several to many amphitropous or anatropous ovules; style 1, glabrous; stigma terminal, usually slightly dilated. Fruit a valvate or circumscissile capsule [or rarely indehiscent]. Seeds several to many, with a small embryo in fleshy albumen.

A family of about 20 genera and approximately 500 species, widely distributed in the Northern Hemisphere, occurring on all continents but most abundant in the north-temperate regions.

The Primulaceae are distinguished by their predominantly herbaceous habit, gamopetalous corollas, epipetalous stamens in a single whorl opposite the corolla lobes, free-central placentation and valvate or circumscissile capsules with numerous seeds.

Vascular evidence indicates that the unilocular condition of the ovary of the Primulaceae, with free-central placentation, is of a derivation similar to that of the Caryophyllaceae; the primulaceous flower is descended from an ancestor having a plurilocular ovary with axile placentation. Several modern systematists have suggested that the primitive condition may well be found among the Centrospermae. However, evidence from the remainder of the plant has not yet been adequately considered.

Generic relationships within the Primulaceae are not clear. Consequently, several different tribal arrangements exist for the family. Objections have recently been raised to the alliance (on the basis of the reflexed corolla lobes) of *Dodecatheon* with *Cyclamen* and the resultant separation of these genera from *Primula*. *Dodecatheon* has been considered on anatomical grounds to approximate more closely the original primulaceous flower than any of the other family representatives, but evidence based upon chromosome numbers raises some question in this regard. *Lysimachia* has also been suggested as the most primitive genus of the family and that nearest the Myrsinaceae, for some species of sect. *Apodanthera* (cf. *L. solanoides* Hand.-Mazz.) are lignescent, with indehiscent or hardly dehiscent capsules, and subsessile, upright anthers which open by terminal pores. There has been no recent study of the problem of generic relationships within the Primulaceae taking into consideration evidence from all available sources.

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machia vulgaris, Anagallis arvensis, Primula vulgaris and *Samolus Valerandii.*]

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KEY TO THE GENERA OF PRIMULACEAE

A. Terrestrial or marsh plants with entire or merely toothed leaves; flowers solitary, umbellate or racemose.

B. Ovary wholly free from the calyx.

C. Scapose; flowers in involucrate umbels.

D. Low, rosulate annuals with pubescent leaves; corolla inconspicuous, the lobes erect or spreading at anthesis; calyx accrescent, the lobes green, not ridged, the tube whitish and prominently ridged; stamens distinct, included. . . . . 1. *Androsace.*

D. Perennials with broad, glabrous or glabrate leaves; corolla conspicuous, the lobes reflexed at anthesis; calyx herbaceous, not ridged, the lobes and tube similar in texture; filaments connate below, the anthers forming an exserted cone. . . . . 2. *Dodecatheon.*

C. Caulescent; flowers solitary in the leaf axils or in racemes.

E. Stem with scale-like alternate leaves below and a single whorl of thin, lanceolate leaves at the summit, subtending the pedunculate, 6–8(mostly 7)-merous flowers; corolla white. . . . . . 4. *Trientalis.*

E. Stem leafy throughout, leaves alternate, opposite or whorled; flowers 4–6-merous.

F. Capsule valvate; corolla yellow; perennials with opposite or whorled leaves; flowers 5–6-merous. . . 5. *Lysimachia.*

F. Capsule circumscissile; corolla scarlet, blue or white; annuals with alternate or opposite leaves; flowers 4–5-merous. . . . . 6. *Anagallis.*

B. Ovary partially inferior, adnate to the calyx tube; inflorescence racemose, the pedicels bracteate or ebracteate. 7. *Samolus.*

A. Aquatic plants with pectinately dissected leaves; flowers in whorls on the conspicuously inflated, floating peduncles. .... 3. *Hottonia.*

1. **Androsace** L. Sp. Pl. 1: 141. 1753; Gen. Pl. ed. 5. 69. 1754.

Small, scapose, pubescent annuals [biennials or perennials, these scapose or caespitose]. Leaves ovate-lanceolate, sparingly denticulate [or quite various]. Scapes 1–many, the inflorescence a simple umbel [or scapes single-flowered]; flowers involucrate, borne on unequal pedicels. Calyx accrescent, the whitish tube broadly ridged, the 5 lobes green and not ridged. Corolla small, white, marcescent, included within the calyx, the lobes obtuse, shorter than the tube [or in perennials surpassing the calyx and conspicuous]. Stamens 5, the anthers oval to oblong, the short filaments attached at or below the middle of the corolla tube. Style short, the stigma capitate-discoid, the ovary superior, ovoid to globose. Capsule valvate to the middle, coriaceous above, membranaceous below. Seeds many, small, blackish. TYPE SPECIES: *Androsace carnea* L. (A name applied by Pliny to some unknown plant.)

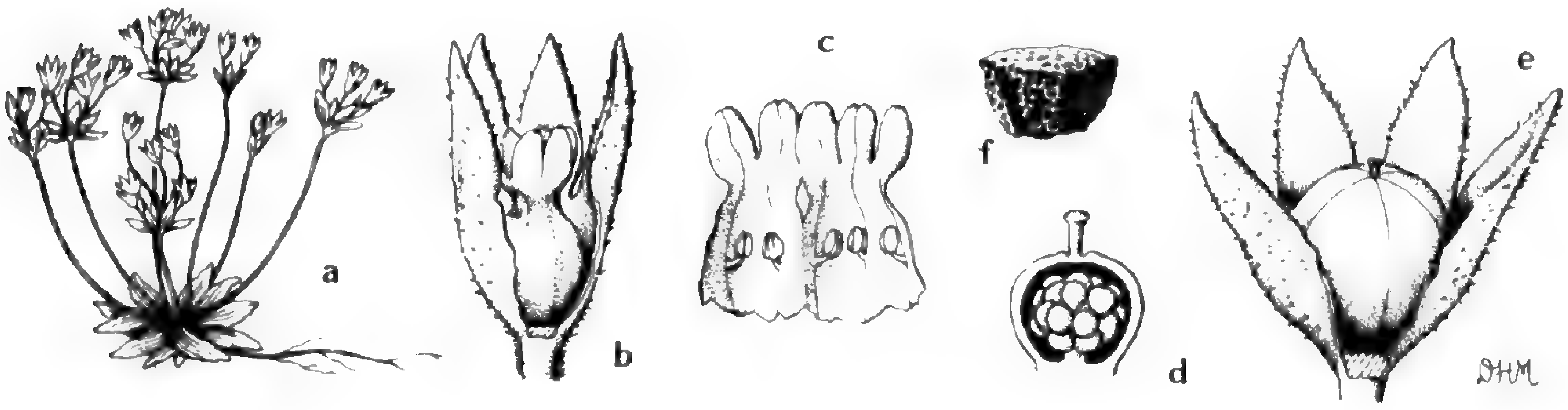

FIG. 1. **Androsace.** a–f, *A. occidentalis* Pursh var. *occidentalis:* a, habit, × ½; b, flower with one sepal removed, × 5; c, corolla opened to show stamens, × 5; d, pistil, semi-diagrammatic, the ovary in vertical section, × 10; e, mature fruit and calyx, one sepal removed, × 5; f, seed, × 10.

About 85–90 species, chiefly of the mountainous and boreal-arctic regions of Eurasia, but with six species and six varieties, all of sect. CHAMAEJASME Koch (sensu Handel-Mazzetti), in North America. The genus barely enters our range in Washington County, Arkansas, where *Androsace occidentalis* Pursh var. *occidentalis* has been collected. This variety with erect or somewhat spreading calyx lobes and erect to arched-ascending pedicels, has a wide range, primarily in the western United States (Mississippi, Missouri, and Arkansas river valleys, foothills of the Rocky Mountains in Colorado, Utah and Montana and into southwestern British Columbia, and also in the mountains of New Mexico and Arizona) in dry sands, gravels and rocky woods. Var. *arizonica* (Gray) St. John, with spreading to arched-reflexed calyx lobes and filiform pedicels, is restricted to the mountains of southeastern Arizona.

The marcescent corollas, often exhibiting a narrow constriction of the tube below the lobes, are inconspicuous in the annual species and are not used taxonomically in this group; here the primary characters are those of calyx and capsule.

Chromosome numbers of $2n = 20$, and 72 have been reported for two Old World species.

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2. **Dodecatheon** L. Sp. Pl. 1: 144. 1753; Gen. Pl. ed. 5. 71. 1754.

Scapose perennial herbs chiefly of calcareous soils. Leaves lanceolate or oblanceolate, entire, the inflorescence a naked scape bearing a simple, involucrate umbel, the pedicels erect in bud, somewhat recurved or arched at anthesis, erect in fruit. Calyx 5-lobed, the lobes equalling or longer than the tube, reflexed at anthesis, erect in fruit. Corolla white or purplish, 5-parted, the tube short, the lobes oblong, erect in bud, reflexed at anthesis. Stamens 5, erect, the filaments short, separate or united into a tube, the anthers basifixed, much longer than the filaments, connivent around the style, the connective prominent, smooth. Stigma slightly if at all dilated, exserted beyond the stamens; style filiform; ovary ovoid, equalling the filaments at anthesis. Capsule ovoid or cylindric-conical, much longer than the calyx, thick-walled, valvate; seeds numerous, spherical or ovoid, ours without membranaceous edges, reticulate, anatropous. TYPE SPECIES: *Dodecatheon Meadia* L. (The name from the Greek *dodeca*, twelve, and *theos*, god, given by Pliny to another plant, probably the primrose, which was allegedly under the care of the twelve superior gods.) — SHOOTING-STARS, AMERICAN COWSLIPS, MEADIAS.

A North American genus of about 15 species, mostly western. Section DODECATHEON, to which our species belongs, differs from sections PURPUREO-TUBULOSA Knuth and CAPITULUM H. J. Thompson by a combination of characters, including the nondilated stigma, valvate capsule (as opposed to operculate), the yellow (rarely dark), separate or united filaments and the seeds without membranaceous margins. There are also developmental differences in the seedlings of the three sections: the first true roots in sect. DODECATHEON develop from the hypocotyl just below ground level, well below the cotyledons; in sect. PURPUREO-TUBULOSA from a subterranean carrot-shaped caudex; and in sect. CAPITULUM from the aerial hypocotyl at the base of the cotyledons.

Dodecatheon Meadia has been variously treated taxonomically. Fassett recognized 5 varieties, some of dubious taxonomic significance, based primarily on quantitative characters of stamen-tube, calyx-lobe and capsule dimensions. Thompson has more recently recognized only three units:

subsp. *Meadia* ($2n = 88$), subsp. *brachycarpum* (Small) Knuth and subsp. *membranaceum* Knuth, the first two of which occur within our area.

Subspecies *brachycarpum* (var. *brachycarpum* (Small) Fassett) (Virginia to northern Georgia, Tennessee, Missouri, Oklahoma and Texas) is characterized by small flowers and fruits. Throughout its range it is sympatric with subsp. *Meadia* with which it intergrades wherever the two come into contact. The latter, however, occurs northward to Wisconsin well into the area of glaciation. Within glaciated territory morphological variation in this species is unimodal, while outside this area variation is bimodal, suggesting the presence of two populations. Populations within glaciated territory are, however, more variable as to flower color than those of unglaciated areas.

The third, subsp. *membranaceum* (var. *Frenchii* Vasey), is restricted in distribution to southern Illinois, adjacent Kentucky and the driftless area of Wisconsin. Characteristically a plant of overhanging, wet or dripping cliffs, where it grows in dense shade, it is characterized morphologically by the abrupt contraction of the leaf blade into the petiole. It occurs within the extensive range of subsp. *Meadia*, which has considerably thicker, noncordate blades. Specimens of the two subspecies have occasionally been found growing within a few feet of one another, although they are easily distinguished morphologically. Ecological experiments, including reciprocal transplantation in the field, as well as greenhouse observations, indicate no change in leaf form as a result of varying light intensities and support the genetical and morphological distinctness of the two taxa.

With the exception of var. *Frenchii* Vasey (subsp. *membranaceum*), the five varieties of *Dodecatheon Meadia* recognized by Fassett on morphological grounds do not occupy different environments. Based primarily on quantitative characters of stamen-tube, calyx-lobe and capsule dimensions, these varieties are of dubious taxonomic significance. Solution of the problems of variation in this complex would appear to require genetic studies.

The taxonomic characters utilized in this group vary considerably. Collectors should record corolla color in the field and such other characters as may be obscured in pressing. The varying shape of the connective and the connation of the filaments have been found to be unreliable as taxonomic characters but no one has suggested the cause of such variation. The red color at the base of the leaves of *D. Meadia* is not lost in herbarium material; in pressing this color consistently disappears from the leaves of *D. radicatum* Greene (*D. amethystinum* Fassett), a species of the East but one apparently not represented in our area. Fruit-texture and -color are reported to be reliable both in the field and in the laboratory.

Although insects have occasionally been observed to visit the flowers of *Dodecatheon*, their role in pollination is unknown. The structure of the flower suggests that self-pollination is frequent, if it is not the primary means of pollination. The observations of collectors in this respect would be helpful. The flower buds are at first erect, but, during anthesis when the sepals and petals are reflexed, the pedicels arch outward and downward, placing the flowers in a nodding position. The erect anthers surrounding the exserted style are thus inverted and, upon dehiscence along their connivent surfaces, a certain amount of pollen falls upon the stigma. In fruit the pedicels reassume an erect position.

The reported chromosome numbers form a polyploid series ($2n = 44$, 66, 88, 132).

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3. **Hottonia** L. Sp. Pl. 1: 149. 1753; Gen. Pl. ed. 5. 72. 1754.

Aquatic herbs with pectinate leaves scattered along the rooting and floating stem and crowded in a whorl beneath the cluster of conspicuous, inflated aerial peduncles; the pedicellate flowers and subtending sepaloid bracts whorled at the constricted nodes, forming interrupted racemes. Calyx of 5 herbaceous, linear-oblong sepals. Corolla white, 5-lobed, the lobes as long as or shorter than the tube. Stamens 5, the filaments short, adnate near the center of the corolla tube; pollen 3-colporoidate. Stigma minutely clavate; style linear; ovary subglobose. Capsule obpyriform to subglobose, membranaceous, 5-valved, the valves sometimes coherent at base and apex; seeds numerous, small, oblong-oval, longitudinally rugose, anatropous. TYPE SPECIES: *Hottonia palustris* L. (The name in honor of Petrus Hotton, 1648-1709, Dutch botanist and professor at Leiden.) — FEATHERFALL, WATER-VIOLET.

Two species, the Eurasian *Hottonia palustris*, and *H. inflata* Ell. of the eastern United States. *Hottonia inflata* is widespread, but of sporadic occurrence, from Florida to Texas and north to New England, New York, Ohio, Indiana, southern Illinois and Missouri. In most areas it is considered rare, although it sometimes occurs in abundance. In New England the species is a winter annual, with the seeds germinating in autumn and the seedlings growing rapidly. Although growth is retarded during the winter months, the plants survive protracted periods beneath a cover of ice. By May the plants reach the surface of the water and the inflated peduncles develop. The flowers appear from late May to mid-June. After flowering, the old plants shed the pectinate leaves and decay as the seeds ripen.

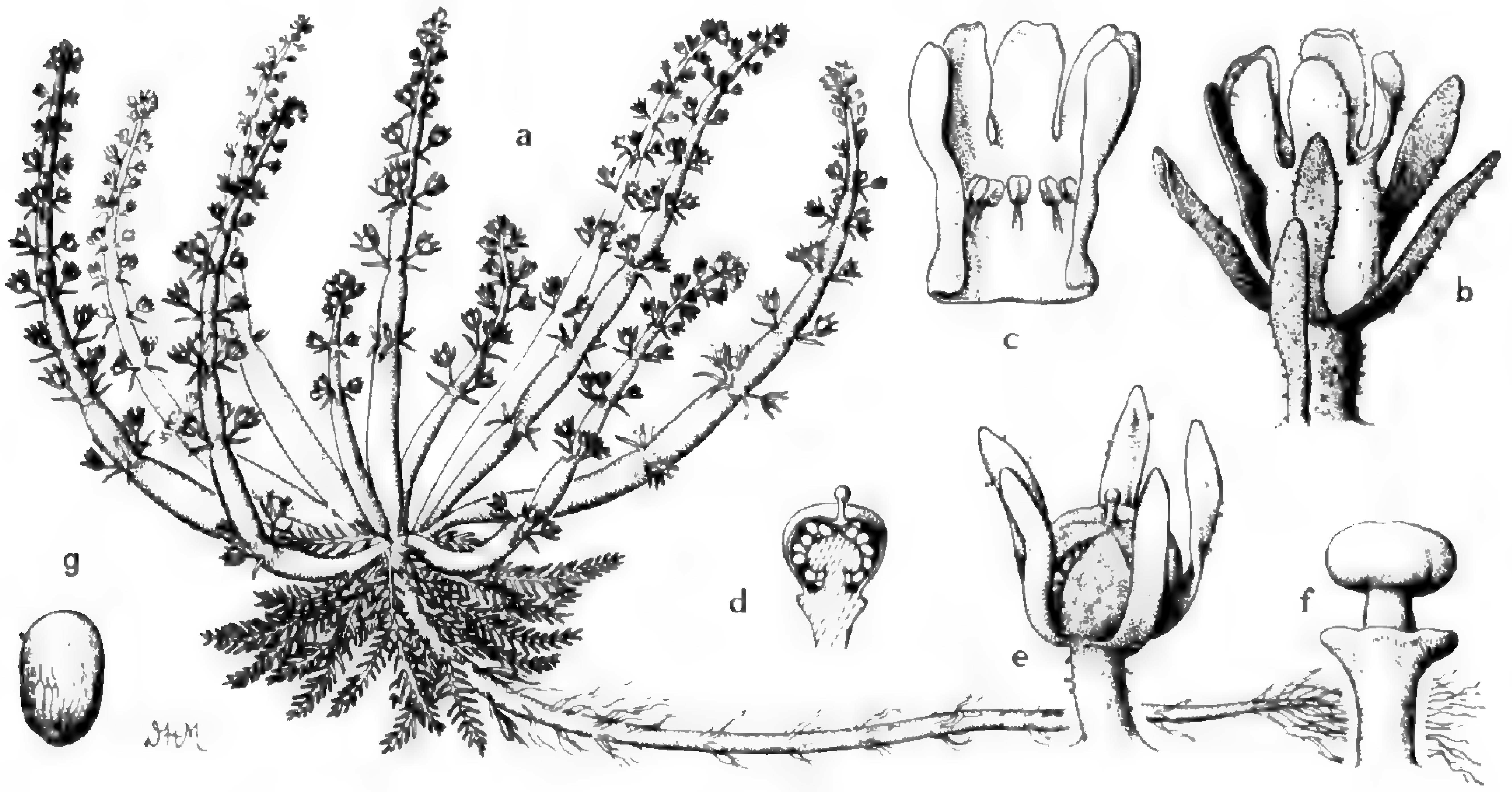

FIG. 2. **Hottonia.** a–g, *H. inflata:* a, flowering and fruiting plant, × ¼; b, flower with bract, × 5; c, corolla, opened to show stamens, × 5; d, pistil, semi-diagrammatic, the ovary in vertical section, × 5; e, mature fruit, × 5; f, pedicel and placenta from a large fruit near base of inflorescence, after dehiscence of fruit, × 5; g, seed, × 15.

Structural and functional dimorphism is reported for *Hottonia palustris* ($2n = 20$) from the British Isles. Pollen grains of the long-styled flowers differ in size as compared with those of short-styled flowers by a proportion of 14 to 9, respectively. (Cf. *Pontederia.*) The significance of the size differences is unknown. Pollination experiments with short-styled flowers indicate that the species is at least partially self-fertile when artificially pollinated. Manual cross-pollination of short-styled flowers with pollen from a long-styled individual of a different source also effects seed production, with a considerably larger proportion of fruit and seed set than in the former instance, suggesting that the heterostylous condition is of functional significance in promoting cross-pollination. In contrast, *Hottonia inflata* exhibits neither heterostyly nor other structural dimorphism. Although the style is quite short, at anthesis the stigma reaches the included anthers and is often seen to be covered with pollen from the same flower, suggesting that self-pollination frequently occurs in this species.

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4. **Trientalis** L. Sp. Pl. **1:** 344. 1753; Gen. Pl. ed. 5. 161. 1754.

Low, nearly smooth, rhizomatous, perennial herbs of woodlands and peaty slopes, spreading by slender, elongate stolons. Stems simple, erect, bearing several inconspicuous alternate bracts and a conspicuous whorl of lanceolate, acuminate, thin-textured, veiny leaves at the summit and a few axillary, slenderly pedunculate, star-shaped, delicate white flowers. Flowers (6)7(8)-merous. Calyx deeply parted, the lobes linear-lanceolate. Corolla deeply parted, rotate, the lobes ovate-elliptic, pointed, coherent at the base as a short, nearly obsolete tube. Stamens with slender filaments, united basally in a short ring on the base of the corolla, the anthers oblong, basifixed, revolutely coiled in anthesis. Stigma only slightly dilated; style filiform, equalling the filaments; ovary globose, about equalling the corolla tube at anthesis. Capsule globose, valvate to the base, the valves recurved, exposing the several grayish-granular seeds persisting temporarily upon the erect placenta. Type species: *Trientalis europaea* L. (The name from the Latin *triens*, one-third of a foot, alluding to the height of the plant.) — Starflower, Chickweed-wintergreen.

Three species of the North Temperate Zone, only one barely entering our area in northeastern Tennessee. *Trientalis borealis* Raf. (*T. americana* Pursh) is distributed from Labrador to Saskatchewan, south to Newfoundland, Nova Scotia, New England, Virginia, West Virginia, Tennessee, Ohio, Illinois and Minnesota. It occurs in shady woodlands southward and on peaty slopes northward, ascending to subalpine regions. *Trientalis latifolia* Hook. occurs in the montane and subalpine regions of Pacific North America from western California into British Columbia. *Trientalis europaea* L. var. *europaea* ($2n$ = ca. 112 or 160) is primarily Eurasian; var. *arctica* (Hook.) Ledeb. enters North America from western Siberia, extending from the Bering Strait and the Aleutians to the mountains of Oregon. Similar in habit, these species differ in the shape of leaves and corolla lobes. *Trientalis* is closely related to *Lysimachia*.

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5. **Lysimachia** L. Sp. Pl. 1: 146. 1753; Gen. Pl. ed. 5. 72. 1754.

Rhizomatous, caulescent, perennial herbs [or rarely shrubs] of decumbent or repent habit and with simple, opposite or whorled (sometimes glandular-punctate) entire leaves. Flowers 5, 6(7)-merous, variously disposed. Calyx herbaceous, of 5 deeply parted imbricate or valvate lobes. Corolla yellow [or white] rotate or somewhat campanulate, of 5 deeply parted, convolute or individually supervolute lobes and a short tube, sometimes with as many alternating staminodia. Filaments of the fertile stamens nearly distinct or united at the base, the 2-loculed anthers basifixed or somewhat versatile. Stigma terminal; style linear; ovary ovoid to globose. Capsule 5-valved, the seeds few to many, oblong, orbicular or angular, sometimes winged, the embryo in evident endosperm. [$2n = 18$, 20, 24, 28, 30, 36, 60, in species beyond our range.] (Including *Steironema* Raf.) TYPE SPECIES: *Lysimachia vulgaris* L. (Named, according to tradition, for King Lysimachus of Thrace, who, when confronted by an enraged bull, waved a loosestrife before it and quieted it; or from the Greek *lysis*, a release, and *mache*, strife, alluding to ancient lore which attributed to the plants the power of conciliation in animals.) — LOOSESTRIFE.

A genus of about 160 species in seven subgenera, of wide distribution, especially in the northern hemisphere (with the largest number of species in eastern India, northern Burma and southern China). Fourteen species, in two subgenera, occur in our area. At various times most of the subgenera have been considered to be independent genera, but on a world-wide basis there seems to be no positive evidence for such separation.

Subgenus SELEUCIA Bigelow (*Steironema* Raf.), with evident staminodia, erose or apiculate corolla lobes supervolute in bud (each inclosing a stamen), and epunctate leaves, includes five species of temperate America north of Mexico, all in our area. The continental-ranging *L. ciliata* L. is closely related to *L. tonsa* (Wood) Knuth, of the southern Appalachians. *Lysimachia radicans* Hook., primarily of the lower Mississippi embayment but with stations in Virginia, approaches *L. lanceolata* Walt., centered in the eastern United States and with two intergrading subspecies, *lanceolata* (including *L. heterophylla* Michx.) and *hybrida* (Michx.) J. D. Ray (var. *hybrida* (Michx.) Gray). Especially distinctive is *L. quadriflora* Sims, mostly of the north-central states but with stations in at least Georgia and Arkansas in our area.

Subgenus LYSIMACHIA (subg. *Cassandra* Bigelow), characterized by absence of staminodia, imbricate corolla lobes with entire margins, and punctate leaves, is a large and complex group centering in southeastern Asia, with only five indigenous American species. Section NUMMULARIA (Gilib.) Klatt includes the repent, very floriferous, but usually sterile and apparently apomictic, *L. Nummularia* L. ($2n = 36$), introduced from Europe, and, to the north of our area, *L. punctata* L. ($2n = 30$), also of European origin. Section LYSIMACHIA (sect. *Lysimastrum* Endl.) is composed of only the distinctive *L. Fraseri* Duby, of the mountains of North Carolina, Georgia, Tennessee and Alabama, the European *L. vulgaris* ($2n = 28$), naturalized in the northern United States and Canada, and *L. salicifolia* F. Muell., of Australia. Section TRIDYNIA (Raf.) Gray includes the widespread *L. quadrifolia* L., primarily of woodlands, its close relative *L. asperulifolia* Poir., restricted to the Carolina coastal plain, *L. Loomsii* Torrey, with a similar distribution in the Carolinas and Georgia, and *L. terrestris* (L.) BSP., of wide northern distribution and unique in producing axillary bulblets. The fertile *L.* × *producta* (Gray) Fern. and the sterile *L.* × *commixta* Fern. are the putative hybrids of this last with *L. quadrifolia* and with *L. thyrsiflora* (subg. NAUMBURGIA), respectively.

Recently evaluated on a morphological basis, some of our species of *Lysimachia* are well marked and easily identified; others are believed to hybridize to a greater or lesser extent and present patterns of variation which are often difficult to interpret. Cytological and genetic investigations would appear to be a source of useful information on the relationships among the variable species.

The generic status sometimes accorded subgenus SELEUCIA (as *Steironema* Raf.) is based in part upon the presence of staminodia. Variously interpreted as sterile filaments and as mere nonvascular excrescences, in the two species studied anatomically these structures as primordia show vascular traces, but there is no further development of the vascular tissue. The floral anatomy of all of the species thus far examined is fundamentally the same, and, except for the presence of staminodia, species of *Steironema* fall naturally into the genus *Lysimachia*.

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6. **Anagallis** L. Sp. Pl. 1: 148. 1753; Gen. Pl. ed. 5. 73. 1754.

Low, erect, spreading or procumbent annual herbs with alternate or opposite entire leaves and peduncled or nearly sessile flowers solitary in the leaf axils; plants of sandy fields, low grounds, damp sands and mud. Corolla (4)5-lobed, conspicuous (rotate with almost no tube) and deciduous, or inconspicuous (the urceolate or globular tube equalling the lobes) and often marcescent at summit of the capsule. Stamens (4)5, the filaments bearded or glabrous, adnate at the base or near the middle of the corolla tube. Ovary ovoid, the style linear, the stigma minutely capitate; capsule membranaceous, globose, circumscissile near the middle, the seeds numerous, angular. (Including *Centunculus* L., *Micropyxis* Duby.) TYPE SPECIES: *Anagallis arvensis* L. (The ancient Greek name, probably from *ana*, again, and *agallein*, to delight in, alluding to the habit of the flowers of opening again in the sunlight after having closed in cloudy weather.) — PIMPERNEL, SCARLET PIMPERNEL, POOR MAN'S WEATHER GLASS.

About 24 species, mostly native to the Mediterranean region, Africa and South America, three widely distributed. The three species known from the United States, representing two of three subgenera, occur within our area.

Subgenus ANAGALLIS, including plants with conspicuous, nearly rotate corollas and opposite or whorled leaves, is represented in our area by *Anagallis arvensis* L. ($2n = 40$), native to the European-Mediterranean region but now a widespread weed on nearly every large land mass. The species includes three subspecies, two of which are known from the United States. Subspecies *arvensis* (subsp. *phoenicea* (Scop.) Vollmann) includes plants with scarlet, salmon, white, lilac, or blue corollas, with relatively large lobes, and comparatively smooth margins, fringed with numerous gland-tipped, 3-celled trichomes. Subspecies *coerulea* (Schreb.) Vollmann (subsp. *foemina* (Mill.) Schinz & Thellung) comprises plants with blue flowers with narrower and smaller corolla lobes which are denticulate-margined and only sparsely glandular with 4-celled hairs. Both scarlet and blue forms of subsp. *arvensis* are well known in the United States. Subspecies *coerulea*, apparently less common, occurs at least in Illinois and Texas and may be expected within our area. Corolla color, rarely indicated, is difficult to determine in dried materials and should be noted by the collector. All blue-flowered plants should be examined carefully while fresh for the small, but important, distinguishing details. The corollas of both subspecies have a purple center produced by cells with purple sap in which small, blue, spicular crystals are aggregated.

Both subsp. *arvensis* and subsp. *coerulea* have been studied in considerable detail. The color variants of subsp. *arvensis* form an interfertile series which shows Mendelian segregation in the hybrids. Subsp. *coerulea* is partially isolated genetically and produces sterile F_1 hybrids with all except the salmon form of subsp. *arvensis*. The F_1 offspring of this last cross have pink flowers and are fully fertile. Segregation for flower color and other characters occurs in the F_2.

The relationship to these of the third, subsp. *gentianea* (Beck) Domac, requires further study. As delimited by Domac (1956), the subspecies includes plants with gentian-blue flowers, the petals of which are almost intermediate between those of the other two subspecies in shape, size and margin, and which are densely beset with 3-celled trichomes like those of subsp. *arvensis*. Trichomes of the stamen-filaments are 8–10(mostly 9)-celled while those of subsp. *arvensis* are 5–8-celled and those of subsp. *coerulea* are 11–12-celled. Although all of the specimens cited by Domac were from Yugoslavia, the distribution is probably much wider.

Anagallis arvensis is an obligate long-day plant, continuing in vegetative growth indefinitely with less than the critical 12-hour light period. Cross-pollination in this species is by Hymenoptera and Diptera. The flowers are also adapted to self-pollination, however, and are fully self-fertile.

Subgenus CENTUNCULUS (L.) P. Taylor, primarily a group of tropical Africa and one traditionally treated as a genus, includes species which combine characters of erect habit, alternate leaves, terminal inflorescences, small, pale flowers, subpersistent corollas and glandular ovaries. In the widespread *A. minima* (L.) Krause (*Centunculus minimus* L.) ($2n = 22$) the corolla is very short and the stamens are connate and adnate to the corolla for about half their total length. The pantropical *A. pumila* Sw. (*Micropyxis pumila* (Sw.) Duby; *Centunculus pentandrus* R. Br.), composed of three varieties, is represented with us by var. *pumila*, confined to low grounds of peninsular Florida. The corolla is longer and the stamens are connate and adnate less than a quarter of their total length (except in *A. pumila* var. *djalonis* (A. Chev.) P. Taylor, of tropical Africa), as in the remainder of the subgenus and genus. Inasmuch as the adnation is merely a matter of degree and varies within a single species, the retention of *Centunculus* as a genus seems unjustified.

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7. **Samolus** L. Sp. Pl. 1: 171. 1753; Gen. Pl. ed. 5. 78. 1754.

Caulescent or subscapose, somewhat succulent, glabrous, perennial herbs with alternate, simple, entire leaves, typically of wet situations in sand, sandy loam or muck, occurring also in salt marshes and on almost bare, eroded limestone. Inflorescences racemose, the wiry pedicels with or without bracts. Calyx herbaceous, campanulate, the 5 triangular lobes acute or acutish, equal to or longer than the adherent tube. Corolla white or pinkish, 5-lobed, the tube shorter or longer than the lobes, the throat sometimes glandular-pubescent. Stamens 5, included, sometimes with alternating staminodia. Stigma terminal, sometimes capitate; style linear; ovary ovoid, half-inferior. Capsule subglobose, the 5 valves thick-textured above, thinner below; seeds small, numerous, angular. (Including *Samodia* Baudo ex Small.) TYPE SPECIES: *S. Valerandii* L. (The name probably of Celtic origin, said to refer to curative properties of the genus in diseases of cattle and swine.) — WATER-PIMPERNEL, MARSH-PIMPERNEL, BROOKWEED.

About ten species, four in North America, the others in the extratropical regions of the southern hemisphere; represented with us by at least two species.

The American representative of the nearly cosmopolitan *Samolus Valerandii* complex, the white-flowered *S. parviflorus* Raf. (*S. floribundus* HBK.), of shallow water and wet soils, is widespread from British Columbia, southern Ontario and Quebec and New Brunswick, southward throughout the United States into Mexico, Cuba and Hispaniola. What is apparently the same species also occurs in southern Brazil, Uruguay, Paraguay, Bolivia, Argentina and Chile. The pedicels are bracteate and the corollas bear staminodia alternate with the stamens. Varying considerably in habit and variously treated taxonomically, the American plant is, in general, more widely and diffusely branched than *S. Valerandii*, with lateral instead of ascending pedicels and setaceous instead of linear-lanceolate bracts. Only the European plant has been investigated cytologically; the $2n$ chromosome number has been reported to be ca. 24 and ca. 36. The pollen grains are 3-colporoidate and subprolate. The development of the embryo has been followed in considerable detail.

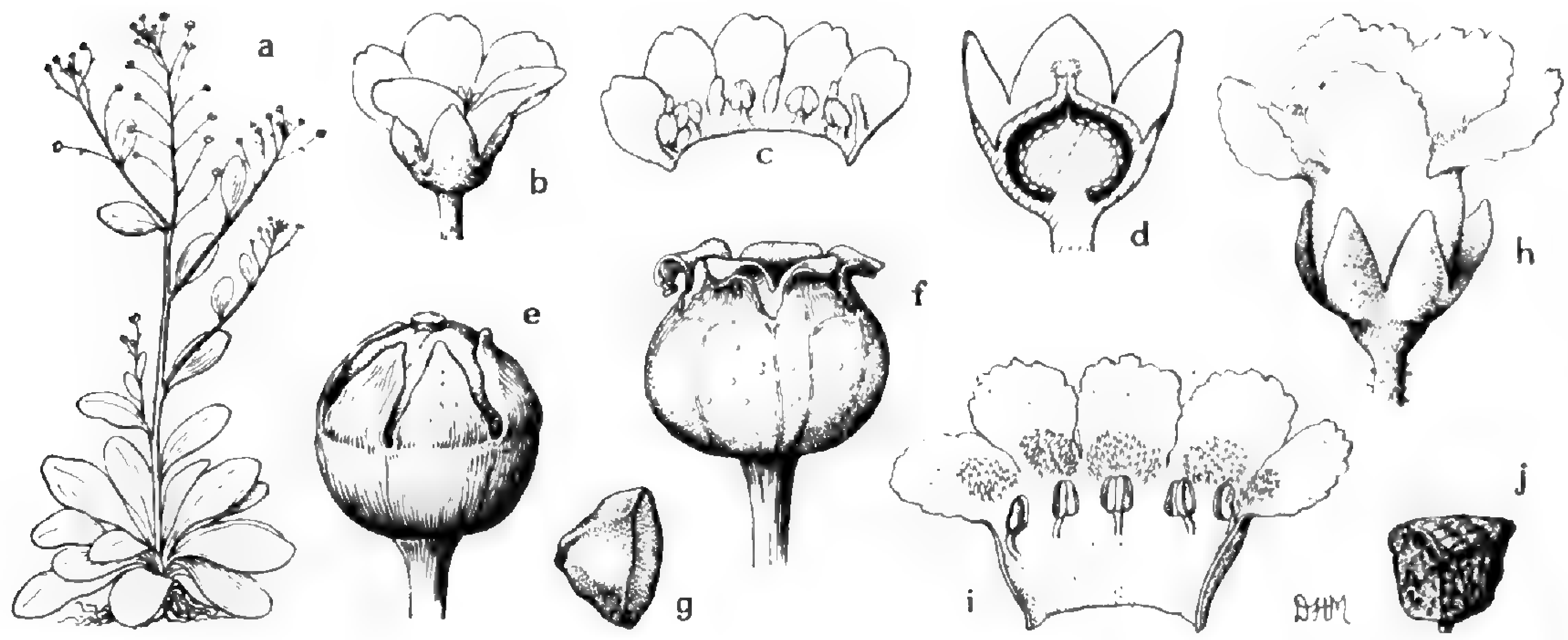

FIG. 3. **Samolus.** a–g, *S. parviflorus:* a, habit, × ¼; b, flower, × 5; c, corolla opened to show stamens and staminodia, × 5; d, flower with corolla removed, the pistil in vertical section, × 10; e, mature fruit before dehiscence, × 10; f, fruit after dehiscence, × 10; g, seed, × 20. h–j, *S. ebracteatus:* h, flower, × 4; i, corolla opened to show stamens and patches of glandular hairs, × 4; j, seed, × 20.

The pink-flowered *Samolus ebracteatus* HBK., lacking floral bracts and staminodia, grows equally well in sand or sandy loam or on almost bare limestone. Thus considerable variation exists in the extent of development of the stem-system and in leaf-shape, flower-size and the form of the inflorescence. Distributed in the West Indies, Florida, Oklahoma, Texas and Mexico, the species is restricted in our area to the southern tip and western coast of peninsular Florida, presumably dispersed from the West Indies. The cause of the gap in distribution between Florida and Texas and Oklahoma is not known. On rich soils the foliage develops a deeper or brighter green; on limestone the foliage is pale or glaucous and sometimes coated with lime.

Samolus alyssoides Heller and *S. cuneatus* Small, both described from Texas, are doubtfully distinct. Glandular-pubescent inflorescences, supposedly characteristic of the latter, appear in populations of *S. ebracteatus* in Florida. The former species is based upon quantitative characters of dubious taxonomic significance. The status of these taxa needs critical evaluation.

The perigynous floral condition characteristic of *Samolus* has been investigated anatomically in *S. parviflorus*. The perianth is firmly attached to the ovary wall, producing an inferior ovary and consequent modification of the perianth pattern. The lower half of the hypanthium is a compound structure consisting of ovary wall and perianth combined. Early anatomical stages show a zonal development of five projecting points which form carpellary walls and five bulbous portions at their bases which unite in forming the central placenta. Ontogenetically the separation between carpel wall and placenta occurs in the embryonic stages and the placenta originates from the fusion of the five basal growing points. A similar situation has been described in *Lychnis* (Caryophyllaceae).

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VANDERBILT UNIVERSITY
AND
THE ARNOLD ARBORETUM

THE CYTOGENETICS OF FACULTATIVE APOMIXIS IN MALUS SPECIES

KARL SAX

SOME OF THE ASIATIC SPECIES OF *Malus* produce predominantly maternal progeny, even when surrounded by other species which bloom at the same time. Since apple species and varieties are generally self-sterile, the production of uniform progeny from trees surrounded by other species or varieties would indicate that these trees are apomictic. The production of occasional variants and the production of occasional hybrids following artificial cross-pollination indicate that apomixis is facultative in these species.

Among the facultative apomicts are *Malus sikkimensis* from northern India, the related *M. rockii* from western China, *M. toringoides* and *M. hupehensis* from China and *M. sargentii* from Japan.

Several of these apomictic apple species are excellent ornamental trees, and *M. toringoides* and *M. sargentii* are usually propagated from seed. For many years the apomictic *Malus* species have been tested as rootstocks for ornamental and horticultural apple varieties. If such seedlings proved to be compatible with the clonal varieties they would provide uniform rootstocks without the expense and long period of time needed to obtain uniform rootstocks by vegetative propagation.

During the past twenty years we have used seedlings of *Malus sikkimensis* as rootstocks for apple varieties. They have proved to be compatible with all ornamental and commercial varieties of apples tested, and for some varieties they are semi-dwarfing. The first seedlings used were from a tree (AA No. 17459) which was raised from seed obtained from the Royal Botanic Gardens, Kew, England, in 1902. The progeny were relatively uniform with only an occasional variant. Unfortunately this tree was cut down before chromosome counts were obtained. The only other source of seed until recent years was a seedling of AA 17459 which was planted in 1936 (AA 50–36–A). Seedlings from the daughter tree proved to be much more variable than those of the original tree.

Malus rockii in the Arnold Arboretum is represented by a tree (AA 8334) grown from seed obtained from the University of California Botanic Garden in 1936. Like *M. sikkimensis* it is slow to come into fruit, and seed has been available only during the past few years. The two-year-old trees in the nursery are very uniform, varying only in size and vigor.

Malus hupehensis (AA 7441) has given the most uniform progeny of all the species tested, but the seedlings are not very compatible when budded with horticultural apple varieties. The occasional variants are usually dwarf forms.

The oldest tree of *M. toringoides* in the Arboretum (AA 17475) is from seed collected in China by Wilson in 1908. It has produced relatively uniform progeny and mature seedlings grown on the Peter Bent Brigham Hospital grounds are duplicates of the mother tree. But seeds sent to Stern in England produced a variant with larger fruit, which was given the varietal name *macrocarpa*. This variety, which is represented in the Arnold Arboretum (AA 11246), flowers about a week earlier than does the mother tree. Seedlings of var. *macrocarpa* grown at the Case Estates of the Arnold Arboretum by Dr. Wyman proved to be very variable in size and, in the several which have borne fruits, these differ in size and shape from either the species or the variety.

The oldest specimen of *M. sargentii* (AA 4681) in the Arnold Arboretum was grown from seed collected in Japan by Sargent in 1892. The variety *rosea* originated as a seedling of the species grown in the Rochester Park. A specimen (AA 11045) was planted in the Arnold Arboretum in 1921. Both *M. sargentii* and var. *rosea* produce 90 per cent or more of maternal-type seedlings when open pollinated. The variants usually differ from their parents primarily in size and vigor. Seedlings of the variety are more vigorous and are more compatible when budded with horticultural varieties than are the seedlings of the species. The variety is being tested as a dwarfing rootstock.

Chromosome counts of these apomictic species and their progeny have been obtained from meiotic divisions of the pollen mother cells and from somatic tissue. The mitotic divisions were obtained from parenchyma cells developed from the medullary rays. A strip of bark was removed from the trunk or branch of the tree and the exposed wood was covered with a strip of polyethylene film. The parenchymatous tissue from the medullary rays develops rapidly and after five or six days can be cut off in thin ribbons and fixed in alcohol-acetic fixative and stained in aceto-carmine. Although the large parenchyma cells provide much better chromosome figures than do root-tip or leaf-tip smears, exact counts are difficult or impossible in the triploids and tetraploids. In most cases the somatic counts reported are accurate to ± 1 or 2. Meiotic counts, particularly in the triploids, are also subject to some error, because of variation in the degree of pairing of the meiotic chromosomes and the great irregularity of meiosis in most of the triploids.

A summary of the chromosome counts is shown in TABLE I. The seedling of the original specimen of *M. sikkimensis* grown in the Arnold Arboretum is a triploid, but it produces both triploid and tetraploid progeny. A meiotic anaphase of one of the tetraploid progeny is shown in FIG. 1. Two seedlings of one of the tetraploid segregates grown in the Bussey Orchard (BO 4), were examined for chromosome counts and both were found to be triploid. The tetraploids generally have larger flowers and fruits than do the triploids and bloom earlier in the spring.

Malus rockii is a tetraploid and relatively good meiotic figures were obtained (FIG. 2). At the first meiotic division there are often several univalents, but the division is quite normal. The seedlings of *M. rockii* grown in the nursery included both tetraploids and, apparently, pentaploids, although only 76 chromosomes could be found in the somatic figure illustrated (FIG. 12). Some of the somatic counts reached 85, but exact counts were impossible.

TABLE I. Chromosome Counts of Facultatively Apomictic Malus Species and their Progeny

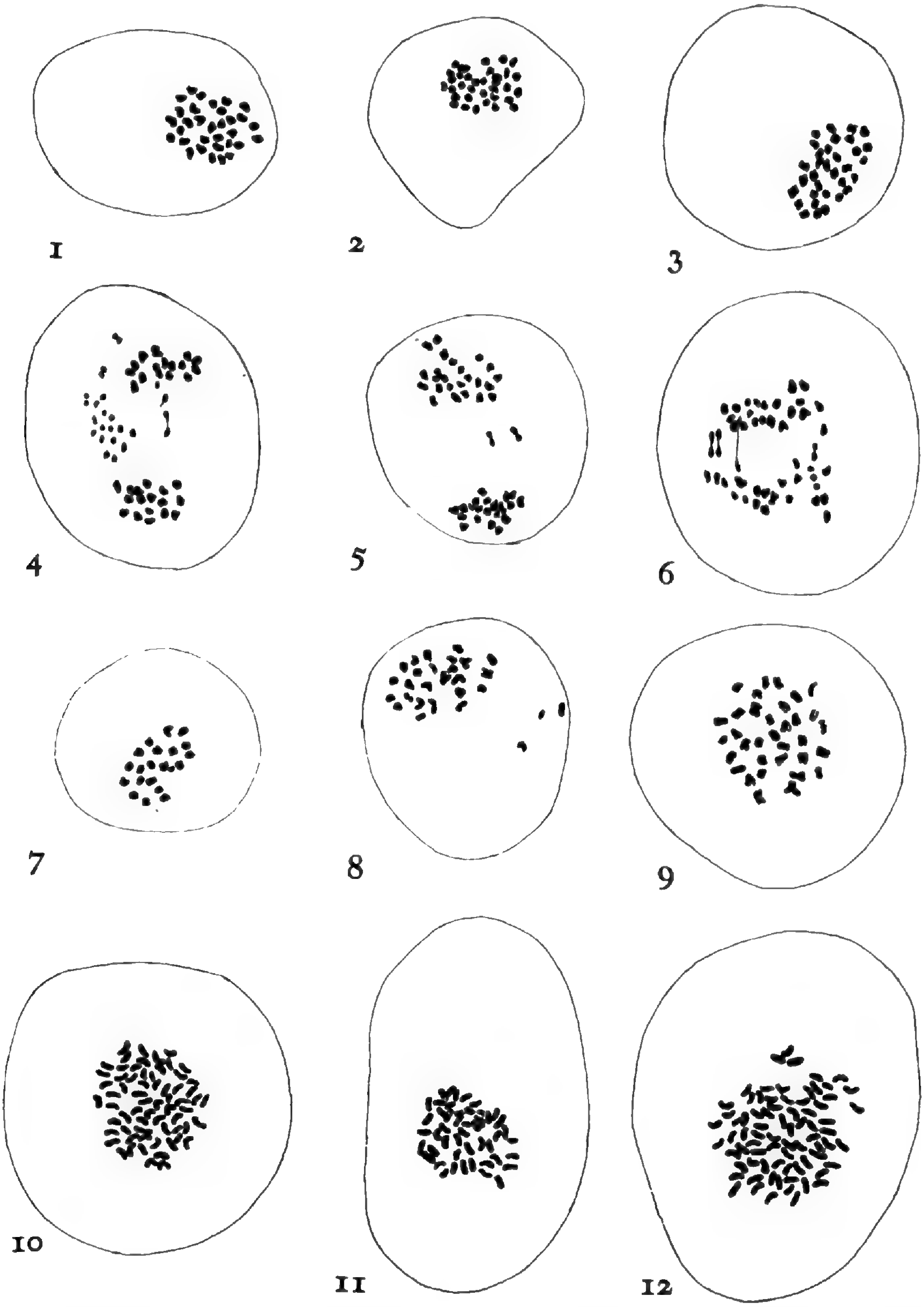
	RECORD NUMBER	CHROMOSOME NUMBERS			
	OF		PROGENY		
SPECIES	SEED PARENT	SEED PARENT	3*n*	4*n*	5*n*
M. sikkimensis	AA 17459	?	1	7	
M. sikkimensis sdlg.	BO 4	4*n*	2		
M. rockii	AA 8334	4*n*		4	2
M. hupehensis	AA 7441	3*n*			
M. toringoides	AA 17475	3*n*			
var. *macrocarpa*	AA 11246	4*n*	6		
M. sargentii	AA 4681	4*n*		3	
var. *rosea*	AA 11045	3*n*	3		

Malus hupehensis is a triploid, as determined from meiotic counts by Dermen (1936) and from our somatic counts. Meiosis in the pollen mother cells is very irregular; the tetrads disintegrate and no mature pollen grains are formed. Among the seedlings of *M. hupehensis*, Dermen found two tetraploids in 39 seedlings, based on somatic counts in root tips.

Malus toringoides also has very irregular meiotic divisions of the pollen mother cells and stages from prophase to tetrads can be found in a single anther. No critical counts could be obtained from meiotic figures, but somatic counts show that this species is a triploid. The var. *macrocarpa*, however, is a tetraploid, as determined from both meiotic and somatic counts. Meiosis in the tetraploid is normal with only occasional lagging univalents. All the seedlings of the variety which were examined were triploids.

Malus sargentii is a tetraploid with about 34 chromosomes at meiosis (FIG. 3) and 68 chromosomes at mitosis. The seedlings from the Arnold Arboretum trees are also tetraploids, but the fact that this species gave rise to the triploid var. *rosea* indicates that some triploid segregates would be found if enough seedlings were grown. The var. *rosea* is a triploid with many univalents at the first meiotic division (FIG. 4). Only three seedlings of the variety were examined cytologically and all were triploids. It is probable that some of the larger progeny of var. *rosea* are tetraploids, but these were not examined.

Many hybrids have been made between *M. sargentii*, or var. *rosea*, and diploid ornamental apples to combine the dwarf growth habit of this species with the superior flowering and fruiting characters of the ornamental diploid varieties. Crosses have also been made with 'McIntosh' as the first step in combining the disease resistance of *M. sargentii* with the fruit size and quality of 'McIntosh.' *Malus sargentii*, or its var. *rosea*, when artificially



Figures 1–12. Meiotic and mitotic chromosomes of *Malus* species and hybrids. 1, *M. sikkimensis*, meiotic anaphase I, 32 chromosomes. 2, *M. rockii*, meiotic anaphase I, 35 chromosomes. 3, *M. sargentii*, meiotic metaphase II, 33 chromosomes. 4, 5, *M. sargentii rosea*: 4, meiotic anaphase I, 3*n*; 5, meiotic anaphase I, 3*n*. 6, *M. sargentii rosea* × 'McIntosh' (5750), meiotic anaphase I, 3*n*. 7, *M. sargentii rosea* × *arnoldiana* (4650), meiotic anaphase I, 21 chromosomes. 8. *M. sargentii rosea* × *astracanica* (33340), meiotic anaphase I, 3*n*. 9, *M. sargentii rosea* × *astracanica* (33340 seg.), meiotic metaphase II, 4*n*. 10, *M. sargentii*

pollinated with pollen of a diploid produces from 0 to about 25 per cent of sexual hybrids. Most of the progeny are maternals in all crosses.

The hybrids were grown to maturity and their progeny from open-pollinated seeds were tested for breeding behavior. Most of them tend to breed true, with a small proportion of variants, indicating that facultative apomixis is a dominant character. The cytology and breeding behavior of the *M. sargentii* hybrids is summarized in TABLE II.

The pollen parents were diploid species and varieties which, when open pollinated, produced extremely variable progeny. Hybrid 19039 ('Henrietta Crosby') is a cross between *M. arnoldiana* (*M. floribunda* × *M. baccata*) and *M. pumila* var. *niedzwetzkyana*; 20139 is *M. arnoldiana* × *M. purpurea* f. *eleyi* (*M. pumila* var. *niedzwetzkyana* × *M. atrosanguinea*); and 6639 is an open-pollinated segregate of *M. spectabilis* f. *riversii*. *Malus astracanica* is a hybrid between *M. pumila* and *M. prunifolia*, and the Hopa Crab is *M. baccata* × *M. pumila* var. *niedzwetzkyana*. As would be expected, the progeny of these hybrids are very variable.

The sexual hybrids produced by crossing *M. sargentii* with 19039 or 20139–2 are triploids, as might be expected (FIG. 5). However, when pollinated with 20139–1 or 20139–3, *M. sargentii* produced aneuploid hybrids with the chromosome number near the diploid level. Hybrid 5650–2 had about 21 bivalents with only occasional univalents (FIG. 7). These hybrids lacked vigor and did not live long.

Crosses between the triploid *M. sargentii* var. *rosea* and the diploid species produced progeny ranging from near-diploid to tetraploid. The hybrid between var. *rosea* and *M. astracanica* was a triploid (FIG. 8). Progeny of this hybrid (33340) produced both triploids and tetraploids (FIG. 9). The tetraploid had larger flowers and fruits and bloomed earlier than did the original hybrid.

When crossed with *Malus arnoldiana*, *M. sargentii* var. *rosea* produced an aneuploid with about 17 bivalents and several univalents at meiosis. An aneuploid also resulted when var. *rosea* was crossed with 6639, but two sister hybrids were approximately triploid. Crosses with 'McIntosh' produced a triploid (FIGS. 6, 11), and three tetraploids or near tetraploids (FIG. 10). Crosses with Hopa Crab produced a tetraploid and two feeble aneuploids.

Progeny tests of the *Malus sargentii* F_1 hybrids indicate that facultative apomixis is a dominant character. The F_1 trees were grown in test plots with diploids and the open-pollinated seeds of the hybrids were presumably pollinated with pollen of both diploids and polyploids, although pollen fertility in the triploids is low. The seeds were stratified and grown in flats in the greenhouse. Some of the progenies were transferred to the nursery for further observation and selection. The percentage of variants was somewhat higher when the progenies were scored as young seedlings,

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var. *rosea* × 'McIntosh' (5750–B), mitotic metaphase, 67 chromosomes. 11, *M. sargentii* var. *rosea* × 'McIntosh' (5750), mitotic metaphase, 48 chromosomes. 12, *M. rockii* segregate, mitotic metaphase, 76 chromosomes.

because some of the variants were weak plants which did not survive or were too small to transfer to the field. In the field there was some variation in size and vigor of the maternal types. The variant seedlings differed from the maternal type in leaf characters and growth habit and generally were quite variable. The proportion of maternals and variants produced by some of the hybrids is shown in Table II.

All of the triploids and most of the tetraploid hybrids produced predominantly maternal progeny when open pollinated. However, one of the tetraploid hybrids between *M. sargentii* var. *rosea* and 'McIntosh' produced twice as many variants as maternals. The tetraploid segregate of *M. sargentii* var. *rosea* × *M. astracanica*, 33340, also produced a high proportion of variants, as did the tetraploid segregates of the triploid species *M. sikkimensis* and *M. toringoides*. Yet the tetraploid *M. sargentii*, when open pollinated, produces nearly 100 per cent of maternals.

Table II. **Cytogenetics of Malus Species Hybrids**

Cross	Record Number	Chromosome Counts		Progeny Segregation	
		Meiotic	Mitotic	Maternal	Variants
Malus sargentii	AA 4681	$4n$	$4n$	+	
× 19039	4751–1	$3n$	$3n$	40	2
× 20139–2	4851–1	$3n$		12	0
× 20139–2	4851–2	$3n$			
× 20139–1	5650–1	$16\text{–}17_{II} + 1\text{–}3_{I}$			
× 20139–1	5650–2	$20\text{–}21_{II} + 1\text{–}3_{I}$			
× 20139–3	5650–3	$16\text{–}17_{II} + 1\text{–}3_{I}$			
M. sargentii var. *rosea*	AA 11045	$3n$	$3n$	259	24
× *astracanica*	33340	$3n$	$3n$	25	2
Segregate of 33340		$4n$	$4n$	28	14
× *atrosanguinea*	17039	$3n$		72	3
× *arnoldiana*	4650–3	$17_{II} + 3_{I}$			
× 6639	5150–0	22_{II}			
× 6639	5150–1	$3n$			
× 6639	5150–2	$3n$			
× 'McIntosh'	5750–1	$3n$	$3n$	16	1
× 'McIntosh'	5750–2	$4n$	$4n$	8	16
× 'McIntosh'	5750–A	$4n$	$4n$	17	2
× 'McIntosh'	5750–B	$4n$	$4n$	33	1
× Hopa Crab	4450–A	$17_{II} + 2\text{–}3_{I}$			
× Hopa Crab	4450–B	$4n$		72	4
× Hopa Crab	4450–C	$18\text{–}20_{II} + 0\text{–}4_{I}$			

DISCUSSION

The facultatively apomictic species of *Malus* include both triploids and tetraploids. The triploids usually produce maternal progeny, presumably as the result of the development of an unfertilized and unreduced egg cell.

The occasional production of tetraploids by triploids would indicate that the unreduced egg cell was fertilized by pollen from a neighboring diploid species. The tetraploid species may breed true with only an occasional variant, as in *Malus sargentii*, but in the tetraploid forms of *M. sikkimensis* and *M. toringoides* the progeny are variable with respect to their morphological characters and, in *M. toringoides*, most or all of the segregates are triploids. Apparently the seeds of *M. sargentii* are derived from an unreduced egg cell, while in the tetraploid forms of *M. sikkimensis* and *M. toringoides* they are often, or perhaps usually, produced from the union of a reduced egg cell and a haploid gamete from pollen of a neighboring diploid species.

The sexual hybrids would tend to resemble the mother plant since in the triploids descended from a tetraploid female parent the latter would contribute two of the three genomes, in the tetraploid descended from a triploid female parent the latter would contribute three of the four genomes, while in the pentaploid *M. rockii* segregates the maternal parent would contribute four of the five genomes. Only in the triploids descended from tetraploid female parents would there be genetic segregation due to the reduction division in megasporogenesis, and then only if the tetraploid is heterozygous.

Often the facultatively apomictic tetraploids may produce some triploids, while the triploids may produce tetraploids, and both types of polyploids will have the major characters of the species. Thus chromosome counts from one or a few individuals may not reflect the true cytological picture. It is probable that this condition may be found in other genera of the Pomoideae. The diversity of types in some of the apomictic species of *Cotoneaster* and *Crataegus*, for example, could be the result of such chromosome irregularities.

In the controlled pollination crosses between the tetraploid *M. sargentii* and diploid species and varieties, the production of triploid hybrids was not unexpected (in view of the breeding behavior of open-pollinated triploid species) but the occurrence of near diploids was not expected. The triploid var. *rosea* also produced some near diploids. Apparently both forms of *M. sargentii* produce some egg cells with near diploid chromosome numbers. It is possible that such near-diploid segregates are produced in open-pollinated segregates, but are eliminated or discarded in the young seedling stage.

Triploid apples crossed with diploids normally produce aneuploid segregates with chromosome numbers ranging from diploid to triploid, regardless of whether the triploid is the female or the male parent, indicating that the triploid parent produced gametes with chromosome numbers ranging from 17 to 34 (Wanscher, 1939). The distribution of chromosome counts of the progeny indicates normal chromosome distribution with the most frequent gametic contributions from the triploid in the 23–25 chromosome classes.

As a result of random distribution of the chromosomes in the meiosis of sexual triploids, the progeny of triploids crossed by diploids usually includes very few diploids or tetraploids, and segregates with 40–42 somatic chromosomes are the most frequent. Yet the triploid *M. sargentii* var. *rosea*, when crossed with diploids, produced tetraploids, triploids and aneuploids near the diploid level in about equal frequencies. Meiosis in the triploids is irregular and could produce egg cells ranging from haploid to diploid, but meiosis in the tetraploid *M. sargentii* does not indicate much irregularity. There is no evidence from microsporogenesis that the tetraploid could produce microspores with one, two or three genomes such as Gottschalk (1958) has described in tetraploid tomatoes. Yet *Malus sargentii* pollinated with diploid species does produce a few hybrids near the diploid level. Apparently megasporogenesis is more irregular than microsporogenesis in these *Malus* species; however, it has not been studied cytologically.

In the progeny of tetraploid *M. sieboldii* crossed with diploid species, Olden (1953) found an occasional diploid or near diploid segregate, some triploids, and an occasional pentaploid. Although *M. sieboldii* usually produces tetraploid maternals, chromosome reduction can occur to produce near haploid or diploid egg cells and the unreduced egg cell can also be fertilized. Even in cultivated clonal varieties of apples, Einset (1952) finds that diploids may produce triploids and triploids may produce tetraploids by the functioning of unreduced egg cells fertilized by haploid male gametes. More recently he has obtained pentaploids from tetraploids.

Some of the progeny of *Malus rockii* which we have classed as pentaploids have less than 85 chromosomes, as is shown in FIG. 12. Olden found counts of 70, 80 and 82 in progeny from open-pollinated *M. sieboldii*. He also found variable chromosome numbers in some segregates as Hegwood and Hough (1958) have found in the 'Winter Pearmain' apple and its segregates. As a rule, however, the facultatively apomictic tetraploid apple species usually produce tetraploid or diploid egg cells.

The dominance of facultative apomixis in the polyploid *Malus* species is in accord with the inheritance of facultative apomixis in other polyploid genera (Stebbins 1950). This dominance should facilitate the production of facultatively apomictic hybrid segregates which could be propagated from seed.

SUMMARY

Facultatively apomictic species of *Malus* include *M. sikkimensis, M. rockii, M. hupehensis, M. toringoides, Malus sargentii* and its var. *rosea*. All are polyploids: the tetraploid species produce maternal tetraploids and hybrid triploids or pentaploids; the triploid species produce maternal triploids and hybrid tetraploids; both tetraploids and triploids also produce some aneuploids near the diploid level. Facultative apomixis is a dominant trait in the F_1 hybrids between the facultatively apomictic polyploids and sexual diploids.

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STUDIES IN ARTOCARPUS AND ALLIED GENERA, III. A REVISION OF ARTOCARPUS SUBGENUS ARTOCARPUS *

FRANCES M. JARRETT

Section **Artocarpus**

Folia adulta et juvenilia simplicia, integra vel pinnatifida; hypodermis absens vel perfecta, cellis isodiametricis composita, rariter imperfecta (*A. blancoi*). *Inflorescentiae* bracteis interfloralibus sparsis vel absentibus. *Capitula mascula* cylindrica vel clavata, rariter ellipsoidea. *Syncarpia* cylindrica vel ellipsoidea, rariter subglobosa, processibus carnosis, firmis vel flexuosis obtecta, vel areolata; ovaria stylis lateralibus vel sub-basalibus; semina testis, pericarpiis, perianthiisque variis inclusa; embryum oblique positum, cotyledonibus aequalibus vel inaequalibus, radicula ventrali.

The classification of this section is discussed in detail above (p. 130). The definition given here does not take into account the characters of the anomalous species.

Series **Incisifolii** Jarrett, ser. nov.

Folia adulta et juvenilia simplicia, integra vel pinnatifida; hypodermis absens vel rariter imperfecta (*A. blancoi*); glandulae immersae, capitibus planis, 8(–16)-cellis. *Inflorescentiae* ramulis latae. *Capitula mascula* superficie plana, floribus fertilibus vel aliquibus sterilis, solidis praelongisque obtecta, bracteis sparsis vel absentibus. *Syncarpia* processibus saepe ex pilis inflatis asperis, aequalibus vel nonnullis solidis praelongisque obtecta; bracteis sparsis vel absentibus; semina testis tenuiter pergamentaceis, rubris vel brunneis, pericarpiis induratis perianthiis tenuisque inclusa.

The rather thick, yellowish, completely indurated pericarp and the relatively well-developed radicle of the embryo are characteristic of this series.

The species of this series are somewhat difficult to define, especially in respect to the vegetative characters and the size of the male heads, but they can readily be identified when bearing syncarps. In all the species pinnatifid leaves may occur on the adult tree, so far as can be judged from the collections seen, whereas such leaves are a juvenile characteristic in the rest of the genus. The indumentum of the leaves and twigs is very variable in both quantity and type. However, the hairs can be classified as follows: short, whitish (if abundant, appearing greyish), rough-walled hairs; short, whitish, smooth-walled hairs with uncinate tips; longer, rufous to

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* Continued from volume XL, p. 155.

whitish, smooth-walled hairs. The uncinate hairs are patent, but the other types may be appressed or patent, and straight or somewhat undulate. Some intergrades occur, but the indumentum can usually be described in terms of these three types of hairs, all of which may occasionally (in *A. communis*) occur on the same leaf. The inflated hairs found on the inflorescences, except in *A. communis*, are characteristic of the series.

In considering the species of this series, *Artocarpus pinnatisectus* and *A. multifidus*, both from the Philippines, can first be distinguished from the rest by their deeply pinnatifid, many-lobed leaves, their large anthers 1.2–1.5 mm. long, and the occurrence of elongate, solid, sterile perianths at least in the male inflorescences. The newly described *Artocarpus multifidus* is a very well marked species, although it is based on only two collections, male and female respectively. The inflorescences of both sexes have numerous elongate, solid perianths (projecting 2 mm. in the male head and 15 mm. in the syncarp) with inflated, strongly recurved hairs, and the leaves have seven to ten pairs of lateral lobes. *Artocarpus pinnatisectus* is based on equally limited material, and is not so well defined as a species. In both the collections examined the leaves have twelve to twenty pairs of lateral lobes. The male heads on one of the collections have slightly elongate sterile flowers (projecting only c. 0.5 mm.). The syncarp on the other has no solid processes but in its dimensions (15 × 5 cm., submature), and in the size of the processes (3 × 2 mm.), as well as in the simple styles, it differs from the other Philippine species of the series. While these inflorescences are referred to the same species primarily on the basis of the shape of the associated leaves, their characters are not incompatible with each other and each can be distinguished from all the other species of the series. It should be noted that the absence of a hypodermis in the leaves, the shape of the gland-hairs, the inflated hairs on the syncarp, and also the characters of the embryo and pericarp in *A. multifidus*, justify the placing of these species in series *Incisifolii*, in spite of the differences between them and the other members of the group.

In the remaining species the leaves have not more than five (rarely up to nine) pairs of lateral lobes with shallower sinuses, and only in *Artocarpus communis* are the adult leaves typically incised. In *Artocarpus blancoi*, *A. treculianus* and *A. horridus* the leaves apparently become entire on the mature tree, at least on the smaller twigs. In these four species the anthers are shorter, 0.3–0.8 mm. long, and all the flowers are fertile. In spite of the great variability of *Artocarpus communis*, especially under cultivation, this species is distinguished from the three others by the larger inflorescences, the slender processes on the syncarp, varying to low facets or mere areolae, and the absence of inflated hairs. *Artocarpus horridus*, a new species from the Moluccas, is distinguished primarily by the remarkable, pungent, rufous hairs on the twigs, stipules, petioles and peduncles, but also by the syncarp, which blackens on drying and usually appears cinereous with inflated hairs covering the short-cylindric processes (3 × 1.5–3 mm.). In the Philippine species these hairs are yellow to brown, and the syncarp is not usually nigrescent. The two other species in the series, *Artocarpus blancoi* and *A. treculianus*, are from the Philippines. Although closely allied to each other, they differ consistently in the characters of the syncarp; the processes in the former are flexuous, projecting 8 to 15 mm., but in the latter they are short-cylindric, projecting to only 4 mm. There also appears to be a difference in the orientation of the embryo, but insufficient material has been examined for this to be certain. The male head in *A. treculianus* is more slender (c. 7 mm. thick instead of 13–20 mm.), and the anthers are shorter (0.3–0.5 mm. instead of 0.8 mm.). The vegetative characters of the two species overlap, but *Artocarpus blancoi* tends to have larger, more pubescent leaves; specimens with small, entire, subglabrous, rhomboid leaves may be assigned with certainty to *A. treculianus*. The two species overlap in their distribution only in central Luzon, and otherwise they occur in areas with a slightly different climate.

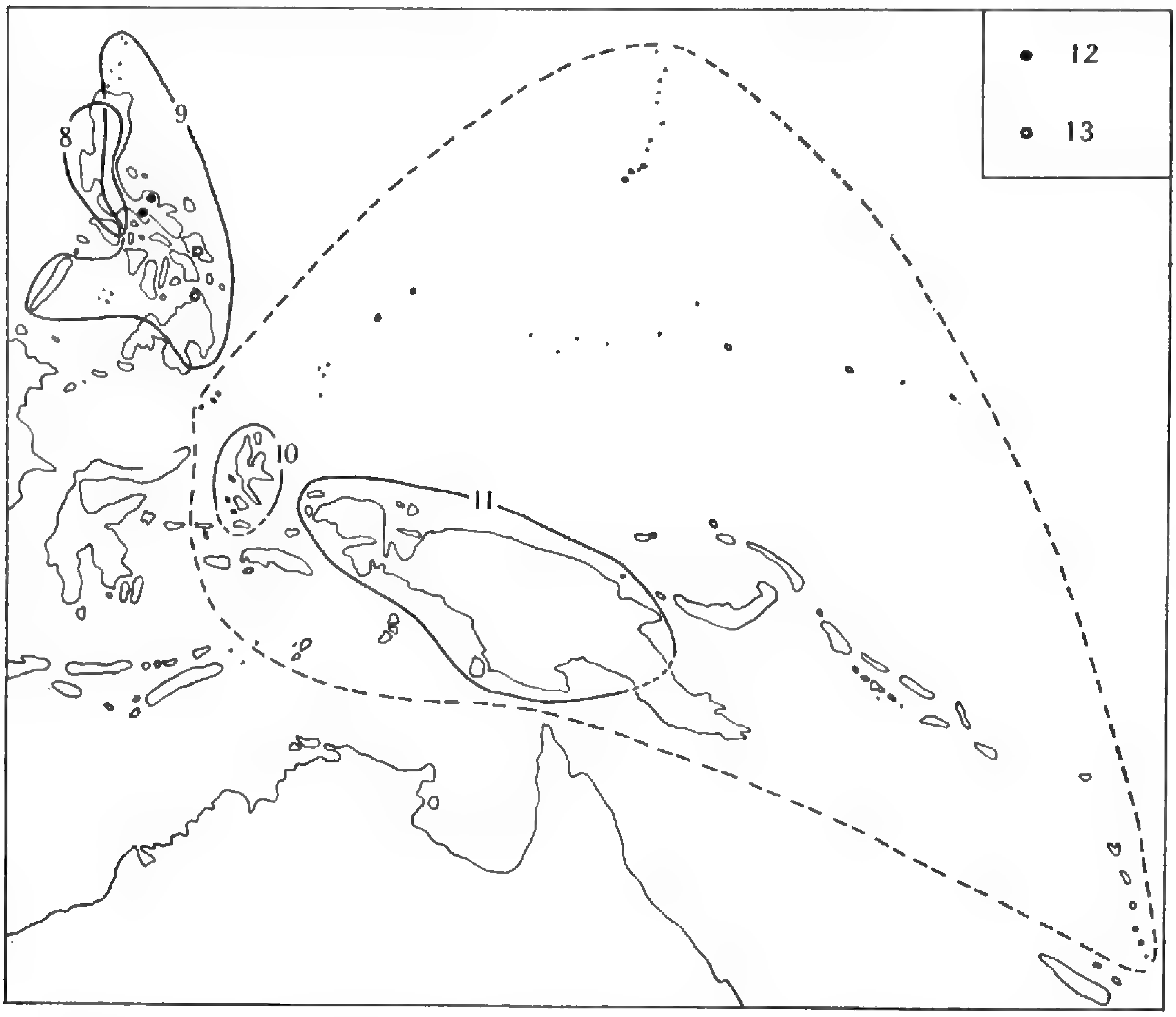

FIG. 12. Distribution of the species of series INCISIFOLII. 8, *Artocarpus blancoi*; 9, *A. treculianus*; 10, *A. horridus*; 11, *A. communis*, distribution as a wild plant — probably indigenous within the area enclosed by the solid line and perhaps also within some part of the region enclosed by the broken line; 12, *A. pinnatisectus*; 13, *A. multifidus*.

There are a few collections referable to this series from the Philippines (all with male inflorescences) which are intermediate in their characters between the species as here defined. It is suggested that these are of hybrid origin, with *Artocarpus treculianus* as one of the parents; they are described and discussed under that species.

8. **Artocarpus blancoi** (Elmer) Merr. Enum. Philip. Pl. 2: 40. 1923; Quis. Med. Pl. Philip. Is. 226. 1951.

Artocarpus communis blancoi Elmer, Leafl. Philip. Bot. 2: 617. 1909. Holotype, Lamao River, Mt. Mariveles, Bataan Prov., Luzon, *Borden 488* (*FB 1682*), Aug. 1904 (PNH, destroyed, no duplicate seen); neotype, Luzon, *Ramos BS 42018* (K).

Artocarpus communis Forst. var., Merr. Sp. Blancoanae, 124. 1918.

Artocarpus incisa Linn. f. var. *blancoi* Elmer ex Merr. Enum. Philip. Pl. 2: 40. 1923, pro syn., sphalm.

Artocarpus incisus auct. non Linn. f., Blanco, Fl. Filip. 668. 1837, ed. 2. 465. 1845, ed. 3. 3: 75. 1879.

Artocarpus communis auct. non Forst., Merr. Philip. Jour. Sci. 1, Suppl. 43. 1906.

Evergreen trees, height to 15 m. *Twigs* 9–22 mm. thick, shallowly rugose, greyish pubescent, hairs patent or appressed, usually also villous below stipular scars with longer (to 3 mm.), patent, greyish or pale rufous hairs; annulate stipular scars 1 mm. broad, prominent, conspicuous; lenticels scattered. *Stipules* 7–21 cm. long, broadly lanceolate, acute, villous with patent greyish or pale rufous hairs to 3 mm. long, varying appressed-pubescent. *Leaves* c. 20–60 × 20–40 cm., ovate-elliptic, acute, base cuneate or rounded, entire or pinnatifid, lateral lobes 1–3 pairs, broad, acute, sinuses fairly broad, extending halfway to the midrib; main veins prominent beneath, intercostals slightly so; glabrous above except for scattered hairs on main veins, greyish subappressed-pubescent throughout beneath, the hairs rough-walled, straight or slightly undulate, often with longer, greyish, patent, smooth-walled hairs on the main veins; lateral veins c. 12 pairs, straight; intercostals parallel; drying pale brown or greenish, varying dark brown; hypodermis sometimes present, irregular, interrupted, the cells isodiametric in surface view; gland-hairs immersed, heads flattened, 8-celled; petiole 35–130 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 100–210 × 12–20 mm., cylindric, smooth, covered by flowers, with or without occasional bracts; perianths tubular, 2 mm. long, bilobed above, the lobes with deflexed, inflated hairs having acute tips; stamen 2.7 mm. long, filament fairly slender, cylindric, anther-cells oblong, 0.7 mm. long; bracts slenderly stalked, heads spathulate, to 0.2 mm. across, pubescent (appearing as tufts of hairs on the surface); peduncle 17–37 × 3 mm., greyish or pale rufous villous, varying appressed-pubescent; *female head* with bifid styles exserted to c. 1 mm. *Syncarp* to 10 × 6.5 cm., ellipsoid, drying yellow-brown to brown, covered by closely set, flexuous, tapering obtuse processes, 8–15 × 1.5 mm., rough from the acute, deflexed tips of dense, inflated hairs; scattered bracts usually present between the processes, slenderly stalked, heads narrowly peltate, to 0.2 mm. across, pubescent; wall c. 2 mm.

thick; fruiting perianths numerous, proximal free region thin, not fleshy, "seeds" (pericarps) ellipsoid, 12 × 9 mm., style sub-basal, testa thinly pergamentaceous, embryo with the radicle ventral, the cotyledons parallel to the median plane of the ovary, equal; core c. 10 mm. across; peduncle 35–60 × 5 mm., indumentum as male.

Vernacular names: *Antipolo* or *Tipolo* (Tagalog, Bisayan).

Distribution: in lowland forest, in areas with a rainfall of at least 80 inches but a distinct dry season, Mindoro, Luzon.

Philippine Islands. Mindoro. Pinamalayan, *Merrill 2138* (NY, US, ♂). Luzon. Abra: Dolores, *Fenix BS 26714* (US, ♂). Ilocos Sur: *Paraiso FB 25825* (A, US, ♀). Isabela: Ilagan, *Vidal 3847* (K, ♂). Zambales: *Curran FB 5805* (US, ♂). Bataan: Mariveles, *Ahern 787* (US, ♂); Mt. Mariveles, Lamao River, *Barnes FB 527* (K, NY, US), *Borden FB 1297* (NY, US), *1380* (US), *Curran FB 7514* (NY), *Williams 360* (K, NY, US, ♂). Bulucan: Angat, *Ramos & Edano BS 34204* (GH). Rizal: Antipolo, *Merrill SB 214* (A, BO, GH, L, NY, P, US, ♀), *Ramos 1819* (BM, BO, GH, L, P, SING, ♂), *Ramos BS 42018* (A, BO, K, L, SING, US, ♀); San Mateo, *Vidal 1547* (A, K, L, ♀). Laguna: Copeland Height, College of Agriculture, Los Banos, *Sulit PNH 15695* (PNH, ♀). **Cultivated.** Luzon. Manila, Hort. Bot., *Loher 5018* (K, US, ♀).

This species has been identified from Elmer's description and from the two collections cited by Merrill (1923) in raising the variety to specific rank (*Merrill SB 214* and *Ramos 1819*). Merrill (l.c.) stated that *Artocarpus blancoi* also occurred in Palawan, the Batanes Islands, Negros and Mindanao, but he may have been misled by the earlier confusion between it and *A. communis*. In his paper "The Flora of the Lamao Forest Reserve" (1906) he listed several collections under the name *A. communis*, but those which have been seen are all here referred to *A. blancoi* (*Borden FB 1531, 1544, 1624, 1682* are unaccounted for; the last is the type of *A. blancoi*). Other references to *A. communis* as occurring wild in the Philippines are discussed under that species.

The names *Antipolo* and *Tugup* seem to belong to *Artocarpus blancoi* and *A. treculianus* respectively, but they are not always strictly applied. They first appear (the former as *Atipolo*) in G. J. Kamel's account of the flora of the Philippines (Ray, Hist. Pl. 3, App. 52. 1704) and the descriptions there do not conflict with this usage, although they are not sufficiently precise for accurate identification of the species intended.

9. **Artocarpus treculianus** Elmer, Leafl. Philip. Bot. 2: 617. 1909, "*tréculiana*"; Merr. Enum. Philip. Pl. 2: 43. 1923. Holotype, Negros, *Elmer 10406* (PNH, destroyed); isotypes (A, BM, BO, L); lectotype (BM).

Artocarpus nigrescens Elmer, Leafl. Philip. Bot. 2: 614. 1909; Merr. Enum. Philip. Pl. 2: 42. 1923. Holotype, Negros, *Elmer 9795* (PNH, destroyed); isotypes (A, BM, BO, L); lectotype (BM).

Artocarpus ovatifolia Merr. Philip. Jour. Sci. Bot. 9: 268. 1914, Enum. Philip. Pl. 2: 42. 1923. Holotype, Luzon, *Ramos BS 15040* (PNH, destroyed); isotype and lectotype (BM).

Artocarpus ovatifolia Merr. var. *dolichostachys* Merr. Enum. Philip. Pl. **2:** 43. 1923. Holotype, Samar, *Ramos 1603* (PNH, destroyed); isotypes (BM, BO, GH, L, P, SING); lectotype (BM).

Artocarpus sorsogonensis Elmer ex Merr. Enum. Philip. Pl. **2:** 42. 1923, et Elmer, Leafl. Philip. Bot. **10:** 3807. 1939, pro syn.

Artocarpus communis auct. non Forster, Merr. Philip. Jour. Sci. Bot. **3:** 401. 1908.

Evergreen trees, height to 20 m. (–40 m., fide Merrill, 1914), with small buttresses, bark grey. *Twigs* 4–12(–20) mm. thick, shallowly rugose, appressed-puberulent, rarely shortly appressed-pubescent and sparsely villous below the stipular scars with patent, pale rufous hairs; annulate stipular scars c. 1 mm. broad, slightly prominent, conspicuous; lenticels scattered. *Stipules* 5–18 cm. long, lanceolate, acute, cinereous with minute appressed hairs, varying greyish appressed-pubescent. *Leaves* 13–35(–40) × 5–25 (–30) cm., ovate, elliptic or rhomboid, acute or short-acuminate, base cuneate or rounded, entire or pinnatifid, lateral lobes 1–3 pairs, narrow, lanceolate, attenuate, sinuses extending up to two-thirds the distance to the midrib, wide or narrow; main veins prominent beneath, intercostals less so, reticulum scarcely prominent; glabrous above, the main veins only appressed-puberulent beneath, varying to shortly greyish subappressed-pubescent throughout, the hairs rough-walled, straight or slightly undulate; lateral veins 9–12 pairs, straight; intercostals parallel; dark green and glossy above, paler beneath, drying yellow-green to dark brown, usually paler beneath; hypodermis absent; glands sunken, heads flattened, 8-celled; petiole (20–)30–80 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 10–210 × c. 7 mm., cylindric, smooth, covered by flowers; perianths tubular, 1–1.8 mm. long, shortly bilobed above, lobes with deflexed, inflated hairs having acute tips; stamen 1.5–2.3 mm. long, filament slender, cylindric, anther-cells oblong, 0.3–0.5 mm. long; peduncle 12–27 × 1–2 mm., appressed-puberulent; *female head* with bifid styles exserted to c. 1 mm. *Syncarp* to 7 × 5 cm. (*Ramos & Pascasio BS 34736,* 11 × 3 cm.; fide *Elmer 9795* to 10 × 7.5 cm.), ellipsoid to cylindric, yellow, drying yellow-brown to brown, covered by closely set, fleshy, cylindric, obtuse processes c. 4 × 2.5 mm., rough from the acute, deflexed tips of inflated hairs; wall c. 2 mm. thick; fruiting perianths numerous, proximal free region thin, not fleshy, "seeds" (pericarps) ellipsoid, 12 × 7 mm., style sub-basal, testa thinly pergamentaceous, embryo with the radicle ventral, the cotyledons transverse to the median plane of the ovary and horizontal or nearly so, the upper one smaller; core c. 10 mm. across; peduncle 20–50 × 2.5 mm., appressed-puberulent.

VERNACULAR NAMES: *Tugup, Togop* and variants (Bisayan). USES: the timber is valuable.

DISTRIBUTION: in forest to 2500 ft. in regions with a rainfall of at least 60 inches and the dry season short or absent, Philippine Islands.

Philippine Islands. PALAWAN. Puerto Princesa, Mt. Pulgar, *Elmer 13135* (A, BM, BO, GH, L, U, US, ♀). BATANES ISLANDS. *Fenix BS 3613* (US, ♀). BABUYAN

ISLANDS. Camiguin Island, *Fenix BS 4069* (US, ♀). LUZON. Cagayan: Mt. Tabuan, Bauan, *Ramos BS 77064* (SING, ♀). Isabela: *Alvarez FB 18566* (US, ♂); San Mariano, *Ramos & Edano BS 46941* (BM, NY, ♀). Quezon (Tayabas): Baler, Cemento River, *Quisumbing PNH 2508* (A, PNH, SING, ♀); Casiguran, *Ramos & Edano BS 45408* (A, BM, BO, K, P, US, ♂, ♀); Pagbilao, *Merrill 2848* (BM, NY, P, US, ♀). Laguna: *Ramos 1390* (A, BO, L, P, SING, ♂); San Antonio, *Ramos BS 15040*, June 1912 (BM, ♀), *20530* (K, US, ♀). Camarines: *Alvarez FB 21424* (BM, K, L, P, ♀), *21438* (BM, K, P, ♀), *Vidal 3843* (K, ♀). Sorsogon: *Vidal 3842* (A, K, ♂, ♀); Irosin, Mt. Bulusan, *Elmer 15785* (A, BM, BO, C, GH, K, L, NY, P, U, US, ♀). SIBUYAN. Magellanes, Mt. Giting-Giting, *Elmer 12468* (A, BM, BO, K, L, ♀). TICAO. *Clark FB 1081* (K, NY). SAMAR. *Ramos 1603*, Apr. 1914 (BM, BO, GH, L, P, SING, ♂). LEYTE. Palo, *Elmer 7097* (A, BO, K, ♂). NEGROS. Oriental, Dumaguete, Cuernos Mts., *Elmer 9795*, Apr. 1908 (A, BM, BO, L, ♀), *10406*, June 1908 (A, BM, BO, L, ♀). PANAY. Iloilo, Miagao, *Vidal 3835* (K, ♀). GUIMARAS. *Gammill 310* (NY, US, ♀), *865* (BM, US). MINDANAO. Surigao: *Ramos & Pascasio BS 34736* (A, US, ♀). Davao: *De Mesa FB 27624* (K, US); Todaya, Mt. Apo, *Elmer 10931* (A, BM, BO, K, L, ♀). Bukidnon: near Tanculan, *Fenix BS 24969* (A, P, ♀). **Cultivated.** OKINAWA. Naha, near Yogi Agricultural Institute, *Walker, Tawada & Amana 6051* (A, ♀).

Three specific names based on this species have been published. Of the two species simultaneously described by Elmer (1909), *Artocarpus treculianus* was based on a specimen with entire, pubescent leaves, while *A. nigrescens* was described from a specimen with incised, subglabrous leaves. The type of the third species, *A. ovatifolia* Merrill (1914), has entire, subglabrous leaves. The name of Elmer's second species was derived from his description of the fruits as blackening on the tree. However, these may have been decayed, since all three types have mature or submature syncarps and in the other two descriptions the fruits are stated to be yellow. This is supported by the only field note available, on *Walker et al. 6051*, "fruits yellowish, fleshy, falling before ripe." Therefore, since *A. nigrescens* was based on an erroneous character, *A. treculianus* is here chosen as the name for the species. (Although it is rather surprising that *A. treculianus* should have been introduced to Okinawa, the vegetative characters of the collection cited above are in agreement and the fruit undoubtedly belongs to this species.)

In addition to the characters of the syncarp, this species is distinguished by the consistently slender male heads, but although these have a nearly constant thickness, their length is very variable. The two collections with male inflorescences seen from mid-Luzon (Quezon and Laguna Provinces) have heads 1 to 2.5 cm. long, while the three seen from farther south (Sorsogon Province, Luzon, Samar and Leyte) have heads ranging from 13 to 21 cm. in length. The latter form was distinguished by Merrill as *A. ovatifolia* var. *dolichostachys*, based on *Ramos 1603* from Samar. He had described *A. ovatifolia* from a female collection, *Ramos BS 15040*, but since this came from Laguna Province, Luzon, the distinction is in accord with the limited evidence, which indicates that the variation has a geographical basis. *Artocarpus treculianus*, on the other hand, was described from Negros and presumably represents Merrill's long-headed variety, so that, if the short-headed form were to be regarded as representing a distinct infraspecific taxon, a new name would be needed. However, since only two collections have been seen with the short male head and there is no other distinguishing character, they are not here separated, although future collecting may show that this would be justified.

The majority of the fertile material from the Philippines which is referable to series *Incisifolii* can be assigned readily to one of the species here recognized, but there are a few anomalous collections, all with subglabrous leaves and male inflorescences. These are described briefly below.

Ramos & Edano BS 49334, Mati, Davao Province, Mindanao (SING, ♂): leaves (detached) pinnatifid, lobes 2 or 3 pairs, sinuses extending halfway to the midrib, subglabrous; male head (detached, at anthesis) 115–145 × 9–12 mm., anther-cells 0.8 mm. long, bracts absent, peduncle 25–35 × 2 mm., appressed-puberulent. *Fox PNH 9171*, Karlagen, Pollilo Island (PNH, ♂); twigs and stipules appressed-puberulent; leaves entire, subglabrous; male head (nearly at anthesis) 65 × 12 mm., anther-cells 0.6 mm. long, bracts absent, peduncle 20 × 2 mm., appressed-puberulent. *Curran FB 10164*, Laguna, Luzon (US, ♂): twigs subglabrous; stipules appressed-puberulent; leaves entire, subglabrous; male head (immature) to 40 × 8 mm., a few solid, sterile perianths projecting 0.3 mm. from the surface, anther-cells 0.6 mm. long, bracts scattered, heads spathulate, peduncle 15 × 1 mm., appressed-puberulent. *Curran 3807*, Palawan (BO, K, ♂): twigs and stipules shortly appressed-pubescent, sparsely villous from patent, pale rufous hairs; leaves pinnatifid, lobes 1–2 pairs, sinuses extending one-third the distance to the midrib; male head (immature) 50 × 9 mm., numerous solid, sterile perianths projecting 0.3 mm. from the surface, anthers 0.8 mm. long, bracts scattered, heads spathulate, peduncle 10 × 2 mm., indumentum as twigs.

All four collections could be referred to *A. treculianus* on their vegetative characters, especially the glabrous leaves, but the male heads are too stout, being intermediate in size to *A. blancoi*, and the anthers are too large, agreeing better with the latter species. The last two collections differ from both these species in having sterile flowers, as well as interfloral bracts. They cannot be assigned to *A. pinnatisectus* or *A. multifidus*, however, because of the small anthers (which in these species measure 1.2–1.5 mm.) and, on present evidence, because of the shape of the leaves. It is suggested that these collections are from trees of hybrid origin and that the characters of the first two can be accounted for if they represent *A. treculianus* × *A. communis*. The difference in the size of the male heads would correspond to the variation in *A. treculianus*. The second two collections could represent hybrids of *A. pinnatisectus*, perhaps also with *A. treculianus*, although the former species has not been collected in Palawan. In *Curran FB 10164* the pollen grains are shrunken, but they are apparently well formed in the first two collections. However, although this is one explanation of the characters of these collections, basing the parentage partly on geographical evidence, the first two collections, at least, may represent merely a wider range of variation in *A. treculianus* than is here recognized.

10. **Artocarpus horridus** Jarrett, sp. nov. Holotype, Halmaheira, *Beguin 1976* (L); isotypes (BO, L).

Soccus silvestris Rumphius, Herb. Amb. **1:** 114. *t. 34.* 1741.

Artocarpus communis Forster var. *pungens* J. J. Smith ex Heyne, Nutt. Pl. Ned. Ind. ed. 2. **1:** 557. 1927, non *Artocarpus pungens* (Lesquereux) Hollick, Geol. Surv. Louisiana Spec. Rep. **5:** 281. *t. 38, figs. 1, 2.* 1899.

Artocarpus elasticus auct. non Reinw. ex Blume, Hassk. Abh. Naturf. Ges. Halle **9:** 158. 1866; Merr. Interpr. Rumph. Herb. Amb. 191. 1917.

Syncarpia cylindrica, ad 9 × 4.5 cm., processibus crebris, brevibus, cylindricis, obtusis, canis ex pilis inflatis, vel glabris obtecta; folia integra vel pinnatifida, glandulis immersis, capitibus planis, 8-cellis; ramuli, stipulae, petioli, pedunculique horridi, pilis patentibus, rigidis, aciculiformibus, rufis, 2 mm. longis.

Arbores ad 35 [–40] m. altae. *Ramuli juniores* 12 [6–15] mm. crassi, rugosi, horridi, pilis patentibus, rigidis, aciculiformibus, rufis, 2 mm. longis, numerosis ad paucis, nec non appresse puberulentes; cicatrices stipularum annulatae, 1 mm. latae, prominulae, conspicuae; lenticellae infra cicatrices circum ramulos dispositae. *Stipulae* 9 [6–27] cm. longae, horridae, pilis ut ramulis, appresseque pubescentes, pilis canescentibus. *Folia* c. 30 × 20 [20–70 × 10–55] cm., ovati- [vel rhomboido-]elliptica, breviter acuminata, basi rotunda vel cuneata, subintegra, laciniis lateralibus utrinque 3, brevissimis, [integra vel pinnatifida, sinusibus angustis, laciniis utrinque ad 9, lanceolatis, acutis vel breviter acuminatis,] supra saepe appresse puberulentia, costa nervis lateralibus transversalibusque subtus prominentibus, undique appresse pubescentibus, [saepe] horridisque, pilis ut ramulis, venulis subtus prominulis, in sicco rufi-brunnea; nervi laterales utrinque 11–18, recti; nervi transversales paralleli; hypodermis absens; glandulae immersae capitibus planis, 8-cellis; petiolus 45–90 mm. longus. *Inflorescentiae* axillis foliorum solitariae. *Ad anthesin: capitula mascula* c. 50 × 15 [50–95 × (5–)15–23] mm., cylindrica, plana, floribus numerosissimis obtecta; perianthia tubulosa, 1 mm. longa, supra bilobata, glabra vel pilis paucis, inflatis, apicibus acutis deflexis; stamina 1.6 mm. longa, filamentis cylindricis cellis antherum oblongis, 0.6 mm. longis; pedunculus 20–35[–50] × 5 mm., indumento ut ramulis; *capitula feminea* stylis bifidis 2 mm. exsertis. *Syncarpia* 5.5–9 × 3(–4.5) cm., cylindrica [vel subellipsoidea], flava, in sicco nigrescentia, processibus crebris, solidis, cylindricis, obtusis, 3 × 1.5–3 mm., canis ex pilis inflatis, apicibus acutis, deflexis, vel glabris, obtecta; pedunculus c. 80 [(–110)] × 6 mm., indumento ut ramulis.

Vernacular names: *Dinga*, Halmaheira, Ternate; *Pongo*, Halmaheira.

Distribution: in evergreen forest to 1000 ft., the Moluccas (Halmaheira group).

Moluccas. Morotai. Totodoku, *bb 33816, 33817, 33864,* (L); W. Pitu, *Beguin 2223* (BO, L, ♂, ♀). Halmaheira. Djailolo, Togoair, *bb 23731* (BO, L); Galela, *Beguin 1954* (BO, L, ♂, ♀); Galela, Soa Tobara, *Beguin 1906,* (BO, L, ♂), *1908*

(BO, L, ♀), *1975*, *1976*, May 1922 (BO, L, ♂, ♀); Kp. Goal, *Pleyte 190* (L); W. Tobelo, *Beguin 2293* (BO, ♀), *2295* (BO, K, L, ♀). TERNATE. Foramadiahi, *Beguin 1233* (BO, L, ♂, ♀). BATJAN. Saoran Domut, *bb 23200*, *23204* (BO, L).

Artocarpus horridus is remarkable for the sharp, rigid hairs on the twigs and peduncles, which make specimens unpleasant to handle, and from which the specific epithet is derived. These hairs, combined with the frequently entire leaves and the relatively small syncarp (as compared with *A. communis*), enable the species to be identified with Rumphius' *Soccus silvestris*, or *Soccun Utan*, with certainty. J. J. Smith labelled the Beguin collections as *Artocarpus communis* var. *pungens*, but the name was not published until Heyne took it up in 1927. The latter, however, did not provide a description or cite Beguin's collections, but identified the variety correctly with Rumphus' description and plate, so that these must be regarded as the type of Smith's name. Rumphius recorded the species from Amboina and adjacent islands.

The collections seen are rather variable in the shape of the leaves and the inflorescences and in their indumentum, but at least a few rigid hairs are always present. Large, pinnatifid leaves and numerous rigid hairs appear to be correlated with stout inflorescences having dense inflated hairs, while specimens with small, entire leaves and sparse rigid hairs have slender, subglabrous inflorescences. The first type may represent collections made from young trees or juvenile shoots.

11. **Artocarpus communis** J. R. & G. Forster, Char. Gen. 101. *t. 51, 51a*. 1776. Holotype, without provenance, *Forster s.n.* (BM); ? isotype, Tahiti (K).

Camangsi, *Rhymay Marianorum* et *Dugdug Marianorum* Kamel in Ray, Hist. Pl. 3, App. 52. 1704.

Soccus lanosus Rumphius, Herb. Amb. 1: 110. *t. 32*. 1741.

Soccus granosus Rumphius, l.c., 112. *t. 33*.

Sitodium-altile [Banks & Solander ex] Parkinson, Jour. Voy. Endeavour, 45. 1773, nomen subnudum.

Rima Sonnerat, Voy. Nouv. Guin. 99. *t. 57–60*. 1776.

Rademachia incisa Thunb. Vet. Akad. Handl. Stockholm 37: 253. 1776; Houttuyn, Nat. Hist. II. Pl. 11: 449. Holotype, Java, *Thunberg s.n.* (UPS, not seen); ? isotype (L).

Sitodium incisum Thunb. Philos. Trans. Roy. Soc. London 69: 465. 1779, nomen illegitimum.

Artocarpus incisus Linn. f. Suppl. Pl. 411. 1781.

Artocarpus incisifolia Stokes, Bot. Mat. Med. 4: 331. 1812, nomen illegitimum.

Artocarpus nucifera [Thompson,] Cat. Maurit. 25. 1816, nomen nudum.

Arctocarpus camansi Blanco, Fl. Filip. 670. 1837.

Arcthocarpus rima Blanco, l.c., 671.

Artocarpus laevis Hassk. Flora 25(2), Beibl. 18. 1842. Holotype, Java, Batavia (cult.), *Hasskarl s.n.* (L).

Artocarpus mariannensis Tréc. Ann. Sci. Nat. Bot. III. 8: 114. 1847. Holotype, Marianas Islands, *Gaudichaud s.n.* (P).

Artocarpus incisa Linn. f. *β laevis* Miq. Fl. Ind. Bat. 1(2): 285. 1859.

Sitodium utile Solander ex Seem. Fl. Viti. 255. 1868, pro syn., errore pro *Sitodium altile*.

Artocarpus incisa Linn. f. var. *muricata* Becc. For. Borneo, 628. 1902. Holotype, New Guinea, *Beccari PP 25* (FI).

Artocarpus leeuwenii Diels, Bot. Jahrb. **67**: 175. 1935. Holotype, New Guinea, *Docters van Leeuwen 11163* (B, not seen); isotypes (BO, L, U).

Artocarpus papuana Diels, l.c., nomen illegitimum, non *A. papuanus* Renner, 1907. Holotype, New Guinea, *Ledermann 7513* (B); [5] isotype (SING).

Artocarpus altilis (Parkinson) Fosberg, Jour. Wash. Acad. Sci. **31**: 95. 1941, nomen subnudum.

Evergreen or deciduous trees, height to 35 m. *Twigs* 5–15 mm. thick, smooth or rugose, greyish appressed-pubescent, with or without patent rufous hairs below the stipular scars or rarely throughout, varying to glabrous; annulate stipular scars c. 1 mm. broad, slightly prominent; lenticels none or scattered. *Stipules* 10–25 cm. long, lanceolate or broadly lanceolate, greyish or rufous appressed-pubescent, varying to subglabrous. *Leaves* 15–17 × 10–50 cm., rhomboid, varying to elliptic or ovate in outline, base rounded or cuneate, pinnatifid, varying to entire; lateral lobes 1–5(–9) pairs, lanceolate, attenuate, sinuses narrow, extending up to two-thirds the distance to the midrib, varying to deeply pinnatifid with broad sinuses; main veins prominent beneath, intercostals slightly so; puberulent to pubescent on both surfaces with straight, white, usually appressed, rough-walled hairs and/or uncinate, white, patent, smooth-walled hairs, with or without longer rufous (rarely white) appressed, smooth-walled hairs on the main veins, varying to glabrous (seedless cultivars usually subglabrous except on the main veins); lateral veins 9–12 pairs, straight; intercostals parallel; green, usually drying brown to pale brown; hypodermis absent; gland-hairs immersed, heads flattened, 8-celled; petiole 30–60 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis: male head* 70–300 (–400) × 15–30(–55) mm., narrowly to broadly cylindric or clavate, rarely ellipsoid, smooth, covered by flowers; perianths tubular, 1–1.5 mm. long, bilobed above, sparsely pubescent or glabrous; stamen 1.6–2.4 mm. long, filament cylindric, anther-cells oblong, 0.6–0.8 mm. long; peduncle 30–60 × 3–6 mm., greyish or rufous villous to glabrous; *female head* with bifid or simple styles exserted up to 2 mm. *Syncarp* (? 10–)15–30 cm. across, cylindric, obovoid, ellipsoid or globose, green to yellow, drying brown to black, covered by closely set, flexuous, attenuate or conical, acute processes, projecting to 15 mm., to 5 mm. across at the base, varying to low facets, or (in seedless cultivars) with the surface merely areolate, pubescent or subhispid with slender patent hairs, varying to glabrous; fruiting perianths numerous, proximal free region thin, not fleshy, "seeds" (pericarps) obovoid-oblong, irregularly compressed, c. 25 × 20 × 15 mm., the style lateral, two-thirds the distance up the ventral face, testa thinly pergamentaceous, embryo with the radicle ventral, the cotyledons somewhat oblique to the median plane of the ovary, the lower one slightly larger

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[5] It is regretted that the name of the Botanisches Museum, Berlin-Dahlem, Germany, (B), was inadvertently omitted from the list of institutions to which grateful acknowledgement is made for the loan of specimens.

and shallowly folded (cultivars frequently with few or no seeds, the perianths hypertrophied to form starchy edible tissue and the undeveloped ovaries surrounding the core); peduncle 35–135 × 5–10 mm., greyish or rufous villous to glabrous.

VERNACULAR NAMES. (1) General: Breadfruit, restricted to the seedless form in Africa and the New World; Breadnut, seeded form, in the latter regions; Arbre à Pain; etc. (2) Malaysia: ***Kulur***, ***Kulor*** or ***Kuror***, seeded, and ***Sukun*** or *Soccun*, seedless (Malay), Malaysia excluding the Philippines; ***Kluwih***, seeded and ***Timbul***, seedless (Sundanese), Java; ***Camansi***, seeded, and ***Rima***, seedless (Tagalog and Bisayan), Philippines; ***Gomo***, Moluccas. Only some common forms of the more widely distributed names are given here; Heyne, Nutt. Pl. Indonesië ed. 3. 1: 555. 1950, gives many local names and variants. (3) Pacific: ***Dugdug***, seeded, and ***Lemai***, seedless, Marianas Islands; ***Mai*** or ***Mei***, Caroline, Marshall, Ellice, Samoa and Marquesas Islands, Niue (e. of Tonga Islands) and Mangareva; ***Uto***, Fiji; ***Ulu***, Tonga, Samoa and Hawaiian Islands; ***Uru*** partially replaced by ***Maiore***, Society and Austral Islands; ***Kuru***, Cook Islands and Mangareva.

USES. The fruit of both the seeded and the seedless forms is an important article of diet in some regions. In New Guinea, Melanesia and the Moluccas the form of chief importance is that with seeds, and these are eaten roasted or boiled. Elsewhere, the seedless form is more commonly cultivated, and in the Pacific it provides the inhabitants of some island groups with a major source of carbohydrate. Different varieties may bear for only a limited period, but a succession of them can provide fresh fruit for most of the year, although the time and length of season, or seasons, varies in the different islands. The fresh fruit is eaten after being cooked by roasting or boiling. The fruit is preserved for the time when it is out of season by being made into a fermented paste which is stored in pits lined with leaves (of *Cordyline* or coconut) and covered with leaves and stones, where it will keep for several months. The paste is called *mar* or *maratan* in the Carolines, *masi* in Samoa and *mahi* in Tahiti. The fruit may also be cut into slices and dried, usually in the sun, for storage. Neither form has become of equal importance elsewhere in the tropics, but the seedless form is widely used as a vegetable, as also is the young fruit of the seeded form in Malaysia. The latex is used in New Guinea and the Pacific for bird-lime and for caulking boats, and the young bark is sometimes used for making *tapa* cloth. The wood is used in the Pacific for building houses and for furniture, but it is of variable quality and is not much valued in other regions.

DISTRIBUTION. Seeded form: probably indigenous in New Guinea, where it is scattered in (?) primary rain forest and is locally abundant in secondary forest on alluvium; perhaps indigenous in Micronesia, where it is a prominent member of the forest on some "high" islands, especially on coralline limestone, and also in Melanesia and the Moluccas; cultivated throughout the tropics (locally naturalized in secondary vegetation, e.g., in Luzon) but rare in Polynesia and generally less frequent than the seedless form, except in New Guinea, Melanesia and the Moluccas. Seedless form: cultivated throughout the tropics; many cultivars are distinguished, especially in Polynesia.

Lesser Sunda Islands. TANIMBAR ISLANDS. Lurumbun, *bb 24430*, P[6] (L). **Moluccas.** TALAUD ISLANDS. Karakelang, Gunong Duata, *Lam 2895*, P (L). SULA ISLANDS. Kali Waj Gaj, *bb 28813*, P (BO).

New Guinea. VOGELKOP. Inanwatan, Tisa, *bb 32639*, P (BO, L); Manokwari, Momi, *Kostermans 189*, P (BO, K, L); Manokwari, Prafi, *NIFS BW 453* (L, ♂, ♀); Manokwari, Warnapi, *bb 33667*, P (BO); Tangion Bair [= Biak], *Beccari PP 25*, Apr. 1872 (FI, ♀); Tanibo, *bb 25517*, P (BO, L). DUTCH NORTH NEW GUINEA. Bernhardbivak, Idenburg River, *Brass & Versteegh 13537*, P (A, ♀), *bb 25680*, P (BO, L, SING, ♂, ♀); Hollandia, n. of Kobroor, *bb 25347* (L); Meervlakte, Motorbivak, Bruine River, *Docters van Leeuwen 11163*, R, Nov. 1926 (BO, L, U, ♂, ♀); Pioneerbivak, Mamberamogebiet, *bb 31100*, P, *bb 31306*, P (BO); Prauwenbivak, *Lam 927* (BO, L, U, ♂, ♀); Sennen, 30 km. inland from Nabire, *Kanehira & Hatusima 12580*, R (A, BO, ♂). DUTCH SOUTH NEW GUINEA. Lorentz River, *Von Römer 154* (BO, L, ♂, ♀); Mimika, Uta, Aria, *bb 32858*, P (L); Mimika, Uta, Najaja, *bb 32851*, P (L). PAPUA. Central Division: near Port Moresby, *Edelfeldt 51* (L); Sogeri, *Forbes 158* (BM, ♀); Veiya, *Carr 11633*, R (A, K, ♀), *11675*, S (A, K, ♂). Gulf Division: Vailala River, Lipokira, *Brass 981*, ? cultivated (A, ♂, ♀). Northern Division: Isuarava, *Carr 15726*, S (A, K, ♀). MANDATED TERRITORY OF NEW GUINEA. Morobe District: Markham Valley, Kajabit, *Clemens 40696* (A, ♂); Sattelberg, *Clemens 1117* (A, L, ♂, ♀, ? mixed collection). Sepik District: mouth of April River, *Ledermann 7513*, R, June 1912 (B, SING, ♂, ♀). ARU ISLANDS. P. Kobroor, *bb 25347*, P (BO).

The nomenclature of the Breadfruit is discussed in detail above (p. 118) where it is concluded that the correct name is *Artocarpus communis* J. R. & G. Forster (1776). The combination *Artocarpus incisus* (Thunb.) Linn. f. (1781), based on *Rademachia incisa* Thunberg (1776), which was made by Linnaeus *filius* when he chose *Artocarpus* over *Rademachia*, is rejected on the grounds that an earlier legitimate name was available for the species and should have been used. The earliest published Linnaean binomial for the Breadfruit, *Sitodium-altile* [Banks & Solander ex] Parkinson (1773)[7] on which *Artocarpus altilis* (Parkinson) Fosberg (1941) is based, is also rejected since the account to which it is attached is considered to be inadequate as a generico-specific description.

Artocarpus communis is based solely on the seedless form of the Breadfruit. The type is presumably the Forster specimen in the British Museum (Natural History) consisting of a single incised leaf without provenance.

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[6] The following abbreviations are used to indicate the type of forest from which the collection was made: P, old or primary; R, riverside; S, secondary.

[7] A comment may be added here on the hyphenation of the Latin names attached to the series of notes on Tahitian plants in Sydney Parkinson's journal. There is no definite reason for supposing that Stanfield Parkinson added the hyphens in editing his brother's work for publication. On the other hand, the hyphenation by Sydney Parkinson of Solander's manuscript names, in adding them to his notes, is probably an insufficient reason for rejecting the work as one in which binomial nomenclature is not used. The hyphens should be regarded as an orthographic error.

Another specimen collected by Forster, also a single leaf, which is in the herbarium at Kew, was collected on Tahiti, and this may be an isotype. The illustrations in the original account show the male head as narrowly cylindric, the syncarp as subglobose with low facets, and the peduncles of both as sparsely villous. *Sitodium-altile* was likewise based on the seedless Breadfruit of Tahiti. Thunberg's *Rademachia incisa* was described from Java and included both the seedless and seeded forms of the Breadfruit, which he designated as "α.) Pericarpio sterili, muricato, sulcis inter germina reticulato, . . . ," and "β.) Pericarpio fertili, germinibus productis & pistillis longis echinato; . . . ," respectively. The vegetative characters appear to be taken from the seeded form, since the leaves, petioles and peduncles are described as villous and the seedless form in Java is glabrous or nearly so.

The Breadfruit is cultivated throughout the tropics in both seeded and seedless forms, but in most areas the seedless form is more commonly grown and is of considerably greater importance. A review follows of the variation exhibited by both forms throughout their present ranges, together with a discussion of the ecological status of the former. This survey can be only preliminary, since in most areas insufficient evidence is available concerning the details of variation. A conservative taxonomic treatment is therefore adopted. The aim here is to draw together from a wide geographical area and range of literature the information that is available, and to present the taxonomic problems, thus providing a basis for future, more detailed studies.

Although further studies may show that two or more subspecies or closely allied species are involved, it is tentatively concluded that the Breadfruit, whether seeded or seedless, represents a natural but rather variable species which has been considerably modified under man's influence. The seeded Breadfruit appears to be indigenous in New Guinea and perhaps also in the Moluccas, Melanesia and Micronesia. Some, at least, of the few-seeded or seedless varieties were developed in New Guinea, but others may have arisen from seeded Breadfruit growing in Micronesia, Melanesia and the Moluccas.

In the literature the place of origin of the Breadfruit has been indicated in general terms as the Sunda Islands or Malaysia (e.g., Alphonse de Candolle, Orig. Pl. Cult. 238. 1882), or else as the Pacific (e.g., Burkill, Dict. Econ. Prod. Malay Penin. 250. 1935). It has often not been made clear whether both the seeded and the seedless forms were under consideration, or the latter alone. The fairly consistent and marked differences which exist over wide areas (but not in New Guinea or the Pacific) between the two cultivated forms have led some authors, including Quisumbing (Philip. Jour. Sci. 70: 331. 1940), to suggest that they originated from two distinct wild species. However, as already indicated, a broad view is here taken of *Artocarpus communis*. Moreover, if two or more taxonomic entities should be involved in the ancestry of the Breadfruit, a complex hybridization between them has apparently taken place. It will be shown below that the differences between the seeded and seedless forms can be accounted for in part by their distribution from different sources.

The distinctions between *Artocarpus communis* and the allied species of series *Incisifolii* are indicated above in discussion of the series. The principal characters in which variation occurs within the species, including cultivars, are the outline and indumentum of the leaves, the shape and size of the male head, the shape, size and surface of the syncarp, and whether or not seeds are formed. Before proceeding with a description of the Breadfruit by geographical areas, the possible causes and consequences of the development of sterility will be discussed.

First, however, it must be pointed out how very inadequate the herbarium material — most of which is sterile — has been as a basis for this survey. For comparative studies over a wide area, material which gives as full a picture as possible of trees representing different variants of the seeded and seedless forms would be of very great interest. The difficulty of making successive collections from a single tree is recognized, but ideally the following material would be necessary: (1) one or more leaves attached to a twig (having a terminal bud enclosed by stipules), with notes on the variation in leaf-shape on different parts of the tree; (2) two or three male inflorescences at anthesis to show the range of variation in shape; (3) a female inflorescence at anthesis; (4) a longitudinal slice of the mature fruit dried rapidly to prevent decay (showing outline, surface, and whether or not seeds are present); (5) drawings or, preferably, photographs to show the habit of the tree and the shape and arrangement of the fruit; and (6) notes on the colour and uses of the fruit and wood, the mode of propagation, vernacular names, etc. If collections can be made only at the time of anthesis, both male and female inflorescences should be gathered. In order to carry out more detailed studies and to establish the cause of the failure to form seeds, field and experimental work in the tropics will be necessary. I am glad to learn from Dr. F. R. Fosberg, Pacific Vegetation Project, National Research Council, Washington, D.C., that such a survey may be carried out in the Pacific region.

The presence or absence of seeds must be treated independently from other variation in the species, and the possible genetic basis and consequences of the sterility considered. Correlations existing between the seeded or seedless character and other variation will be indicated below. The evidence available from the literature shows that triploidy occurs in the seedless form. Chromosome numbers equivalent to a diploid number of 56 have been recorded in *Artocarpus heterophyllus* (Subba Rao, Half-Yearly Jour. Mysore Univ. Sect. B. Sci. **1**: 63. 1940; Janaki-Ammal in Darlington & Wylie, Chromosome Atlas ed. 2, 184. 1955), *A. lakoocha* (Banerji & Hakim, Proc. Ind. Acad. Sci. B. **38**: 128. 1954) and seeded *A. communis* (Nishiyama & Kondo, Seiken Zihô **1**: 26. 1942, reference not seen; Janaki-Ammal in Darlington & Janaki-Ammal, Chromosome Atlas, 184. 1945). A somatic chromosome number of c. 81 has been recorded for seedless *Artocarpus communis* (Nishiyama & Kondo, l.c.). These counts suggest that the basic number for *Artocarpus* is 28 and that the seedless Breadfruit is triploid ($3n = 84$), at least in the example under study. As a genus, *Artocarpus* appears to be tetraploid with respect to the basic number of 14 that occurs widely in the Urticales. Darlington and Wylie gave the basic number of *Artocarpus* as 14, but their data were derived in part from Krause's study of chromosome numbers in the Moraceae (Planta 13: 29. 1931), and unfortunately the only species studied by the latter was *A. cannonii* W. Bull ($2n = 28$), which had been transferred correctly to *Ficus* by N. E. Brown in 1888. Thus there is as yet no evidence that the diploid number of 28 occurs in *Artocarpus*.

Further investigation will be required to determine whether or not triploidy is the primary cause of the failure to form seeds. The simple occurrence of triploidy would not necessarily result in the formation of a fleshy, edible fruit and it is more likely to have been a secondary development as, for example, in the banana. Some fruits with very few seeds have been seen on collections from New Guinea (e.g., *Carr 11633*), and in Tahiti and Java varieties are recorded with fruits which are eaten for their flesh but which usually have a few seeds. This tendency to develop only a few seeds may well be due to genetic factors other than polyploidy. Both of the latter varieties are propagated by vegetative means, and Heyne (Nutt. Pl. Indonesië ed. 3. 555. 1950) states that the seeds are not viable in the Javan variety. If triploidy were to arise in such a variety it might be expected to produce more complete sterility and, other things being equal, the triploid plant would presumably tend to be selected.

The seedless varieties of the Breadfruit are most commonly propagated by means of root cuttings and root suckers and the formation of the latter is stimulated by deliberate injury of the roots. Each variety is thus a clone within which the primary source of variation is presumably somatic mutation. This will be the chief means by which new varieties can arise in areas where the seeded form is rare or absent, and that such mutations do occur is evident from comments given with lists of varieties from the Pacific. As suggested by Fosberg (Botanical Report on Micronesia. U. S. Commercial Company Economic Survey of Micronesia. 1946), back-crossing may occur between the seedless and seeded forms of the Breadfruit. If fertile pollen is produced by a seedless variety it may fertilize a seeded variety and carry over characters of the former, including those that have arisen by somatic mutation, thus adding to the general pool of variability in the seeded form. If a genetically determined inability to produce seeds is also transmitted, a new seedless variety may be formed that combines characters of both the seedless and the seeded parents. A triploid seedless variety might be expected to produce occasional haploid and diploid grains which could result in diploid and triploid progeny (the latter, at least, seedless) on successful pollination of the seeded form. Conversely, though less frequently, diploid and triploid (and presumably also tetraploid) progeny might be grown from occasional seeds formed in a usually seedless variety.

The range of variation exhibited by seedless varieties must depend primarily on that of the seeded plants from which they have arisen. The variation observed indicates that only autotriploidy has occurred, if the broad view here taken of *Artocarpus communis* is accepted. There is no taxonomic evidence from the characters observed that hybridization with the allied species here recognized has occurred during the development of the seeded or seedless Breadfruit. In addition, historical evidence, outlined below, makes it unlikely that the Philippine species, at least, could have taken part in any hybridization. However, although no infra-specific taxa are here proposed within *Artocarpus communis*, this does not exclude the possibility that, when more detailed evidence based on a wide range of vegetative and inflorescence characters is available, two or more subspecies, or closely allied species, in the New Guinea and western Pacific regions may be shown to have been involved in the ancestry of the Breadfruit as it is known today. Many varietal names have been proposed for the seedless as opposed to the seeded form of Breadfruit, but such taxa can only be descriptive, since in different areas there is great and overlapping variation in both forms and the origin of the seedless form is probably complex.

The following subdivision of the areas in which the Breadfruit occurs, according to the status and relative importance of the seeded and seedless forms, is given as a basis for the review which follows: (1) area in which the seeded form is predominant, very variable and probably indigenous — New Guinea and perhaps the Moluccas and Melanesia; (2) area in which the seedless form is predominant and very variable — the Pacific; (2a) area in which the seeded form is a conspicuous and possibly indigenous component of the vegetation — Micronesia; (2b) area in which the seeded form is rare — Polynesia; (3) area in which the seeded and seedless forms are rather constant in their characters and distinct from each other — the remainder of the tropics.

In New Guinea the Breadfruit is of widespread occurrence, especially in its seeded form. It was recorded by Miklouho-Maclay (Proc. Linn. Soc. N. S. Wales **10**: 348. 1885; as *A. incisa* and *A. integrifolia*) in the Astrolabe Bay area of Northeast New Guinea, both in cultivation and in the forest, and by Warburg for Finschhafen and the Bismarck Archipelago (Bot. Jahrb. **13**: 295. 1891). Lauterbach (l.c. **63**: 421, 438, 444, 447. 1930) stated that wild Breadfruit occurred in the Astrolabe Bay area both on the hillside in rainforest and in the secondary alluvial forest. On the Ramu River, he recorded it as characteristic of the latter, being found in places in pure stands. In Papua, White (Proc. Roy. Soc. Queensland **24**: 23. 1922) noted that the Breadfruit was "common wild or cultivated through the whole of the coastal country," while Lane-Poole (Forest Resources of Papua and New Guinea, 81. 1925) recorded it as one of the more permanent members of the regrowth on cleared land. In the "Results of the Archbold Expeditions," the Breadfruit was recorded from the Fly River region as common on flooded riverbanks and in second growth forest (Rand & Brass, Bull. Am. Mus. Nat. Hist. **77**: 366, 376. 1940). It was also recorded from the Meervlakte in Dutch North New Guinea as occurring along waterways and as a marginal constituent of periodically inundated *Timonius*-forest, one of the successional communities of this flood plain (Archbold, Rand & Brass, l.c. **79**: 233, 235, 1942). A photograph of this community was published by Van Steenis (in Nieuw Guinea, ed. Klein, Pt. II. Veg. en Flora, 228. *t. 2.* 1954). Lam had earlier noted its abundance in this region (Fragmenta Papuana, transl. Lily M. Perry. Sargentia 5. 1945), and in his review of the vegetation and flora of the whole of New Guinea (Blumea 1: 120. *map.* 1934) he described the Breadfruit as a locally frequent constituent of the extensive freshwater swamps. Further west, the Breadfruit was recorded as frequent in the inner part of MacCluer Gulf by Engler in the enumeration of plants collected by Naumann on the voyage of the *Gazelle.* (Bot. Jahrb. 7: 451. 1886). However, Rand and Brass have expressed doubt as to whether the Breadfruit is indigenous in New Guinea, and they took its presence in the Fly River area as "an indication of the presence of human population." As they stated, it is indeed difficult to establish its occurrence in undisturbed climax forest. Nevertheless, several collections have been seen which do appear to be from such forest. The best attested of these is *Brass & Versteegh 13537,* "frequent tree of primary rain-forest, on slope of a ridge, 650 m. alt." There seems to be no conclusive reason for doubting that the Breadfruit is truly indigenous in New Guinea; moreover, the seeded form shows a wider range of variation there than anywhere else. It evidently is capable of competing with other indigenous species, although its presence is admittedly most conspicuous in the secondary forest.

The seeded Breadfruit shows in New Guinea the full range of variation indicated in the description of the species, except, perhaps, in the shape and surface of the syncarp and in the shape of the male head. It may be noted once more how variable the indumentum is in colour, distribution, abundance, and type and length of hair. The collections listed above include all that were seen from New Guinea. Their provenance is indicated and none was stated to be cultivated, except possibly *Brass 981,* although some of those from secondary or riverside forest, or for which there are no data, may have been planted. With the exception of *Carr 11633, 11675, 15726* (secondary or riverside forest) and *Clemens 1117* (no data), which will be discussed below, their inflorescences may be described as follows. The syncarps are ellipsoid to cylindric, with slender flexuous processes projecting to 5–15 mm., and the male inflorescences are narrowly cylindric, 20–30 (–37) × 1.5–2 cm. This appears to be the indigenous form of the Breadfruit in New Guinea. *Artocarpus leeuwenii* and *A. papuana* of Diels both represent this form. The type of *Artocarpus leeuwenii* (*Docters van Leeuwen 11163*) has a dense indumentum throughout, and the syncarp processes (erroneously called styles) project to 12 mm., whereas the type of *A. papuana* (*Ledermann 7513*) has less indumentum and the syncarp processes project only 5–7 mm. Intermediate collections have been seen, however. The type of *Artocarpus incisa* Linn. f. var. *muricata* Beccari resembles that of *A. leeuwenii* in the syncarp characters, but has a sparser indumentum.

The four collections which were excepted above show a wider range of variation. The syncarp on *Carr 15726* has low, broad, obtuse processes on the surface and a number of apparently well-developed seeds. *Carr 11633* has a syncarp covered by conical processes projecting to 3 mm. and has only one seed. A similar, possibly entirely seedless, syncarp was seen on *Clemens 1117*. This collection is also of interest since on the specimen at the Arnold Arboretum some of the male inflorescences measure only 11–13 × 1.5–1.8 cm. at anthesis, although on that at Leiden there is one measuring 25 × 1.6 cm. A note on the label at Leiden suggests that this may be a mixed collection. *Carr 11675* has a male inflorescence measuring 15 × 1.1 cm., at anthesis, so that there is evidently fairly wide variation in both male and female inflorescences in collections from secondary and riverside forest. It must be pointed out that all the syncarps seen are ellipsoid to cylindric and that none is undoubtedly seedless. Thus the "characteristic" seedless Breadfruit of the Pacific, with a globose head and a nearly smooth surface has not been seen in New Guinea. Too much emphasis should not be placed on this apparent absence since so few syncarps have been seen, and none is definitely from a cultivated plant. Brass (Bull. Am. Mus. Nat. Hist. 111: 97. 1956) notes that the seeded Breadfruit is cultivated on the Cape Vogel Peninsula for its seeds, and Barrau (Subsistence Agriculture in Melanesia. Bishop Mus. Bull. **219**: 59. 1958) states that, especially in New Guinea, the seeds are preferred to the flesh, although the latter is also eaten. It is of interest to note that Ochse and Backhuizen van den Brink (Veg. Dutch E. Ind. 489. 1931) record that F. J. F. van Hasselt, a missionary at Manokwari, stated that the Papuans sliced Breadfruit (presumably few-seeded or seedless) and dried it for storage over a period of time. In view of the variability and apparent overlapping of characters, there is no reason why the few-seeded or (?) seedless varieties should not have arisen in New Guinea.

There is no definite evidence as to whether the Breadfruit is indigenous in Melanesia and the Moluccas. In Melanesia, Guillaumin's observation that it is common in the rainforest on Eromanga in the New Hebrides (Jour. Arnold Arb. **13**: 106. 1932) is based on a field note, the only one seen from the whole region, on *Kajewski 394* (A, K). This collection has deeply incised leaves with broad sinuses. The inflorescences are at anthesis; the male head is clavate, measuring 13 × 2 cm., and the female head is obovoid with conical processes projecting 1 mm. However, too much significance cannot be attached to this single record of the status of the Breadfruit, since it is possible that the forest was secondary. Daniker (Viert. Naturf. Ges. Zürich 77: Beibl. **19**: 125. 1932) recorded the Breadfruit as doubtfully spontaneous on the Loyalty Islands. The only other fertile collection seen from Melanesia is *Mosely s.n.* (BM, K) from the Admiralty Islands, with male heads measuring 20–26 × 3 cm. at anthesis. It may be noted that the single fertile collection seen from New Caledonia, *Balansa 3233* (P), has a seeded fruit with low facets and a clavate male inflorescence 7 × 2.3 cm.

In the Moluccas, the only source of detailed information is Rumphius, who described (c.1660–1680) distinct seeded and seedless forms in the "Herbarium Amboinense." The former, *Soccus granosus*, had narrowly conical processes on the syncarp and more or less pubescent twigs and leaves, while the latter, *Soccus lanosus*, had low facets on the syncarp and was glabrous. Rumphius recorded that he had been told that the Breadfruit grew wild on Banda. All the collections from the Moluccas cited above are stated to be from either old or primary forest, but all are sterile, and no other fertile collections from these islands have been seen. In their vegetative characters the collections lie within the range of variation shown by those from New Guinea, but none is as densely pubescent as the type of *A. leeuwenii* and most are subglabrous. Both to the east and west of New Guinea, therefore, the range of variation is apparently fairly wide, but whether these forms could have been derived solely from the apparently indigenous Breadfruit of New Guinea cannot be determined until more adequate material is available. This problem will be discussed further below under Micronesia.

In the Pacific region (i.e., Micronesia and Polynesia) the Breadfruit is chiefly of importance in its seedless form and the variation exhibited by this will first be indicated briefly, since more evidence is available concerning this form than the seeded form. A list follows of the more important references which give lists of Breadfruit varieties under their vernacular names. In the ensuing discussion, where only the date is given after an author's name, it refers to a work in this list.

Christian, F. W. The Caroline Islands, 386. 1899. [43 varieties (two seeded) on Ponape, with brief notes on the fruits.]

Seemann, B. Flora Vitiensis, 255. 1868. [13 varieties (one seeded), with short notes on the fruits and leaves.]

Christopherson, E. Flowering Plants of Samoa. Bishop Mus. Bull. **128:** 72. 1935. [30 varieties, with brief notes on the fruits and leaves.]

Bennett, G. Gatherings of a Naturalist in Australasia, 396. 1860. [24 varieties in Tahiti, with some brief comments.]

Henry, T. Ancient Tahiti. Bishop Mus. Bull. **48:** 39. 1928. [40 varieties listed, with some short notes. The Tahitian legend of the origin of the Breadfruit is also given (p. 423).]

Wilder, G. P. The Breadfruit of Tahiti. Bishop Mus. Bull. **50.** 1928. [31 varieties described (one seeded), with photographs of the fruits and leaves. A number of the vernacular names in these three works are the same.]

Christian, F. W. Eastern Pacific Islands, 208. 1910. [34 varieties listed from the Marquesas without descriptions.]

Wester, P. J. Philip. Agr. Rev. **17:** 24. 1924. [A compilation of earlier lists incorporating further data from Tahiti and the Marquesas.]

The variation recorded for the seedless form of the Breadfruit in the Pacific covers the full range indicated for the species in the shape, size and surface of the syncarp, and in the outline of the leaves. The latter are usually incised and glabrous or nearly so except on the main veins, but there are a few entire-leaved varieties. These observations are based on the descriptions of Wilder (1928), on the brief notes of other authors, and on rather sparse herbarium material. On the basis of this evidence it has not been possible to distinguish any obvious groups of varieties. With closer study, however, lines of development between different varieties may well prove to be traceable and it may then be possible to determine the routes of distribution. At present it can be noted only that some of the seedless varieties show quite a close resemblance to the seeded form of New Guinea in their elongate, "prickly" syncarps. They may be contrasted with other varieties having round, nearly smooth fruits, but all gradations and combinations of characters seem to occur between these two extremes. Seeded varieties of the Breadfruit are rare in Polynesia but have been recorded from Fiji (*uto sore*, Seemann, 1868) and Tahiti (*huero*, Wilder, 1928). It was noted above that the second of these is usually propagated by vegetative means. The fruit is globose, with few seeds and low facets, and the leaves are incised and "slightly pubescent."

The Breadfruit was distributed throughout the Pacific before the arrival of Europeans. The earliest description that has been found of it was given by Quiros, who went as the pilot on Medaña's voyage of 1595 through the southern Pacific Ocean and who, after the death of Medaña on Santa Cruz, guided the survivors of the expedition to Manila (Penrose, Travel and Discovery in the Renaissance 1420–1620, 165. 1952). Quiros recorded the Breadfruit from the Marquesas, in the east, and Santa Cruz, in the west, in an account of the voyage which he wrote in the form of a letter to De Morga, then governor of the Philippines, and which the latter included in his "Sucesos de las Islas Filipinas," published in 1609. There can be no doubt that the Breadfruit was introduced into Polynesia by man, and it may be noted that this opinion was expressed as early as 1784 by Forster in his little book "Vom Brodbaum."

In Micronesia, on the other hand, it has been stated that the seeded form is an important constituent of the lowland vegetation on some of the "high" islands. In the eastern Caroline Islands the seeded form has been recorded from all the "high" islands. Kanehira listed two seeded varieties from Truk (edible, *mei chon*; not edible [?], *aroyas*; Jour. Dep. Agr. Kyushu Univ. **4**: 306. 1935). Glassman noted two seeded varieties in Ponape, which frequently grew without any cultivation (*mai-pa*, *mai-kohlch*, Bishop Mus. Bull. **209**: 11. 1952; cf. *pa*, *koli*, Christian, 1899). On Kusaie, Volkens (Bot. Jahrb. **31**: 416. 1901) recorded the Breadfruit (not stating whether it was seeded) from lowland forest. He also mentioned that there were seeded varieties on Yap, but apparently regarded them solely as planted in mixed groves of useful and strand trees. Volkens stated that in the Carolines as a whole most of the primary forest had been destroyed, except on very steep slopes, and Glassman also noted that on Ponape most of the vegetation at low elevations was secondary. Although the seeded form is evidently able to maintain itself, as in New Guinea, in secondary vegetation, authentic records of its occurrence in virgin forest in the Carolines are lacking. Seeded varieties are also recorded from "low" islands in this group, namely, Pingelap Atoll (*mei sabarak*, St. John, Pacif. Sci. **2**: 109. 1948), and Namonuito and the Hall Islands (Stone, l.c. **13**: 89, 90, 100. 1959). These records indicate that seeded as well as seedless varieties must have been distributed by man in this area; Stone notes that the seeds are a favourite article of diet.

In the Marianas, a seeded form of the Breadfruit called *dugdug* was stated by Safford to be very abundant on Guam (Contr. U. S. Natl. Herb.

9: 55, 190. 1905). Dr. F. R. Fosberg, who has studied this form in the field, has been kind enough to send me the manuscript of a paper he has written on the Breadfruit in Micronesia. He also expresses the doubts indicated above as to the status of seeded varieties of the Breadfruit in the Carolines, but he states that in Guam the *dugdug* is dominant in some of the least disturbed original forest, especially in limestone areas. Its characters are somewhat distinctive and Dr. Fosberg describes the leaves as often entire (although very variable in their outline on the same tree) with conspicuous, brown, appressed hairs on the main veins beneath, the male inflorescences as short (to c. 10 cm. long), and the syncarps as more or less short-cylindric with low facets at maturity. This form was described by Trécul as *Artocarpus mariannensis* from a collection made by Gaudichaud, *sine numero*, in the Marianas Islands. The collection probably comes from Guam, which Gaudichaud visited in 1819 with the Freycinet expedition. The type specimen in the Muséum National d'Histoire Naturelle, Paris, has entire leaves, which are glabrous except for appressed colourless or pale rufous hairs on the underside of the main veins, and an immature male inflorescence with a cylindric head measuring 7 × 1 cm.; the vernacular name is given as *doug-doug*. The few fertile collections seen from Guam indicate that the seedless form of the Breadfruit there, called *lemai*, likewise has rather short, stout male inflorescences, but that the leaves are incised.

From this review it is evident that, throughout the Pacific, the Breadfruit exhibits a range of variation, at least in the shape of the syncarp, beyond that seen so far in collections from New Guinea. On the other hand, in the Pacific region the leaves tend to be subglabrous except on the main veins, and no specimens have been seen with such a dense indumentum as the type of *A. leeuwenii*, which may be regarded as representing almost the extreme of variation in this direction of the presumed indigenous form in New Guinea.

Nevertheless, until additional fertile collections are available, especially from New Guinea and the Carolines (none at all has been seen from the latter area), it is felt that the pattern of variation in the Pacific cannot be established with sufficient certainty to justify the separation of the Guam form of the seeded Breadfruit as a distinct subspecies or species. If this should be a distinct indigenous form and if it has hybridized with an introduced form of the Breadfruit in the Micronesian area, as is suggested by Dr. Fosberg, the characters of the Guam form could account for the greater range of variability of the Breadfruit in the Pacific than in New Guinea. However, it has been indicated in the course of this review that there is a considerable scatter of the characters of this form in the western Pacific area and that most of them (entire leaves, rufous hairs, fairly short male inflorescences and low anthocarp apices) also turn up in collections from New Guinea. There is a possibility that the *dugdug* of Guam represents a very early introduction of a rather distinctive type, developed in the Carolines or in New Guinea, which became naturalized and flourished in part due to lack of competition from the relatively small indigenous flora.

It must be pointed out in this connection that the Breadfruit has a large seed with no powers of dormancy. Furthermore, only two other species of the genus extend farther east into New Guinea than the Vogelkop; of these one extends into the Solomon Islands.

Dr. Fosberg discusses and has drawn my attention to the considerable range shown in the Pacific and elsewhere in the minute details of the indumentum of the leaves (even when consisting of only scattered hairs on the main veins), and differences in the hairs may be of great assistance in tracing the alliances of the different varieties.

In spite of the lack of material from the Carolines it seems that this scattered group of islands may have been a centre of differentiation and of distribution for seedless varieties of the Breadfruit. This is also suggested by the distribution of the names for the Breadfruit which is outlined below, and by the wide range of variation in fruit characters indicated by Christian's notes on seedless varieties in Ponape (1899). This range is apparently as wide as that found farther east and includes the characters of the seeded forms of both Guam and New Guinea. To show to what extent Micronesia was a centre of origin for seedless varieties from seeded trees requires further study, both there and in New Guinea.

Two names for the Breadfruit are widespread in the Pacific, as was pointed out by Christian in 1897 (Jour. Polynes. Soc. **6**: 127. 1897). Their distribution is northerly and southerly respectively, but they overlap somewhat, especially in eastern Polynesia. The more northerly of the names is *mai* or *mei*, which occurs in the Caroline and Marshall Islands (Christian, l.c. and 1899, and other authors), in Niue, east of the Tonga Islands (Yuncker, The Flora of Niue Island. Bishop Mus. Bull. **178**: 46. 1943) and in Samoa, the Marquesas, and Mangareva in the Tuamotu Archipelago (Christian, 1910). It is also found as *lemai* in the Marianas and as *rima* in the Philippines. The southern name appears as *ulu* in Samoa (Christopherson, 1935), as *kuru* in the Cook Islands (Wilder, Flora of Rarotonga. Bishop Mus. Bull. **86**: 40. 1931), and as *uru* in Makatea. In the Tuamotu Archipelago *ura* is recorded from Anaa (Brown, Flora of Southeastern Polynesia — III. Dicotyledons. Bishop Mus. Bull. **130**: 37. 1935) and *kuru* from Mangareva (Christian, 1910). Wilder (1928) records that in Tahiti the name for the Breadfruit used to be *uru* ("head"), but that it is now *maiore*. In Hawaii the Breadfruit is called *ulu* and MacCaughey (Torreya **17**: 37: 1917) states that the plant was probably introduced there from Samoa. In Fiji, the word for Breadfruit is *uto*, meaning "heart," according to Seemann (1868). Two names which are somewhat similar to those of wide distribution in the Pacific are recorded on collections from New Guinea — *momu*, *momoi*, and *mow* from the Vogelkop, and *unu* from Papua. However, in view of the many and various local names that have been noted for the Breadfruit in New Guinea and Melanesia (Christian, Jour. Polynes. Soc. **6**: 128. 1897; Barrau, Jour. Agr. Trop. Bot. Appl. **4**: 119. 1957) it would not be justifiable to assume that there is necessarily a direct relationship. Although in the Carolines the Breadfruit is most frequently called *mai*, in the Palau Islands and Yap, which are in the western part of the group, it is known by the names *medu*, *methu*, *thu*, *su* and other variants which are all probably cognate (Christian, l.c.; Barrau, l.c.). Further east in the group, in Kusaie, it is called *mos* or *mosse*, and this name is also recorded, as *mossi*, for Northeastern New Guinea (Christian, l.c.). No obvious correspondences can be traced in the names of varieties, except between neighbouring islands; thus Niue has evidently received its varieties from Samoa (? or Tonga), while Makatea shows some relationship with Tahiti.

The status and variability of the Breadfruit in the rest of Malaysia, apart from New Guinea and the Moluccas, which have already been discussed, will now be considered. In the Philippines the seeded and seedless forms of the Breadfruit are rather different from each other and they were described by Blanco in 1837 as *A. camansi* and *A. rima* respectively, the specific epithets being derived from their Tagalog vernacular names. (He applied the name *Artocarpus incisus* to the indigenous species now called *A. blancoi.*) The Breadfruit has been regarded as an introduced plant in the islands by some authors, including Merrill (Fl. Manila, 176. 1912, Enum. Philip. Pl. **2**: 40. 1923), and this view of its status is supported by the absence of any definite records, either in the literature or on field labels, of its occurrence in the wild, except in secondary vegetation. This may be contrasted with the fairly abundant herbarium material of *A. blancoi* and *A. treculianus*. Merrill's record of *Artocarpus communis* from the Lamao Forest Reserve, Luzon (Philip. Jour. Sci. **1**: Suppl. 43. 1906), and Whitford's records of the species as a constituent of dipterocarp forest in various parts of the Philippines (Philip. Jour. Sci. **1**: 373–431, 637–679. 1906; l.c. Bot. **4**: 699–723. 1909; Bull. Bur. For Philip. **10**(1): 23, (2): 29. 1911) must, for the most part, be referred to other indigenous species of this series. However, it appears that the Breadfruit does occur in the degraded forest called *parang* (Whitford, Philip. Jour. Sci. **1**: 391. *t. 4, 5.* 1906).

Quisumbing, however, in 1940 (Philip. Jour. Sci. **72**: 331) revived the name *Artocarpus camansi* Blanco for the seeded form of the Breadfruit in the Philippines and expressed the opinion that it was an endemic species, closely related to, but specifically distinct from, the ancestor of the Polynesian Breadfruit. The *camansi* has a narrowly oblong-obovoid male head, 15–25 cm. long, and narrowly conical processes on the syncarp, projecting 5–8 mm., whereas the *rima* (which Quisumbing referred to *A. communis*) has a club-shaped male head (8–15 cm. long in the collections examined in this study) and a nearly smooth syncarp. However, specimens representing the *camansi* which have been examined (*e.g.*, *Merrill SB 830*) resemble rather closely others seen from New Guinea and, although the seeded breadfruit is apparently naturalized in Luzon, it seems most probable that it has been introduced from New Guinea or the Moluccas. The rather marked differences shown by the seedless *rima* are due to its introduction from a different source, which was almost certainly the Marianas. The seedless *lemai* of Guam resembles the *rima* in the club-shaped male head, the names are cognate, and there was contact with Manila through the Spanish galleons. Wester made this suggestion in 1924 (Philip. Agr. Rev.

17: 24) on the basis of the absence of any mention of the Breadfruit in the Philippines in de Morga's "Sucesos de las Islas Filipinas" (1609) and the inclusion by G. J. Kamel of ***Rhymay Marianorum*** (together with *Dugdug Marianorum* and *Camangsi*) in his list of Philippine plants (in Ray, Hist. Pl. **3**: App. 52. 1704).

The seeded and seedless forms of the Breadfruit are both cultivated in western Malaysia, and they are similar to the forms described by Rumphius in the "Herbarium Amboinense" from the Moluccas and noted above. The seeded form has distinct processes on the syncarp and more or less abundant indumentum, while the seedless form (which may have a few inviable seeds) has an almost smooth syncarp and is glabrous or nearly so. The latter was described by Hasskarl in 1842 as *Artocarpus laevis*. The earliest mention of the Breadfruit in western Malaysia was made in 1642 in a brief description in Bontius' "De Medicina Indorum" (p. 52), which apparently refers to this species, although a remark on the objectionable odour of the fruit suggests some confusion with the Chempedak (*Artocarpus integer*). This description reappeared in Bontius' "Historiae Naturalis & Medicae Indiae Orientalis Libri Sex" (p. 119), as edited and published by Piso in 1658 in his "De Indiae Utriusque Re Naturali et Medica." An illustration of the Breadfruit was added, but the vernacular name was given as *Champidaca*; further reference is made to this confusion under *A. integer*. The three works mentioned in this paragraph, together with Kamel's list, contain the only references in pre-Linnaean botanical writings to the Breadfruit.

The differences just given between the seeded and seedless forms of the Breadfruit seem to hold, with minor variations, throughout the rest of the tropics, but the specimens and descriptions available are not adequate for this to be stated with certainty.

It is not known when the Breadfruit was first carried westward from Malaysia, but it is cultivated in Ceylon and along the western coast of the Deccan peninsula. According to Thunberg (Philos. Trans. Roy. Soc. London **69**: 470. 1779) it was introduced into Ceylon in 1727 or 1728 from the Maldive Islands, but no confirmation of this statement has been found in the later literature.

The Breadfruit was introduced to Mauritius from Luzon in the eighteenth century by Sonnerat, who described it under the name *rima* (Voy. Nouv. Guin. 99. *t. 57–60*. 1776), but it was not established on the African continent until the nineteenth century, according to Chevalier (Revue Bot. Appl. Agr. Trop. **20**: 29. 1940). It was mentioned by Ficalho in 1884 (Pl. Uteis Afr. Port. 273) for the Portuguese dependencies and Chevalier (l.c.) states that it was introduced into French Guinea in 1897. It is now common along the coastal region of west tropical Africa.

In the New World, the Breadfruit was introduced into the West Indies at the end of the eighteenth century, following representations by the planters as to its potential value in providing a staple food for the slaves (see Howard, Scientific American **188**: 88. 1953). The Society of Arts, in London, offered rewards for its introduction and establishment, and details of these, with reports on the progress of the trees, appeared in their Transactions for the period 1783–1807. The seeded form was brought to Martinique from Mauritius by a French ship in 1792 (Robley, Trans. Soc. Arts **20**: 357. 1802). The introduction of the Breadfruit by Captain William Bligh is, however, far better known. In 1787 he set out from London in the *Bounty*, largely through the influence of Sir Joseph Banks (see Cameron, Sir Joseph Banks, K.B., P.R.S., The Autocrat of the Philosophers. 1952), to collect young plants from Tahiti and carry them westward to the West Indies, but soon after the *Bounty* left Tahiti in 1789 this attempt terminated in the famous mutiny. In 1791 Bligh set out once more in the *Providence* and arrived at St. Vincent and Jamaica in 1793, bringing with him the seedless form of the Breadfruit from Tahiti, together with a few plants of the seeded form from Timor. An illustrated account of both forms, based on material from St. Vincent was published by W. J. Hooker in 1828 (Bot. Mag. **55**: *t. 2869–71*).

In South America, Tavares (Broteria, Ser. Vulg. Sci. **13**: 25. 1915) states that the Breadfruit was first cultivated in French Guiana in 1811, and that it was introduced from there to Brazil, where only the seedless form is known. The Breadfruit is also frequently grown in the coastal regions of Central America and, as Standley and Steyermark observe (Fieldiana Bot. **24**(4): 12. 1946), it may have been introduced there from the west by early Spanish voyagers.

12. **Artocarpus pinnatisectus** Merr. Philip. Jour. Sci. **18**: 50. 1921, "*pinnatisecta*," Enum. Philip. Pl. **2**: 43. 1923. Holotype, Luzon, *Escritor BS 20789* (PNH, destroyed); isotypes (K, US); lectotype (US).

Tall tree (fide Merrill). *Twigs* 15–20 mm. thick, shallowly rugose, glabrous except for tufts of patent greyish or pale rufous hairs to 3 mm. long below the stipular scars and petioles; stipular scars 2 mm. broad, not prominent, conspicuous; lenticels in a ring below scar. *Stipules* 10–20 cm. long, lanceolate, acute, villous with patent, pale rufous hairs, to 3 mm. long. *Leaves* c. 40–100 × 35–60 cm., oblong to oblong-ovate in outline (fide Merrill), deeply pinnatifid, lateral lobes c. 12–20 pairs, lanceolate, attenuate, to 18 × 2 cm. (*Escritor BS 20789*) or to 38 × 6 cm. (*Ramos & Edano BS 33536*), sinuses narrow, extending to within 1.5 cm. of midrib; midrib and main veins of lateral lobes prominent beneath, reticulum slightly so; glabrous above, main veins appressed-puberulent beneath, and with scattered longer hairs; lateral veins of lobes to c. 25 pairs; intercostals few, parallel or not; drying pale to dark brown; hypodermis absent; gland-hairs immersed, heads flattened, c. 16-celled; petiole 70–100 mm. long.

Inflorescences solitary in leaf-axils (only male head seen attached). *Male head* (immature, deformed on both sheets) of two laterally connate lobes each to 70 × 25 mm., smooth, covered with flowers, a few of these sterile, and occasional interfloral bracts, the sterile perianths solid and projecting c. 0.5 mm. from the surface; perianths tubular, 2.4 mm. long, bilobed, lobes with deflexed inflated hairs having acute tips; stamen immature, filament fairly slender, anther-cells oblong, 1.2 mm. long; bracts slenderly stalked, heads narrowly peltate, 0.2 mm. across, with a tuft of hairs 1 mm. long; peduncle (two laterally fused) 25 × 5 mm., with sparse patent rufous hairs. *Syncarp* (submature) 15 × 5 cm., cylindric, drying red-brown, covered by closely set, fleshy, short-cylindric, obtuse processes, 3 × 2 mm., rough from the acute, deflexed tips of inflated hairs; simple styles exserted to 1.5 mm.; scattered bracts present between the processes, slenderly stalked, heads narrowly peltate, 0.2 mm. across; wall 1.5 mm. thick; seeds . . . ; core 25 mm. across; peduncle . . . .

DISTRIBUTION: Philippine Islands (Luzon and ? Mindanao).

Philippine Islands. LUZON. Quezon (Tayabas): Guinayangan, *Escritor BS 20789*, Mar. 1913 (K, US, ♂). Camarines: Paracale, *Ramos & Edano BS 33536* (A, K, US, ♀).

This species is based on very inadequate material. Only two collections have been seen, these bearing immature male inflorescences and a detached, submature syncarp respectively. However, although the specimens differ in the size of their leaves, they agree in the large number of lateral lobes (12–20 pairs as compared with 7–10 pairs in *A. multifidus*), and their association seems justified in view of the differences from the other species already noted under the series. In the original description Merrill cited a third collection, *Cruz FB 27751*, Davao, Mindanao, but no duplicates of this have been found and it was not stated whether it was fertile. Both the isotypes show the same abnormality of the male inflorescence, which has the appearance of two inflorescences fused laterally and presumably developed from a partially divided rudiment. Merrill made no reference to this and gave the dimensions of the head as 10 × 3 cm., and the length of the peduncle as 3 to 4 cm.

13. **Artocarpus multifidus** Jarrett, sp. nov. Holotype, Samar, *Sulit 6462* (PNH); isotype (A).

Inflorescentiae floribus fertilibus, plerisque perianthiis solidis praelongis, bracteisque raris obtectae; folia profunde pinnatifida, laciniis utrinque 7–10, glandulis immersis, capitibus planis 8-cellis, sine hypoderme.

Arbores ad 10 [–20] m. altae. [*Ramuli juniores* 15–20 mm. crassi, rugosi, infra cicatrices stipularum annulatas, 2 mm. latas, prominulas, conspicuas, villosi, pilis patentibus, pallidi-rufis, 3 mm. longis, lenticellisque circum ramulos dispositis. *Stipulae* 18–23 cm. longae, late lanceolatae, acutae, tenuiter villosae, pilis patentibus, pallidi-rufis, 3 mm. longis.] *Folia* [40–] 90 cm. longa, ovati-oblonga, [profunde pinnatifida,] sinusibus angustis, costa tenuiter villosa, in sicco brunnea; laciniae utrinque [7–]10, lanceolatae, leviter falcatae, attenuatae, ad 32 × 7 cm., nervis mediis lateralibusque subtus prominentibus, nervis transversalibus venulisque subtus prominulis, nervis mediis tenuiter villosis, nervis lateralibus utrinque ad

FIG. 13. Left, *Artocarpus pinnatisectus*, paratype, *Ramos & Edano 33536* (K); right, *A. multifidus*, holotype, *Sulit PNH 6462* (PNH).

25, rectis, pubescentibus, pilis [rectis vel] uncinatis, nervis transversalibus non parallelis; hypodermis absens; glandulae immersae, capitibus planis, 8-cellis; petiolus [70–]130 mm. longus.

Inflorescentiae axillis foliorum solitariae. [*Capitula mascula* (immatura) ad 80 × 25 mm., clavata, plana, floribus fertilibus numerosissimis, plerisque sterilibus, 2 mm. exsertis, obtecta; flores fertiles perianthiis tubulosis, 2.5 mm. longis, supra bilobatis, puberulentibus, staminibus filamentis cylindricis, cellis antherum oblongis, 1.5 mm. longis; flores steriles cylindrici, solidi, 4.5 mm. longi (ad 2 mm. prominentes), apicibus clavatis, pilis recurvatis; pedunculus 50 × 3 mm., tenuiter villosus.] *Syncarpium* (maturum) 12 × 5 cm., cylindricum, in sicco brunneum, processibus crebris duarum longitudinum, carnosis, teretibus, obtusis, asperis, pilis recurvatis, subinflatis, inaequalibus, longioribus crispis, obtectum; processus longiores flexuosi, 15 × 1 mm., solidi, breviores 5 × 1 mm., perforati, stylis bifidis, 2 mm. longis exsertis; bracteae interflorales rarae, tenuissimae, anguste peltatae, capitibus 0.2 mm. latis, pubescentibus; stratum externum syncarpii c. 2 mm. crassum; "semina" (pericarpia indurata) numerosa, ellipsoidea, 10 × 7 mm., stylis sub-basalibus, perianthiis liberis tenuisque inclusa; embryum radicula ventrali, cotyledonibus aequalibus fere in longitudinem positis, testa tenuiter pergamentacea inclusum; axis syncarpii c. 20 mm. diametro; pedunculus 50 × 7 mm., tenuiter villosus.

DISTRIBUTION: in forest to 2000 ft., Philippine Islands (Samar, Mindanao).

Philippine Islands. SAMAR. Mt. Calbiga, Taft. *Sulit PNH 6462*, May 1948 (A, PNH, ♀). MINDANAO. Surigao: Mt. Kabatuan, *Mendoza & Convocar PNH 10563* (A, PNH, ♂).

The characters of this rather distinctive species are discussed above, under the series.

(*To be concluded*)

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STUDIES IN ARTOCARPUS AND ALLIED GENERA, III. A REVISION OF ARTOCARPUS SUBGENUS ARTOCARPUS *

FRANCES M. JARRETT

Series **Cauliflori** Jarrett, ser. nov.

Folia simplicia, adulta integra, juvenilia ad 5-lobata; hypodermis et cellae resinosae absentes (hic in ceteris speciebus subg. *Artocarpi* inventae); glandulae immersae capitibus globosis 6–10-cellis. *Inflorescentiae* trunco et ramis, masculae etiam ramulis, latae. *Capitula mascula* superficie plana, floribus fertilibus vel paucis sterilibus solidis obtecta, omnibus aequalibus, bracteis absentibus. *Syncarpia* processibus puberulentibus ad minute hispidis, omnibus aequalibus obtecta, bracteis absentibus; semina testis tenuis, brunneis, pericarpiis membranaceis (*A. integer*) vel endocarpiis corneis et exocarpiis subgelatinosis (*A. heterophyllus*), perianthiisque crassis, carnosis inclusa.

TYPE SPECIES: *Artocarpus integer* (Thunb.) Merr.

In a paper entitled "Notes on the systematy and distribution of Malayan phanerogams, II. The Jack and the Chempedak," Corner discussed in detail the nomenclature and distinguishing characters of the two species included in this series (Gard. Bull. Singapore **10**: 56–81. *t. 1, 2.* 1939). The descriptions given below are based in part on this paper. The nomenclatural studies are reviewed above (pp. 119–122). They showed that the name *Artocarpus integer* (Thunb.) Merr. (*Rademachia integra* Thunb.), with its illegitimate synonym *A. integrifolia* Linn. f., should have been applied to the Chempedak, rather than to the Jack, as had been the universal practice since the beginning of the nineteenth century. *Artocarpus heterophyllus* Lamarck was then chosen by Corner as the correct name for the Jack.

A detailed analysis was given by Corner of the distinctions between *Artocarpus integer* (including var. *silvestris*) and *A. heterophyllus*, and the chief characters are enumerated below. The variety of the latter which is said to resemble *A. integer* is excluded from consideration here. Vegetatively, *A. integer* and *A. heterophyllus* are differentiated by the colour (when fresh) and the shape of the leaf blade (the base being abrupt in the

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* Continued from volume XL, p. 326.

former and decurrent onto the petiole in the latter) and by the frequently hirsute versus subglabrous shoots.

The inflorescences in *Artocarpus integer* are somewhat smaller in all their parts than in *A. heterophyllus*, and in the latter alone the top of the peduncle is expanded to form a narrow fleshy flange or annulus at the base of the male and female heads. The syncarp in *A. integer* becomes characteristically "baggy" at maturity, due to the separation of the wall from the free, fleshy region of the fruiting perianths. The perianths also become detached from the core, so that they fall out when the syncarp is cut open. This separation does not occur in *A. heterophyllus* and the edible fruiting perianths must be cut away from the rest of the syncarp. There are considerable differences in the details of the fruiting perianths and of the enclosed structures in the two species. In *A. integer* the ripe, free, hypertrophied region of the perianth is soft, without a stalk, and the enclosed pericarp is membranous with the style attached one-third of the way up the ventral face. The embryo has somewhat unequal cotyledons and the radicle is immersed between their short basal lobes. In *A. heterophyllus* the fruiting perianths are firm with a fleshy, thickened stalk. The pericarp is clearly differentiated into a subgelatinous exocarp, 1 mm. thick (which apparently persists until the decay of the syncarp), with the style attached two-thirds the distance up its ventral face, and a horny endocarp [8] which becomes completely free from the exocarp at maturity. The embryo has very unequal cotyledons and the radicle is superficial, being well developed and directed down towards the hilum. Figures illustrating these various differences are given in Corner's paper.[9]

The characters of greatest taxonomic significance in distinguishing the species are probably those provided by the pericarps and embryos and the presence or absence of the annulus. The presence of a well-developed endocarp in *A. heterophyllus* but not in *A. integer* is especially noteworthy. The difference in the embryos is considerable, but it is difficult to determine its significance in view of the lack of complete information for section *Artocarpus* and the variation which is found in the other series. The annulus is likewise difficult to evaluate as a taxonomic character since it is developed only in *A. heterophyllus*. It is presumably equivalent morphologically to the slight expansion of the peduncle at the base of the inflorescence head that is found in various other species of *Artocarpus*, and perhaps also to the basal involucre in *Parartocarpus*. Although the cumulative effect of these differences is to make the two species rather distinct from each other, none of them is, in itself, sufficient to justify the creation of a separate series for each species, with the possible exception of the endocarp character.

On the other hand, the characters uniting *Artocarpus integer* and *A. heterophyllus* are equally marked, as is pointed out in the discussion of section *Artocarpus* (p. 131 above). Nevertheless, none of these — namely,

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[8] Referred to as the outer testa on p. 128 above, and by Corner.

[9] TEXT-FIGURES 3 and 4 were accidentally transposed; the legend on p. 66 refers to the figure on p. 67 and *vice versa*.

cauliflory and the very large size of the syncarps, the hypertrophied fruiting perianths, the lack of resin-cells in the leaves and perhaps the separation of the cotyledons to allow the emergence of the plumule in germination — is again sufficient to warrant the placing of the species in a separate section. In the shape of the inflorescences, the position of the style and the orientation of the embryo, the general alliances of series *Cauliflori* are with the other members of sect. *Artocarpus*, and the group is perhaps nearest to series *Angusticarpi*.

14. **Artocarpus integer** (Thunb.) Merr. Interpr. Rumph. Herb. Amb. 190. 1917, non sensu Merrill; Corner, Gard. Bull. Singapore **10**: 56. *t. 1, 2.* 1939.

Saccus arboreus minor Rumph. Herb. Amb. **1**: 107. *t. 31.* 1741.

Rademachia integra Thunb. Vet. Akad. Handl. Stockholm **37**: 254. 1776; Houttuyn, Nat. Hist. II. Pl. **11**: 453. 1779. Holotype, Java, *Thunberg s.n.* (UPS, photograph in Corner, 1939); ? isotype (L).

Sitodium macrocarpon Thunb. Philos. Trans. Roy. Soc. London **69**: 467. 1779, nomen illegitimum.

Artocarpus integrifolia Linn. f. Suppl. Pl. 411. 1781, nomen illegitimum; Panzer, Beitr. Geschichte Brodbaums, 35. 1783, et in Panzer & Christmann, Pflanzensyst. **10**: 371. 1783; Murray, Syst. Veg. ed. 14. 838. 1784; Persoon, Syst. Veg. ed. 15. 882. 1797.

Sitodium cauliflorum Gaertn. Fruct. **1**: 345. 1788, nomen illegitimum.

Artocarpus jaca Lamarck, Encycl. Méth. **3**: 209. 1789.

Artocarpus pilosus Noronha, Verh. Batavia. Genoot. **5**(5): 7. 1790, nomen nudum.

Polyphema champeden Lour. Fl. Cochinch. 546. 1790, pro maxima parte, "spathis" exclusis.

Artocarpus polyphema Persoon, Syn. Pl. **2**: 531. 1807, nomen illegitimum.

Artocarpus champeden (Lour.) Stokes, Bot. Mat. Med. **4**: 330. 1812; Sprengel, Syst. Veg. **3**: 804. 1826.

Artocarpus pilosa Reinw. ex Blume, Cat. Bog. 101. 1823, nomen nudum.

Artocarpus hirsutissima Kurz, Natuurk. Tijdschr. Ned. Ind. **27**: 182. 1864. Holotype, Bangka, *Kurz 1017* (CAL); isotype (CAL).

var. **integer**

Evergreen trees, height to 20 m., not or scarcely buttressed, bark greyish brown, somewhat scaly. *Twigs* 2.5–4 mm. thick, shallowly rugose or smooth, pilose with sparse to dense, patent, rufous hairs to 3 mm. long, often also with shorter, whitish hairs; annulate stipular scars c. 0.5 mm. across, not or slightly prominent; lenticels scattered. *Stipules* 1.5–9 cm. long, ovate, acute, indumentum as twigs. *Leaves* 5–25 × 2.5–12 cm., obovate-elliptic, varying obovate- or elliptic-oblong or elliptic, acuminate, base cuneate or rounded, abrupt, margin entire; juvenile leaves elongate, or with 1–2 pairs lateral lobes; main veins only prominent beneath, or intercostals slightly so; main veins pilose beneath or on both surfaces, lower surface often appressed-pubescent throughout, rarely also above, the hairs rufous; lateral veins 6–10 pairs, curved; intercostals few, to c. 10, parallel, markedly oblique; dull mid-green, midrib pale, drying red-brown; hypodermis absent; gland-hairs deeply immersed in pits contracted at the mouth, heads globose, c. 10-celled; petiole 8–30 mm. long.

Inflorescences solitary in leaf-axils; cauliflorous and ramiflorous, flowering on short leafy shoots; male heads sometimes borne on the ultimate twigs. *At anthesis*: *male head* 30–55 × 9–12 mm., cylindric, varying clavate, smooth, covered by flowers; perianths tubular, 0.7–1.0 mm. long, very shortly bilobed above, minutely pubescent; stamen 1.0–1.3 mm. long, filament cylindric, anther-cells ellipsoid, 0.25 mm. long; peduncle 25–60 × 1.5–3 mm., indumentum as twigs; *female head* with simple, filiform styles exserted to 1.5 mm. *Syncarp* 20–35 × 10–15 cm., cylindric, somewhat "baggy" at maturity, yellow, drying brown, with a strong, harsh, penetrating odour (like durian and *Mangifera foetida*), covered by closely set, firm, tapering, obtuse, minutely hispid processes, 2–4 × 3 mm.; wall c. 10 mm. thick; fruiting perianths numerous, proximal free region yellow, markedly fleshy, soft, becoming detached from wall and core, "seeds" (membranous pericarps) ellipsoid to oblong, c. 30 × 20 mm., style one-third the distance up the ventral face, testa thin, embryo with the radicle ventral, immersed, enclosed by the basal lobes of the cotyledons, these oblique to the median plane of the ovary, unequal, one cotyledon two-thirds to three-quarters the length of the other; peduncle 55–65(–90) × 4–7 mm., indumentum as twigs.

Vernacular names: *Sone-ka-dat*, Moulmein, Burma; *Chempedak*, *Tjempadak*, *Champada*, *Tjampada* and variants (Malay), peninsular Siam, Malaysia. Uses: the fleshy perianths, "with a strong, sweet taste of durian and mango," which surround the seeds are eaten and the flavour is considered superior to the Jackfruit; the seeds are also eaten roasted or boiled.

Distribution: Apparently indigenous in evergreen forest to 1500(–4000) ft., Sumatra, Borneo, Celebes, Moluccas, New Guinea (Vogelkop); cultivated in Tenasserim (Moulmein), and throughout Malaysia, except central and eastern Java, the Philippines and eastern New Guinea; restricted both when indigenous and cultivated to regions without a marked dry season.

Sumatra. Atjeh. Gunong Caoutchouc, Langsa, *bb 2574* (BO, L). Tapanuli. Barus, Pankalan Tapus, *bb 28454* (BO, L, SING); Padang Lawas, Batang Baruhar, *bb 6442* (BO); Padang Lawas, Purbasinamba, *bb 6201* (BO, ♀). West Coast. Padang Pandjang, near Pajakumbuh, *Meijer 7116* (L); Sidjundjung, Muaro, *bb 9064* (BO, L); Solok, Sulangko, Gunong Batu Kunit, *Koorders 10666* (BO). East Coast. P. Berhala, *Lörzing 6989* (BO, L, ♀). Indragiri. Damar Mengkuang, *bb 27539* (BO); Kwala Belilas, *bb 27594, 27606* (BO). Palembang. Banjuasin and Kubustreken, Banjunglintjir, *NIFS T 54* (BO, L, ♀); Lematang Ilir, Semangus, *bb 31736* (BO, L), *32006* (BO); Rawas, *Grashoff 1026* (BO).

Borneo. Brunei. Mile 3, Kuala Abang road, *Ashton BRUN 85* (L, ♀). East and northeast Borneo. E. Kutei: Tandjong Bangko, near Mahakam River estuary, *Kostermans 7091* (L, ♀). W. Kutei: Longbleh, *bb 16081, 16120* (BO); Mujup, *bb 16733* (BO), *16754* (A, BO, SING). British North Borneo. Beaufort, Lumat, *Cuadra A 1334* (SING).

Celebes. Central Celebes. Malili, Usu, *NIFS Cel./III–70* (BO, ♂, ♀), *127*

(BO), *128* (A, BO, SING), *129, 130* (BO). P. MUNA. Wapai, *bb 21731* (A, BO). **Moluccas.** SULA ISLANDS. Sanana, Kabauw, *bb 28869* (BO, L, SING). AMBON. Pula, Hatu, *bb 14268* (BO). **New Guinea.** VOGELKOP. Kali Kamundan, *bb 21882* (BO, ♀); Manokwari, Sidai, *Schram BW 1741* (L); Tavui, *bb 22318* (A, BO, L, ♀).

var. **silvestris** Corner, Gard. Bull. Singapore **10**: 76. 1939. Holotype, Malaya, *Corner SFN 32988* (SING).

Differs from var. *integer* as follows: twigs, leaves and peduncles varying to entirely glabrous; *leaves* withering green, yellowish green or dingy yellow, not rich ochre or orange, drying blackish brown to red-brown; *syncarp* 15–30 × 10–15 cm., without any odour; fruiting perianths more or less tasteless.

VERNACULAR NAMES: *Bankong*, Malaya; *Barok*, Johore, Lingga Archipelago.

DISTRIBUTION: Malaya, Sumatra, Lingga Archipelago, Borneo.

Siam. PENINSULAR SIAM. Patalung, Kao Soi Dao, *Kerr 19234* (BM, ♀); Pattani, Banang Sta, *Kerr 7422* (BM, ♀). **Malaya.** PERAK. Tapah, *Wray 1356* (K, SING, ♂, ♀). PAHANG. Raub, Batu Talam, *Burkill & Haniff SFN 17030* (SING, ♀); Fraser's Hill, *Corner SFN 33205* (SING, ♂), *Corner s.n.*, Aug. 1937 (SING), *Nur SFN 11254* (BO, SING, ♀), *Strugnell CF 14627* (SING, ♀); Kuala Teku, *Corner SFN 33688* (SING, ♀); Sungei Tahan, *Corner s.n.*, Sept. 1937 (SING), *Ridley s.n.*, June 1891 (SING, ♀). SELANGOR. Kuala Lumpur, Weld Hills Res., *Ahmad CF 4586* (SING, ♀); Simpang mines, *Ridley s.n.*, Aug. 1904 (SING). JOHORE. Mawai-Jemalaung road, Sungei Kayu, *Kiah s.n.*, Oct. 1936 (SING); 18th mile, Mawai-Jemalaung road, *Corner SFN 32988*, May 1937 (SING, ♀). PENANG. *King 1636*, (CAL, SING, ♂). SINGAPORE. Changi, *Ridley 5028* (CAL, SING, ♀).

Sumatra. PALEMBANG. Lematang Ilir, Gunong Megang, *NIFS T 814* (BO, ♂, ♀). LINGGA ARCHIP. P. Sinkep: Djago, *bb 3943* (BO); Selewar, *bb 4067* (BO); Sungei Bajur, *bb 2072* (BO); Sungei Buluh, *bb 4081* (BO); Sungei Manggu, Muara Ketjil, *bb 3927* (BO); Sungei Pulak, *bb 4030* (BO); Tandjong Batang, *bb 4020* (BO); Tandjong Sembilang *bb 2047* (BO, L). **Borneo.** SOUTH AND SOUTH-EAST BORNEO. Tanah Bumbu, Kampong Baru, *bb 13374* (BO, ♂, ♀).

Artocarpus integer appears to be indigenous over a wide area in Malaysia, and all the collections cited above are recorded as having been made in primary or, less frequently, "old" forest. There is, however, some variation within the species, and in Malaya this was related by Corner in 1939 to the wild or cultivated status of the plant. Wild trees in Pahang and Johore were found to differ from the typical cultivated form of Malaya in the absence of odour from the syncarp and in the insipid fruiting perianths — both characters being in strong contrast to those of the cultivated Chempedak — and also in the lack of "autumn colours" in the withering leaves. Corner described these trees as *A. integer* var. *silvestris* and assigned to this entity all the specimens listed above from Malaya, with the exception of *Burkill & Haniff SFN 17030* and *Ridley 5028*. which were not cited. He also stated that, whereas the cultivated form was consistently pilose, the wild trees varied to glabrous. The only entirely glabrous collections that have been seen are the type of var. *silvestris* (*Corner SFN 32988*) from Johore, *Ridley 5028* from Singapore, and the specimens listed above under var. *silvestris* from the Lingga Archipelago. These glabrous collections differ further from the others cited under var. *silvestris* in the rather small, elliptic leaves, which often dry a distinctive, blackish brown. The remaining collections cannot be distinguished with certainty on herbarium characters from the range of variation exhibited by var. *integer*, as represented by both cultivated trees and the wild specimens listed above. Furthermore, most collections of *Artocarpus integer* from eastern Malaysia (Celebes to New Guinea) are rather sparsely pilose. In addition to the collections from Malaya and the Lingga Archipelago, two collections from Siam are listed under var. *silvestris* on geographical grounds, as well as one each from Sumatra and Borneo which are stated to have inodorous fruits, although it must be pointed out that in both the female heads on the herbarium sheets were at anthesis. It is likely that var. *silvestris*, as defined by the inodorous, insipid fruits, is more widely distributed in Malaysia than is here indicated and further study of *Artocarpus integer*, both in the wild and in cultivation, is needed to elucidate the variation which it shows.

The male inflorescences of var. *silvestris* were described by Corner from his collection *SFN 33205*. The heads are conical, 3–4.5 × 2–2.5 cm., with a shallowly and irregularly rugose surface, perianths 1–1.5 mm. long and stamens 1.7–2.4 mm. long. There is no appearance of abnormality in the inflorescences, which have been seen preserved in spirit, but in all other collections of both varieties with male heads these are more or less cylindric, with a smooth surface.

As is indicated in the nomenclatural discussion at the beginning of the treatment of the genus *Artocarpus* (p. 122, above), there is some doubt as to the sources of Loureiro's description of *Polyphema champeden* which is here cited in synonymy under *Artocarpus integer*. It has generally been assumed that Loureiro's account was based on the Chempedak, and his name is the basionym of two names that have been used widely for this species, *Artocarpus champeden* (Lour.) Stokes and the illegitimate *A. polyphema* (Lour.) Persoon.

Loureiro stated that *Polyphema champeden* occurred in both Indochina and Malaya — "Habitat in altis sylvis Cochinchinae. Colitur etiam, & Champedèn vocantur a populis Malaiis circa fretum Malaccense habitantibus." — and he gave as synonyms "Champidaca. Bont. Jav. l. 6. cap. 31. pag. 119. Saccus arboreus minor: Tsjampadaha. Rumph. Amb. l. 1. cap. 26. tab. 31." However, *Artocarpus integer*, the Chempedak, is absent from Indochina, according to Gagnepain (in Lecomte, Fl. Gen. Indoch. **5**: 734. 1928),[10] and this is confirmed by the material seen in herbaria, none of

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[10] The records of *Artocarpus polyphema* from Indochina given by Lanessan (Pl. Utiles Colon. Fr. 742. 1886) and by Crevost and Lemarié (Cat. Prod. Indoch. **1**: 266. 1917) were derived from Loureiro, although the second included information from another source, perhaps referring to varieties of the Jack (*A. heterophyllus*) that had been confused with the Chempedak.

which comes from farther north on the continent of Asia than peninsular Burma and Siam. Gagnepain also stated that Loureiro's plant did not correspond to any Indochinese species. Merrill accordingly concluded, in his commentary on the Flora Cochinchinensis (Trans. Am. Philos. Soc. **24**(2): 135. 1935), that the description had been based on plants that Loureiro had seen near Malacca. He further stated that there was a type specimen in the British Museum (Natural History).

The question of the source of Loureiro's description of *Polyphema champeden* was discussed in some detail by Corner in 1939 (Gard. Bull. Singapore **10**: 73). He stated that it had not been possible to find any type specimen and a further search in the herbarium of the British Museum (Natural History) has confirmed this. On the other hand, he showed that some phrases of Loureiro's description could be derived from Rumphius' account of *Saccus arboreus minor* and, since he felt certain that Loureiro had not seen any specimens from Malacca (see below), he concluded that the rest of the description must have been made from an undetermined Indochinese species, and that the name should be treated as a *mixtum compositum*. It is desirable that Loureiro's sources should be determined as exactly as possible, in order that the nomenclature of the species of *Artocarpus* from Indochina may have a secure basis.

In the course of this study it has been possible to examine the first reference cited under *Polyphema champeden*, which is to Piso's edition of Bontius' "Historiae Naturalis & Medicae Indiae Orientalis Libri Sex," published by the former in 1658 in his "De Indiae Utriusque Re Naturali et Medica." This shows that Loureiro also used the illustrations as a source for his description. As noted above under *Artocarpus communis* (p. 322), Bontius had apparently confused the Chempedak with the Breadfruit in his brief account of the latter and to this Piso added, under the erroneous name *Champidaca*, a drawing of a twig of *A. communis* bearing two syncarps and a pair of opposite, incised leaves below them. These are the source of Loureiro's puzzling "Spathae saepe repando-incisae." A re-examination of Rumphius' plate and description shows that rather more of Loureiro's account can be derived from them with some certainty than was assumed by Corner. An extension of his analysis of the description in the Flora Cochinchinensis is given below, with the various sources indicated, the Latin extracts in brackets from the "Herbarium Amboinense."

Sp. 2. POLYPHEMA CHAMPEDEN. α Cây Mít nai.

Differ. spec. Pol. foliis oblongis, integerrimis, pilosis, rugosis, sparsis [diagnosis derived from the following].

Hab., & notae. *Arbor supra mediocrem: trunco, & ramis rectis, ascendentibus.* Folia oblonga, sub-acuta, integerrima, venosa [Rumphius' illustration], rugosa, pilosa, superius obscuro-viridia, subtus flavescentia [rugosa & pilosa, . . . superius obscure virentia, inferius flava], sparsa, petiolis longis [Rumphius' illustration]. Spathae saepe repando-incisae [leaves of *Artocarpus communis* in Piso's illustration]. Amenta oblongo-ovato [? male head in Rumphius' illustration], scabra, flosculis propriis tecta, ut in Polyph. Jacâ. Baccae compositae vix pedem longae, 4 pollices latae, muricatae, flavo-virides [Fructus . . . pedem nempe modo longus, quatuor vel quinque crassus digitos . . . Exterior

> flavo-viridis ac pilosus cortex obsessus quoque est angulosis & acuminatis tuberculis seu verruculis]: baccis partialibus plurimis, *ovatis*, *sub-angulatis*, flavis, humescentibus, parvis [nuclei . . . usque ad octuagenarium & centesimum numerum, quae obducuntur quoque succosa ac mucosa carne instar nucleorum, uti *Nanca*, nuclei hi autem multo sunt minores, caro etiam multo magis flava est, ac succosior, gratique saporis] edulibus, nimiâ dulcedine, & intenso odore parum gratis [? information from Malacca — this character is not made clear in Rumphius' account]. Tota arbor humore lactescente scatet [Rumphius in various places]. Fructus pendent ex summo trunco, & ramis pedunculis [fructus crassissimis ex ramis excrescunt uti quoque ex summo trunco propriis ex pedunculis] longis [? Rumphius' illustration].

The words in italics, referring to the habit of the tree and the shape of the fruiting perianths, and perhaps also the description of the "ament" (probably the male head), were apparently derived from personal observation and may have been based on the Indochinese species which Loureiro confused with the Chempedak. The identity of this cannot now be determined: the only species which is at all similar is the Jack, *Artocarpus heterophyllus*, but the variety somewhat resembling the Chempedak is not recorded from Indochina. The Annamese vernacular name *cay mit nai* is applied to the two other members of *Artocarpus* subg. *Artocarpus* occurring in the area. The major part of the description, including the diagnostic characters, was based on the Chempedak. Thus it seems justifiable to treat *Polyphema champeden* as a synonym of *Artocarpus integer*, although it is recognized that the description of the "spathes," and perhaps those of some other characters, were derived from different species.

Stress was laid by Corner on Loureiro's description of the hairs on the leaves of *Polyphema champeden* as sparse, and this supports his contention that Loureiro had not seen the cultivated Chempedak in Malaya, which is characterized by markedly pilose twigs, stipules and peduncles. Loureiro, on the contrary, stated in his comparison of *Polyphema* with *Artocarpus* (in a note under the first of his two species, *Polyphema jaca*) that in *Polyphema* the peduncles were always glabrous. This may be accounted for by this part of his description of *Polyphema champeden* apparently having been taken from Rumphius, who was describing the more sparsely hairy eastern Malaysian form of the Chempedak and who showed, in his illustration, scattered hairs on only one twig and pair of stipules.

15. **Artocarpus heterophyllus** Lamarck, Encycl. Méth. **3**: 210. 1789, "*heterophylla*"; Corner, Gard. Bull. Singapore **10**: 56. 1939. Syntypes, Isle de France [Mauritius], *Commerson s.n.* (P-JU), *sine nom. et num.* [? Philippines, *Sonnerat*] (P-LA); lectotype, *Commerson s.n.* (P-JU).

Arbor pala, pomo ariena Pliny, Nat. Hist. lib. XII. cap. xii. circa A.D. 77, foliis exceptis.
Jaca Garcia da Orta, Coloquios, 110. 1563.
Iaca Acosta, Trata Drogas & Medicinas Indias, 264. 1576.
Iaacas Linschoten, Itinerario **1**: 73. 1596.
Palma fructu aculeato ex arboris trunco prodeunte Bauhin, Pinax, 511. 1623.

Jaaca Bontius, De Medicina Indorum, 52. 1642.
Tsjaka-maram Rheede, Hort. Ind. Malab. 3: 17. *t. 26–28.* 1682.
Jaca Indica Ray, Hist. Pl. 2: 1440. 1688.
Nanca Kamel in Ray, Hist. Pl. 3, App. 52. 1704.
Saccus arboreus major Rumph. Herb. Amb. 1: 104. *t. 30.* 1741.
Artocarpus philippensis Lamarck, Encycl. Méth. 3: 210. 1789. Holotype, *sine nom. et num.* [? Philippines, *Sonnerat*] (P-LA).
Artocarpus nanca Noronha, Verh. Batavia. Genoot. 5(5): 7. 1790, nomen nudum.
Polyphema jaca Lour. Fl. Cochinch. 546. 1790. Holotype, Cochinchina (cult.), *Loureiro s.n.* (BM).
Artocarpus integrifolia Linn. f. *β heterophylla* Persoon, Syn. Pl. 2: 531. 1807.
Artocarpus brasiliensis Gomez, Mem. Acad. Sci. Lisbon 3, Mem. dos Corresp. 84. 1812.
Arctocarpus maxima Blanco, Fl. Filip. 669. 1837.
Artocarpus integrifolia mult. auct. non Linn. f.
Artocarpus integer mult. auct. non (Thunb.) Merr., sensu Merr. Interpr. Rumph. Herb. Amb. 190. 1917.

Evergreen trees, height to 10(–15) m., not or scarcely buttressed, bark greyish brown, somewhat scaly. *Twigs* 2–6 mm. thick, finely rugose to smooth, glabrous; annulate stipular scars c. 0.5 mm. broad, not or slightly prominent; lenticels none or scattered. *Stipules* 1.5–8 cm. long, acute, ovate, appressed-puberulent or glabrous. *Leaves* 5–25 × 3.5–12 cm., obovate-elliptic to elliptic, varying subrotund, obtuse to short-acuminate, base cuneate, decurrent, glabrous, margin entire; juvenile leaves elongate or with 1–2 pairs lateral lobes, slightly scabrid; main veins only prominent beneath or intercostals slightly so; lateral veins 6–10 pairs, curved; intercostals c. 10–14, parallel, oblique, nearly perpendicular to the midrib; dark green with pale main veins, drying greenish or pale brown, venation often straw-coloured; hypodermis absent; gland-hairs immersed, heads globose, c. 6-celled; petiole 8–25 mm. long.

Inflorescences solitary in leaf-axils; cauliflorous and ramiflorous, flowering on short leafy shoots; male heads sometimes borne on the ultimate twigs. *At anthesis*: *male head* 25–70 × 8–28 mm., narrowly clavate, rarely ellipsoid, smooth, covered by flowers, a few sterile, the perianths solid, not elongate; fertile flowers with perianths tubular, 1–1.5 mm. long, bilobed above, minutely pubescent; stamen 1.5–2 mm. long, filament cylindric, anther-cells ellipsoid, 0.3 mm. long; peduncle 12–55 × 1.5–2 mm., glabrous, expanded into a narrow flange or annulus 1.5–2.5 mm. wide at the base of the head; *female head* with simple, spathulate styles exserted to 1.5 mm. *Syncarp* 30–100 × 25–50 cm., cylindric or somewhat clavate, yellow, drying brown, with a sickly, sweet odour (like ripe bananas), covered by closely set, firm, tapering, obtuse, puberulent to minutely hispid processes, 4–10 × 4 mm.; wall c. 10 mm. thick; fruiting perianths numerous, proximal free region yellow, markedly fleshy, firm, with a thickened stalk, remaining attached to wall and core, "seeds" (separated horny endocarps enclosed by subgelatinous exocarps 1 mm. thick) oblong-ellipsoid, c. 30 × 15–20 mm., style two-thirds the distance up the ventral face, testa thin, embryo with the radicle ventral, superficial, and the cotyledons almost transverse to the median plane of the ovary, very unequal, the upper cotyledon one-third to one-half the length of the lower; peduncle c. 50–100 × 8–10 mm., glabrous, expanded into a flange or annulus to 5 mm. wide at the base of the head (sometimes obscure at maturity).

VERNACULAR NAMES. (1) General: Jack, Jak, Jaquier, Jaca, etc. (2) India: *Panasa* (Sanskrit, Uriya, Telugu), peninsular India; *Phanas* (Marathi), Bombay; *Kanthal* (Hindi), *Kanthar* (Santali), northeastern India; *Halsu*, *Heb-halsu* (Kanarese), west coast; *Pila*, *Pilavu* (Malayalim, Telugu), Malabar and southern peninsular India; *Chakki*, general for the fruit; *Cos* (Sinhalese), Ceylon. (3) Southeastern Asia: *Peignai,* Burma; *Khanum*, Siam; *Knor prey*, Indochina; *Po-lo-mih*, *Po-lo-mat*, *Po-lo-shue*, China. (4) Malaysia: *Nangka*, as *Nongko* in Java, sometimes as *Langka* in the Philippines.

USES: The sweet, fleshy perianths enclosing the seeds are eaten, and the latter are also eaten roasted or boiled; the wood is highly valued for cabinet work and general house-building purposes; wood chips are used to provide a yellow dye.

DISTRIBUTION: Possibly indigenous in evergreen forest from 1500 to 4000 ft. on the Western Ghats of India; becoming naturalized sparingly in evergreen and semi-evergreen forest and tolerant of a dry season; cultivated throughout the tropics.

It is unlikely that the region within which *Artocarpus heterophyllus* was indigenous can now be determined, but it seems most likely that this was in India, probably along the Western Ghats. Wight (Ic. Ind. Or. **2**: *t. 678.* 1843) made the general comment that the Jack appeared to be an indigenous plant in India. Beddome (For. Man. 219. 1873) recorded it from western mountain forests, and Gamble (Man. Ind. Timb. ed. 2. 653. 1902) and Talbot (For. Fl. Bombay **2**: 527. 1911) stated definitely that they had seen it growing wild in rain forest on the Western Ghats, remote from human habitations. No collections annotated as having been made from such plants have been seen, but this is not surprising, since the species would be universally familiar.

The Jack may also be found apparently wild in evergreen and semi-evergreen forest in Assam and Burma, according to Kanjilal *et al.* (Fl. Assam **4**: 268. 1940) and Brandis (Ind. Trees, 611. 1906), respectively. However, these authors state that it is always either on the site of deserted villages, or an escape from cultivation. In Ceylon, where the Jack is extremely common, it has always been regarded as an introduced plant.

The Jack has long been known from India. It is probably the plant referred to in the following passage from Theophrastus, dating from about 300 B.C.: "There is also another tree which is very large and has wonderfully sweet and large fruit; it is used for food by the sages of India who wear no clothes" (Enquiry into Plants IV, iv. 5, transl. Hort. 315. 1916). This was incorporated by Pliny (circa A.D. 77) into a longer account:

"Maiore alia pomo et suavititate praecellentiore, quo sapientes Indorum vivunt. folium alas avium imitatur longitudine trium cubitorum, latitudine duum. fructum cortice emittit admirabilem suci dulcedine, ut uno quaternos satiet. arbori nomen palae, pomo arienae. plurima est in Sydracis, expeditionem Alexandri termino" (Nat. Hist. XII. xii, Loeb ed. **4**: 16. 1945). Yule and Burnell (Hobson-Jobson, Glossary of Anglo-Indian Words and Phrases, 335. 1886, ed. 2. revised Crooke, 440. 1903), who identified these passages as referring to the Jack, pointed out that Pliny's second sentence was derived (though apparently indirectly) from the next paragraph in Theophrastus, which could refer to the banana: "There is another tree whose leaf is oblong in shape like the feathers of the ostrich; this they fasten on to their helmets, and it is about two cubits long." (Hort, l.c.). This sentence caused the entire description to be applied to the banana by Bauhin (Pinax, 507. 1623) and by many later authors. The derivation of Pliny's names is uncertain, but Yule and Burnell suggested that *pala* might be the Sanskrit *phala* (fruit), while *ariena* was possibly *hiranya* (golden). The Sanskrit name for the Jack is *panasa*. The name *chakki* for the fruit is widespread in India, and it is from this that the European name is taken. Its source is doubtful, although it has been suggested that it may have come from the Malayalim word *chakka* (round).

In Malaysia, although the Jack is widely cultivated, it rarely occurs spontaneously, and then only in secondary vegetation. It thus gives the appearance of being an introduced plant and has always been regarded as such, although the introduction must have taken place at a very early date. It is generally known by an indigenous name, *nangka*, the origin of which is unknown. Ochse and Bakhuisen van den Brink (Fr. & Fr. Cult. Dutch E. Ind. 69. 1931) and Heyne (Nutt. Pl. Indonesië, ed. 3. **1**: 560. 1950) record the Sanskrit name and variants from Sumatra and Celebes.

In southeastern Asia, the Jack is recorded only in cultivation. According to Lacouperie (Babylon. & Orient. Rec. **7**: 169. 1894) it was mentioned from Indochina under the name *pa-na-so* in a Chinese account of Cambodia in the sixth century. He stated that it was first recorded from China in the herbal "Pen-ts'ao Kang Mu," which was compiled between 1552 and 1578, and he derived the Chinese names *po-lo-mih* and *po-lo-mat* from the Sanskrit *pala*, stating that they meant "honey *pala*."

The Jack is now cultivated through most of the tropics, though it is generally of less importance than the Breadfruit, *Artocarpus communis*. In the New World it was brought to Brazil, according to Tavares (Broteria, Ser. Vulg. Sci. **13**: 24. 1915), by the Portuguese in the middle of the seventeenth century. In 1782, plants taken from a French vessel destined for Martinique, but captured by Admiral Rodney, were introduced into Jamaica (Howard, Scientific American **188**: 88. 1953).

In India and Malaysia two main forms of the Jack are found, although there is apparently variation within each. In the more esteemed form the ripe fruit is firm, and the wall remains attached to the fruiting perianths and the core. The flesh of the fruiting perianths is firm and the seeds are enclosed by a horny endocarp. This is the form which was studied by Corner and which has been described above. In India it is known as *varaka* or *barca*, meaning best, and in Malaysia it is called *nangka bilulang*. The second form, which is called *gerissal*, *vela* or *papa* in India and *nangka bubor* in Malaysia, is stated to have a soft, "baggy" fruit when ripe, as in the Chempedak. It appears to have other characteristics of *Artocarpus integer*, since Corner recorded that he had been informed by C. X. Furtado that, in fruits of this form from near Goa, the pulp surrounding the seeds was soft and the testa [pericarp] thin. Rumphius also described the soft pulp of *nangka bubor* and stated that the fruit had a stronger odour. These resemblances led Corner to suggest, no specimens being available, that it might be a glabrous variety of the Chempedak. However, all herbarium material seen from India has the decurrent leaf lamina and the annulus of the Jack. These characters are also shown by two collections, *Meijer 7117* (L, ♀) and *7142* (L, ♂), from Padang Pandjang, near Pajakumbuh, West Coast, Sumatra, which have the vernacular name *tjempedak bubur* and thus may represent this form. The female inflorescence is at anthesis and has the ligulate style found in *A. heterophyllus*. Nevertheless, the similarities between this form and the Chempedak are suggestive of some hybridization between the two species in the past. No genetical data are available beyond the record of a diploid number of 56, apparently the basic number for the genus, in *A. heterophyllus* (Subba Rao, Half Yearly Jour. Mysore Univ. Sect. B. Sci. **1**: 63. 1940). In Ceylon there is a third well-marked variety with small, round fruits called *kuru*.

Mendiola (Philip. Agric. **28**: 789. 1940) reported possible hybridization between the Jack and the Chempedak in the Philippines. He stated that plants raised from the seed of a few introduced Chempedak trees growing near *nangka* (Jack) trees produced fruits with mainly *nangka* characteristics, and that seedlings grown from these fruits were intermediate between those of the two species in several characters. This is the only report of such hybridization, but it is of interest in the light of the previous paragraph.

Series **Angusticarpi** Jarrett, ser. nov.

Folia simplicia, adulta integra, juvenilia praelonga vel trilobata, raro pinnatifida; hypodermis absens; glandulae semi-immersae, capitibus depresso-globosis, c. 6-cellis. *Inflorescentiae* ramulis latae. *Capitula mascula* superficie plana, floribus fertilibus vel aliquibus sterilibus, solidis praelongisque obtecta, bracteis absentibus. *Syncarpia* processibus appresse puberulentibus, aequalibus vel paucis solidis praelongisque obtecta, bracteis absentibus; semina testis pergamentaceis, rubris, pericarpiis pergamentaceis (? maturatis induratis), perianthiis tenuisque inclusa.

TYPE SPECIES: *Artocarpus teysmannii* Miq.

The characters of the pericarps are taken from *Artocarpus teysmannii*, and from the collections probably representing a new species which are briefly described under *Artocarpus lowii*. The differences between the two species at present recognized in the series are also noted under *A. lowii.*

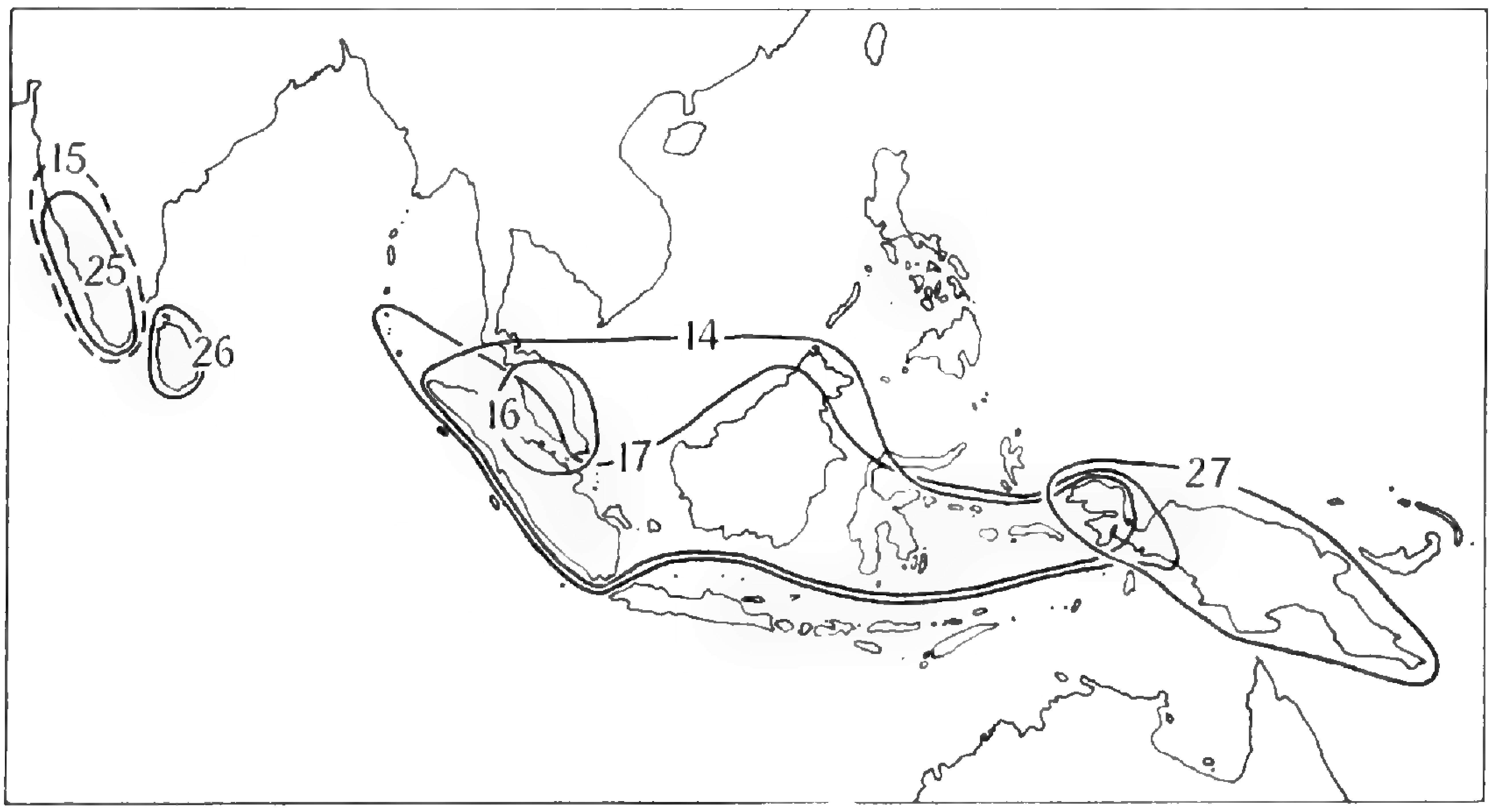

FIG. 14. Distribution of the species of series CAULIFLORI and ANGUSTICARPI and of the anomalous species. 14, *Artocarpus integer*; 15, *A. heterophyllus*, possible distribution as a wild plant; 16, *A. lowii*; 17, *A. teysmannii*; 25, *A. hirsutus*; 26, *A. nobilis*; 27, *A. sepicanus.*

16. **Artocarpus lowii** King in Hook. f. Fl. Brit. Ind. **5**: 542. 1888, et in Ann. Bot. Gard. Calcutta **2**: 10. *t. 7A.* 1889, pro maxima parte, flosculis bracteisque masculis exclusis; Ridley, Fl. Malay Penin. **3**: 353. 1924; Burkill, Dict. 257. 1935; Corner, Gard. Bull. Singapore **10**: 283. 1939, Wayside Trees, 656. 1940. Holotype, Perak, *King 7737* (CAL, not seen); isotypes (BM, K, SING).

Evergreen trees, height to 25 m., bark grey, smooth. *Twigs* 3–6 mm. thick, finely and shallowly rugose, appressed-puberulent; annulate stipular scars c. 0.5 mm. broad, prominent; lenticels few or absent. *Stipules* 2–12 cm. long, lanceolate, attenuate, appressed-puberulent. *Leaves* 11–36 × 4–13 cm., elliptic or narrowly elliptic, acute to short-acuminate, base cuneate, margin entire or shallowly crenate; juvenile leaves to 55 cm. long, narrowly elliptic, with an acumen to 2.5 cm. long, entire or trilobed; main veins prominent beneath, intercostals slightly so; glabrous above, appressed-puberulent on main veins beneath; lateral veins 11–16 pairs, straight; intercostals parallel; dark green, drying pale to dark red-brown above, lighter beneath; hypodermis absent; gland-hairs half immersed, heads depressed-globose, c. 6-celled; petiole 20–35 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 20–25 × 5 mm., cylindric, smooth, covered by flowers; perianths tubular, 0.8 mm. long, shortly bilobed above, minutely appressed-pubescent; stamen 1.5 mm. long, filament slender, cylindric, anther-cells ellipsoid, 0.2 mm. long; peduncle c. 40 × 1.5 mm., appressed-puberulent, also with subpatent, recurved hairs hooked at the tips; *female head* with simple styles exserted to 0.5 mm. *Syncarp* to 6.5 × 3.5 cm., cylindric, yellow, drying brown, covered by closely set, fleshy, conical, appressed-puberulent processes c. 1.5 × 2 mm., or their apices becoming depressed and the surface hence areolate; wall c. 2 mm. thick; fruiting perianths numerous, proximal free region thin-walled, "seeds" (pericarps) ellipsoid, 10 × 8 mm., style subbasal, testa and embryo . . . ; core c. 5 mm. across; peduncle 35–55 × 2.5 mm., indumentum as male.

VERNACULAR NAME: *Miku*, Malaya. USES: the sap, which is apparently unique in this genus in being greasy, is used as an ointment.

DISTRIBUTION: In lowland evergreen forest, Malaya, Sumatra (East Coast).

Malaya. PERAK. Larut, Gunong Pondok, *King 7737*, June 1885 (BM, K, SING, ♀). PAHANG. Kuantan, *Munnick s.n.*, Aug. 1914 (SING); Putat reserve, *Alwi CF 10711* (SING); Raub, *Burkill & Haniff SFN 16649* (SING, ♀). SELANGOR. Kuala Lumpur, *Ridley 4708* (SING); Kuala Lumpur, Public Gardens, *Corner SFN 30775* (K, SING, ♀), *33542* (SING), *Foxworthy CF 4600* (K, ♀), *Hamid & Ja'amat CF 9982* (SING, ♀), *Omar CF 9512* (K, ♀), *Strugnell CF 12612* (SING); Kuala Lumpur, Weld Hills Res., *Hamid CF 986* (SING), *4966* (K, SING, ♀). NEGRI SEMBILAN. Tampin, *Nur 1315* (K, SING, ♀). MALACCA. *Maingay 1477* (K, ♀); Brisu, *Derry 30* (K, SING, ♀); near Durian Tunggal, *Corner SFN 30752* (SING); Sedanan, *Goodenough 1412* (P, SING); Selandar forest near Tebong, *Burkill SFN 534* (SING); Tebong, *Burkill SFN 1336* (SING). SINGAPORE. Bukit Timah, *Forbes s.n.*, Mar. 1893 (BM, ♀), *Kiah SFN 34964* (A, BO, K, L, P, SING), *Ridley 4719* (SING, ♀), *6810b* (SING); Chan Chu Kang, *Ridley 6810a* (SING), *Ridley s.n.*, June 1895 (BO, ♂); Garden Jungle, *Ridley s.n.*, 1907 (BO, ♀). **Sumatra.** EAST COAST. Huta Padang estate, near Kisarin, *Krukoff 322* (BM, BO). **Cultivated.** SINGAPORE. Hort. Bot., *Burkill s.n.*, June 1924 (SING), *Nur 1676* (SING), *Ridley 6810* (BO, SING, ♀).

King accidentally transposed the descriptions and drawings of the details of the male flowers in *Artocarpus lowii* and *A. teysmannii* (called by him *A. peduncularis* Kurz). The "ligulate scales" which he described for *A. lowii* are the sterile flowers of *A. teysmannii.*

In 1939, Corner pointed out that *Artocarpus lowii* and *A. teysmannii* (as *A. peduncularis*) differed in the elliptic versus ovate outline of the leaves and in the larger number of lateral veins present in the former. In addition, *A. teysmannii* has solid sterile flowers in both male and female inflorescences, stamens with larger anthers and broader filaments, and longer pubescence on the stipules. The appearance of the hooked hairs found on the peduncles in *A. lowii* is distinctive. The single collection of *A. lowii* cited from Sumatra is sterile and has no stipules, but it matches those from Malaya closely, having elliptic leaves with 12–17 pairs of lateral veins.

The following four collections probably represent a new species closely allied to, but distinct from, *Artocarpus lowii.* However, they are not being described as such until more adequate material, including the male inflorescence, is available. Three of the collections, all bearing submature syncarps, are from British North Borneo: *Clemens 27131*, Tenompok trail, Mt. Kinabalu, 5000 ft. (A, BO, L, SING, ♀); *Carr SFN 27141*, Tenompok-Dallas path, Mt. Kinabalu, 4200 ft. (SING, ♀); *Wood SAN 16994*, Kandasan-Tenompok path, 12 miles w. of Ranau, 4750 ft. (L, ♀). The fourth collection, which is from Indochina, bears immature inflorescences with malformed flowers: *Poilane 35982*, near Dak Bro, Ngok San, Kontum prov., Annam, 1500 m. (P). The discontinuity in distribution is apparently similar to that shown by *Artocarpus melinoxylus*. The specimens match each other closely in their vegetative characters and in the appearance of the syncarps. The leaves are rather small, 9–18 × 3–5.5 cm., and elliptic to oblong-elliptic in outline. They are narrower than in *A. lowii* and have more widely spreading lateral veins (12–17 pairs). The leaf anatomy agrees well with *A. lowii*, since the glands are immersed, with depressed-globose, 6–8-celled heads, and there is no hypodermis. As in this species the shoots are glabrous except for the appressed-puberulent stipules and young twigs, but the peduncles lack the characteristic hooked hairs. The submature syncarps are similar to those of *A. lowii*, being cylindric, to 5 × 3 cm., and covered by low, conical processes, c. 1 × 2 mm., with a peduncle measuring up to 25 × 3 mm. (and also, in *Clemens 27131*, simple styles exserted to 1 mm.). Partly matured ovaries in *Wood SAN 16994* are subglobose, with the style one-third the distance up the ventral face, the wall becoming indurated, and a reddish, pergamentaceous testa.

17. **Artocarpus teysmannii** Miq. Fl. Ind. Bat. Suppl. 418. 1861, "*Teysmanni*"; Boerl. Handl. Fl. Ned. Ind. **3**: 333, 371. 1900; Heyne, Nutt. Pl. Indonesië ed. 3. 1: 565. 1950. Holotype, Sumatra, *Teysmann HB 4387* (U); isotypes (BO, L).

Artocarpus peduncularis Kurz, Jour. Bot. **13**: 331. 1875; King in Hook. f. Fl. Brit. Ind. **5**: 541. 1888, et in Ann. Bot. Gard. Calcutta **2**: 10, *t. 6*. 1889, pro maxima parte, flosculis bracteisque masculis exclusis; Becc. For. Borneo, 632. 1902; Ridley, Fl. Malay Penin. **3**: 353. 1924; Burkill, Dict. 258. 1935; Corner, Gard. Bull. Singapore **10**: 283. 1939. Holotype, Nicobar Islands, *Kurz s.n.* (CAL); ? isotype (K, numbered *Kurz 26906*).

Evergreen trees, height to 45 m. *Twigs* 2.5–5 mm. thick, rugose, appressed-puberulent; annulate stipular scars c. 0.5 mm. broad, prominent; lenticels absent. *Stipules* 2–9 cm. long, lanceolate, acute or attenuate, appressed-pubescent, hairs yellow. *Leaves* 5–25 × 3–13 cm., ovate to ovate-elliptic, obtuse to acute or short-acuminate, base rounded to broadly cuneate, margin entire or shallowly crenate; juvenile leaves to 60 × 25 cm., elliptic, base cuneate, rarely pinnatifid; main veins prominent beneath; glabrous or nearly so above, appressed-puberulent on main veins beneath; lateral veins 6–12 pairs (–18 in juvenile leaves), straight; intercostals parallel; dark green, drying pale brown when mature, dark brown when immature; hypodermis absent; gland-hairs half immersed, heads depressed-globose, c. 6-celled; petiole 10–35 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 35–75 × 5–7(–9) mm., narrowly cylindric, smooth, covered by flowers, many sterile, the perianths solid, filiform, projecting to 1 mm. from the surface (total length to 2.4 mm.); fertile flowers with perianths tubular, 1.4 mm. long, bilobed above, minutely pubescent; stamen 1.9 mm. long, filament broad, abruptly contracted above, anther-cells oblong, 0.5 mm. long; peduncle 20–80 × 3 mm., appressed-puberulent; *female head* with simple styles exserted to 1.5 mm. *Syncarp* to 8.5 × 2.2 cm., cylindric, yellow, nigrescent on drying, covered by closely set, fleshy, conical, appressed-puberulent processes, mostly perforate, c. 1.5 × 1.5 mm., a few solid, attenuate, to 4 mm. long; wall c. 1 mm. thick; fruiting perianths numerous, proximal free region thin-walled, "seeds" (pergamentaceous pericarps, ? submature) ellipsoid, 7 × 6 mm., style sub-basal, testa pergamentaceous, embryo (shrunken) with the radicle ventral and the cotyledons transverse to the median plane of the ovary, the upper cotyledon one-third the length of the lower; core c. 7 mm. across; peduncle 30–100 × 4 mm., appressed-puberulent.

Vernacular names: *Chempedak ayer* (Malay), Malaya, Sumatra, Borneo; *Sali saling, Tipulu,* Celebes. Uses: Heyne (1950) states that the timber is used for boats, and the latex as bird-lime.

Distribution: In evergreen forest to 1000 ft., often on swampy ground, Nicobar Islands, Malaya, Sumatra, Borneo, Celebes, Moluccas (Sula Islands), western New Guinea.

Nicobar Islands. Kamorta, *Kurz s.n.*, Feb. 1875 (CAL, ♂, ♀), [? =] *Kurz 26906* (K, ♂, ♀). **Malaya.** Perak. Ulu Bubong, *King 9530* (BM, CAL, K, L, ♀). Selangor. Sungai Tinggi, Kuala Selangor, *Nur SFN 34150* (A, SING, ♂), *Symington CF 44051* (SING). **Sumatra.** Atjeh. Singkel, Djangkar-kaling, *bb 10253* (BO); Singkel, Kampung Pamuka, *bb 3162* (BO, L, ♀). East Coast. Karolanden, Lao Solu, *bb 9295* (BO, ♀); Labuan Batu, Kola Napong, *bb 7382* (BO, ♀); Labuan Batu, Simatakasi, *bb 9761* (BO); Langkat, Pantei Tjermin, *bb 9123* (BO, ♀). Indragiri. P. Gelang, *bb 29160* (A, BO, L, SING). Djambi. Simpang, *bb 12868* (BO). Palembang. Lematang Ilir, Gunong Megang, *NIFS T 887* (BO, L, ♀); Musi Ilir, Petaling, *bb 8087* (BO). Lampongs. Kebang, *Teysmann HB 4387* (BO, L, U, ♀).

Borneo. Sarawak. *Beccari PB 3937* (K, ♂); Baram, *Lumbor S 1252* (SING). West Borneo. Kapuas, *Teysmann HB 7895* (BO, L); Sukadana, Kualan, *bb 6295* (BO, L, ♀). South and southeast Borneo. Bandjermasin, *Motley 880* (K, ♂, ♀); Beneden Dajak, *Meegan VIII* (BO); Beneden Dajak, Pahandut, *bb 5551* (BO, ♂, ♀); Pasir, S. Ongka, *bb 25639* (A, BO, L, SING); Sampit, Kandan, *bb 2653* (BO, ♂, ♀); Sampit, Tampudan, *bb 2157* (BO); Sungei Kahajan, *bb 2094* (BO, L). East and northeast Borneo. W. Kutei, near Lahum, *Endert 1879* (K, L).

Celebes. Gulf of Boni, *Heyne 2856* (BO, L, ♀). Central Celebes. Luwu, *Heyne 2551* (BO, ♂); Malili, Angkona, *bb 32359* (BO, L); Malili, Labose, *bb 11423* (BO, ♂); Malili, Usu, *bb 32607* (BO, L, ♀), *NIFS Cel./III–69 no. 131* (BO, L, ♂), *69 no. 186* (BO, ♀), *NIFS Cel./III–85* (BO, ♀), *86* (BO, ♂, ♀), *87* (A, BO, L), *88* (A, BO, L, ♀); Palopo, Baramamase, *bb 22983* (BO); Palu, Tomado, near Lindumeer, *bb 28240* (A, BO, L, SING, ♂, ♀); Poso, Kalora, *bb 28738* (A, BO, L); Tapalang, *Noerkas 443, 456* (BO, L). Southwest peninsula. Kp. Palima, *Noerkas 270* (BO, L). Southeast peninsula. Kolaka, Anaiwoi, *bb*

32545 (BO, L). P. MUNA. Raha, Wasalangka, *bb 21110* (BO, L), *21121* (BO). P. BUTON. Near Wakallea, *bb 4988* (BO, L, U, ♀). **Moluccas.** SULA ISLANDS. Mangoli, Tjapalulu, *bb 29908* (BO, L).

New Guinea. VOGELKOP. Manokwari, Momi, *Kostermans 347* (BO, L, SING); Ransiki, *Koster BW 1204* (L); Sorong, near Remu, *Pleyte 729* (A, K, L, SING, ♀); Wermenu, *bb 22524* (BO, L, ♀). DUTCH SOUTH NEW GUINEA. Sungei Aëndua, near Uta, *Aet 490* (K, L), [? =] *bb 32910* (L). SALAWATI. Kaloal, *Koster BW 1340, 1470* (L). **Cultivated.** JAVA. Bogor, Hort. Bot. *VIII B 52* (BO, L, ♂, ♀).

The appearance of the syncarp at maturity in *Artocarpus teysmannii* is somewhat variable, depending on the conspicuousness of the elongate solid perianths. In some collections these are not distinguishable, and this is so in the Kurz collection from the Nicobars which is the type of his *Artocarpus peduncularis*. However, the specimen has the ovate leaves characteristic of *A. teysmannii* and the syncarp peduncle measures 9–10 cm.; the male inflorescence is also typical of the species.

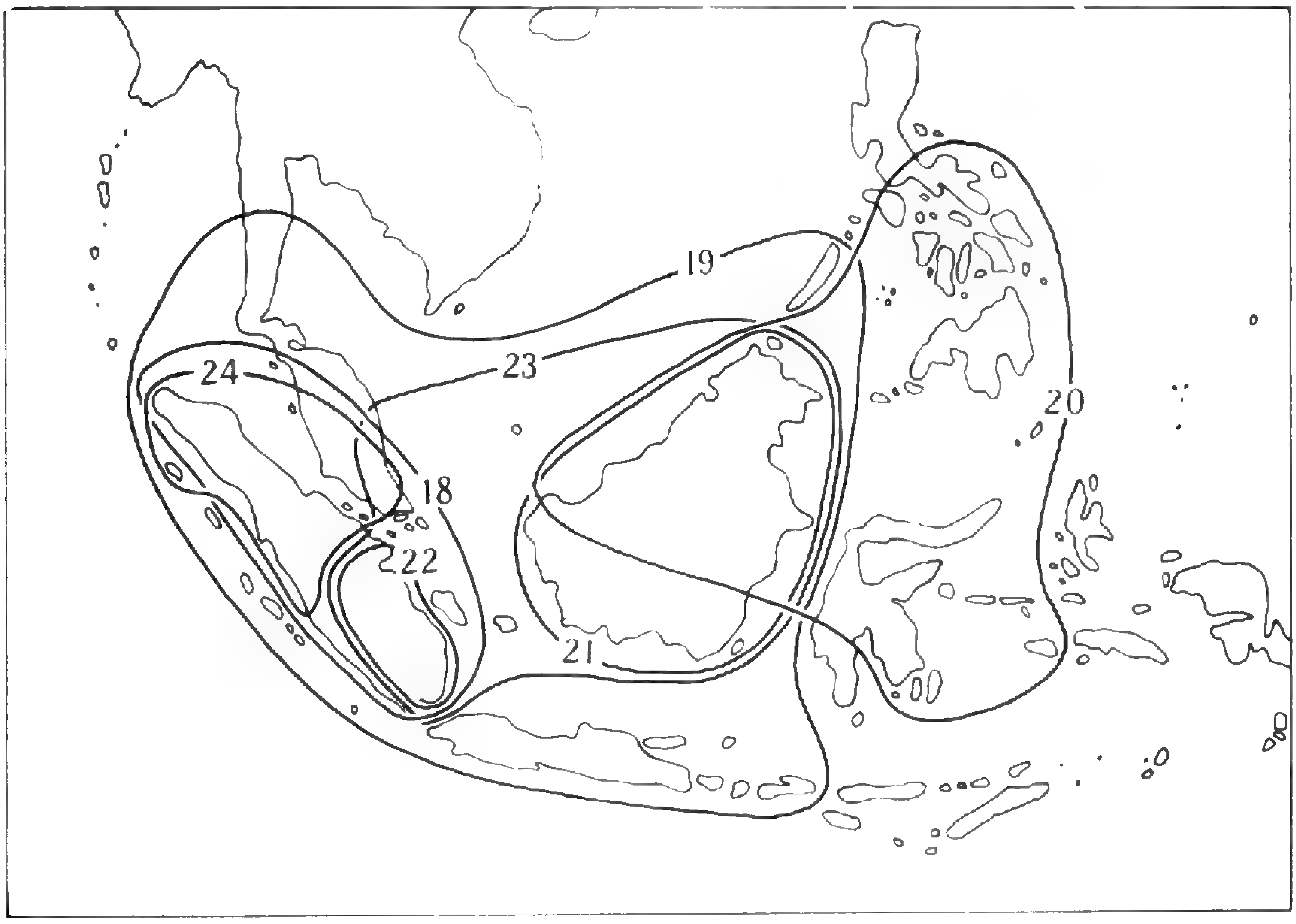

FIG. 15. Distribution of the species of series RUGOSI. 18, *A. scortechinii*; 19, *A. elasticus*; 20, *A. sericicarpus*; 21, *A. tamaran*; 22, *A. sumatranus*; 23, *A. kemando*; 24, *A. maingayi*.

Series **Rugosi** Jarrett, ser. nov.

Folia simplicia, adulta integra, juvenilia pinnatifida; hypodermis perfecta, strato unico ad triplico cellis isodiametricis composita; glandulae superficiales vel subimmersae, capitibus depresso-globosis, 4-cellis. *Inflorescentiae* ramulis latae. *Capitula mascula* superficie rugosa (sulcata ad tuberculata), floribus fertilibus obtecta, bracteis absentibus. *Syncarpia* processibus pubescentibus vel hispidis, aequalibus (in *A. kemando* obsolescentibus) vel nonnullis solidis praelongisque obtecta, bracteis sparsis vel absentibus; semina testis carnosis, rubri-purpureis, pericarpiis corneis perianthiisque tenuis vel subcarnosis inclusa.

TYPE SPECIES: *Artocarpus elasticus* Blume.

It has been possible to examine the internal structure of the mature syncarp in only three out of the seven species recognized in the series (*Artocarpus elasticus*, *A. sericicarpus* and *A. kemando*), but in these the appearance of the thin, horny pericarp and the rather thick, fleshy, reddish-purple testa is distinctive. The embryo is consistently somewhat curved, but the orientation is variable. In *Artocarpus sericicarpus* the long axis is vertical, with the radicle about halfway down the ventral face. In *Artocarpus elasticus* and *A. kemando*, on the other hand, the long axis is horizontal and the embryo is subreniform, with the lower face concave over the sub-basal hilum and the radicle also sub-basal.

As is indicated above in the key to the species, the members of this series may be divided into two groups on the basis of the size of their parts. The first four species have more or less massive shoots and, in all except one, the processes on the syncarp are markedly dimorphic. They are readily separable from each other on the size and indumentum of these processes, on the surface of the male head, and on the texture, indumentum and number of lateral veins of the leaves. The remaining three species are rather slenderly constructed, and the syncarp has short or obsolescent processes, all similar to each other. These species are more closely related to each other, but they can be distinguished by the surface of the syncarp, and usually also by minor characters of the peduncles and leaves, which are commented on in the notes on *Artocarpus sumatranus* and *A. kemando*.

18. **Artocarpus scortechinii** King in Hook. f. Fl. Brit. Ind. **5**: 542. 1888, et in Ann. Bot. Gard. Calcutta **2**: 12. *t. 9.* 1889; Ridley, Fl. Malay Penin. **3**: 355. 1924; Corner, Wayside Trees, 657. 1940. Syntypes, Perak, *King 7792* (CAL, not seen; duplicates examined, BM, K, SING), *Scortechini s.n.* (CAL, not seen).

Evergreen trees, height to 35 m. *Twigs* 8–15 mm. thick, rugose, minutely appressed-hispid; annulate stipular scars c. 1 mm. broad, slightly prominent; lenticels in an irregular ring below scar. *Stipules* 5–17 cm. long, broadly lanceolate, acute, subappressed-pubescent, hairs yellow to rufous. *Leaves* 15–40 × 8–20 cm., elliptic to ovate-elliptic, short-acuminate, base rounded to broadly cuneate, margin entire or shallowly crenate; juvenile leaves pinnatifid; main veins and intercostals prominent beneath, lower surface usually bullate between the meshes of the reticulum; glabrous or nearly so above, subappressed pubescent or hispid-pubescent beneath; lateral veins 12–14 pairs, straight; intercostals parallel; bright green, drying pale or reddish brown; hypodermis of 1 or 2 cell-layers present, complete, cells isodiametric in surface view; gland-hairs slightly immersed, heads depressed-globose, 4-celled; petiole 25–50 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 65–105 × 10 mm., cylindric, the surface sulcate, with long, shallow, sometimes few grooves, covered by flowers; perianths tubular, 0.6 mm. long, bilobed above, minutely pubescent; stamen 0.9 mm. long, filament cylindric, anther-cells oblong, 0.25 mm. long; peduncle 35–50 × 3 mm., shortly appressed-pubescent; *female head* with bifid styles exserted to 0.5 mm. *Syncarp* to 8.5 × 5.5 cm. (to 13 cm. long, fide King, 1889), cylindric, yellow, drying brown, covered by closely set, fleshy, cylindric, obtuse or truncate, shortly hispid-pubescent processes, mostly c. 3 × 2 mm., a few sometimes to 4 mm. long; wall c. 3 mm. thick; "seeds" (pericarps) numerous, ellipsoid, 8 × 7 mm.; core c. 12 mm. across; peduncle 55–95 × 5 mm., short-pubescent.

VERNACULAR NAME: *Terap* (Malay), Malaya, Sumatra.

DISTRIBUTION: In evergreen forest to 2500 ft., Malaya, Sumatra, Lingga Archipelago.

Malaya. PERAK. Batang Padang District, Turu, *King 7792*, July 1883 (BM, K, SING, ♀). PAHANG. Kuala Lipis, *Burkill & Haniff SFN 15680* (K, SING). SELANGOR. Kuala Lumpur, Public Gardens, *Ahmad CF 4990* (K, ♀). NEGRI SEMBILAN. Bukit Sutu, *Alvins 1896* (SING, ♀). MALACCA. *Griffith 4660* (K, ♂, ♀). PENANG. Government Hill, *Burkill 2892* (K, SING, ♂, ♀), *Curtis s.n.* (SING). SINGAPORE. Kranji, *Goodenough 3379* (CAL, SING, ♀); Tangka, *Ridley 11366* (K, SING, ♀); behind Tyersall, *Hullett s.n.*, 1893 (SING, ♀).

Sumatra. ATJEH. Wassenar, *Batten-Pooll s.n.*, July 1939 (SING). TAPANULI. Lapian, Sibolga, *bb 3801* (BO). EAST COAST. Boven Lankat, *bb 9149* (BO, ♂); Ulu Tesso, *bb 27661* (BO, L); Sigati River, *Koorders 10452* (BO). INDRAGIRI. Belimbing, *bb 28499* (BO, L); Danau Mengkuang, *bb 27520* (BO); Muara Serangge, *bb 30009* (BO, L, SING), *30072* (A, BO, L). PALEMBANG. *Castillo & Valderrama 4* (A, K); Banjuasin and Kubustreken, *Grashoff 824* (BO, L); Banjuasin, Bajunglintjir, *NIFS E 787* (BO, L, ♂, ♀); Lematang Ilir, Gunong Megang, *NIFS T 811* (BO, L, ♀); Lematang Ilir, Semangus Reserve, *bb 31677* (BO, L). LAMPONGS. *Teysmann s.n.* (BO). LINGGA ARCHIP. Manggu, *bb 5616* (BO, L, ♂, ♀). **Cultivated.** MALAYA. Singapore, Hort. Bot., *Corner s.n.*, Feb. 1937 (SING, ♀), *Nur 265* (SING, ♀), *Ridley 5690* (BM, SING, ♀), *6431* (CAL, K, SING, ♂), *6543* (CAL, SING, ♂).

Artocarpus scortechinii is smaller in all its parts than *A. elasticus*, and may usually be distinguished from the latter, when sterile, by the upper surface of the leaf, which is smooth or nearly so. A few of the processes on the syncarp may be slightly elongate, but all are perforate and have styles exserted at anthesis.

One collection seen from the Kanching Forest Reserve, Selangor, Malaya, *Nur SFN 34427* (A, SING, ♀), has characters which are somewhat intermediate between *Artocarpus scortechinii* and *A. elasticus*. It has the general appearance of *A. scortechinii* but the dimensions are rather large: the leaves measure up to 36 × 20 cm. and are slightly scabrid above, the twigs are about 15 mm. thick, and the syncarp measures 11 × 4.5 cm., with a peduncle 7 cm. long, and has many somewhat elongate, solid processes about 5 mm. long. The collection appears to be from a hybrid between the two species and, if so, this is the only naturally occurring hybrid in *Artocarpus* which has been recognized in the material examined in the course of this study. Seeds are present in the syncarp and are apparently fully developed.

19. **Artocarpus elasticus** Reinw. ex Blume, Cat. Bog. 101. 1823, nomen nudum, Bijdr. 481. 1825, "*elastica*"; Miq. Fl. Ind. Bat. 1(2): 285. 1859, Ann. Mus. Lugd.-Bat. 3: 211. 1867, pro parte excl. spec. *De Vriese*, Batjan; Koord. & Val. Bijdr. Boomsoort. Java 11: 13. 1906; Van Steenis, Bull. Jard. Bot. Buitenzorg III. 13: 12. 1933; Burkill, Dict. 251. 1935; Corner, Wayside Trees, 653. *t. 193, 194.* 1940; Backer, Beknopte Fl. Java 6: 13. 1948. Holotype, Java, *Reinwardt s.n.* (L).

Artocarpus blumii Tréc. Ann. Sci. Nat. Bot. III. 8: 111, *t. 4, fig. 116.* 1847; Miq. in Zoll. Syst. Verz. Ind. Archip. 2: 89. 1854; Miq. Fl. Ind. Bat. 1(2): 285. 1859, Ann. Mus. Lugd.-Bat. 3: 211. 1867; Kurz, Natuurk. Tijdschr. Ned. Ind. 27: 182. 1864; Becc. For. Borneo, 632. 1902; Renner, Bot. Jahrb. 39: 366. 1907. Syntypes, Java, *Blume s.n.*, *Zollinger 1058* (P); lectotype, *Zollinger 1058* (P).

Artocarpus kunstleri King in Hook. f. Fl. Brit. Ind. 5: 540. 1888, et in Ann. Bot. Gard. Calcutta 2: 9. *t. 4.* 1889; Ridley, Trans. Linn. Soc. Bot. II. 3: 355. 1893, Fl. Malay Penin. 3: 353. 1924. Syntypes, Malaya, *King 3494, 6799, 6967, 10965, Maingay 1484* (CAL, not seen; duplicates examined, K, SING, etc.).

Artocarpus blumei Tréc. var. *kunstleri* Boerl. Handl. Fl. Ned. Ind. 3: 370. 1900.

Artocarpus pubescens auct. non Willd., Blume, Bijdr. 481. 1825; Moritzi, Syst. Verz. 75. 1846.

Evergreen (? or deciduous) trees, height to 45 m. (–65 m., fide *bb 8769*), strongly buttressed when old (fide Corner, 1940), bark dark grey, *Twigs* 10–20 mm. thick, rugose, short-hispid, hairs patent or appressed; annulate stipular scars c. 1 mm. broad, slightly prominent; lenticels in an irregular ring below scar. *Stipules* 6–20 cm. long, broadly lanceolate, attenuate, hispid-pubescent, hairs yellow to rufous, patent or appressed. *Leaves* 15–60 × 10–35 cm., ovate-elliptic, short-acuminate, base rounded or cuneate, margin entire or shallowly crenate; juvenile leaves twice or thrice pinnatifid, to 200 cm. long; main veins and intercostals prominent beneath, reticulum slightly so, lower surface bullate between the meshes of the reticulum; very shortly appressed-hispid above with the main veins pubescent, subappressed hispid-pubescent beneath; lateral veins 12–14 pairs, straight; intercostals parallel; dark green above, pale green beneath, drying purplish to reddish brown above, red-brown beneath; hypodermis of 1–3 cell-layers present, complete, cells isodiametric in surface view; gland-hairs slightly immersed, heads depressed-globose, 4-celled; petiole 40–100 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* 60–150(–200) × 15–25 mm., cylindric, the surface sulcate with long, deep grooves, covered by flowers; perianths tubular, 0.8 mm. long, bilobed above, appressed-pubescent; stamen 0.9 mm. long, filament broad, flattened, anther-cells oblong, 0.4 mm. long; peduncle 40–75 × 3 mm., short-pubescent; *female head* with bifid styles exserted to 1 mm. *Syncarp* to 11.5 × 5.5 cm. (to c. 17 × 10 cm. including processes), cylindric, yellow-brown, drying brown, covered by closely set, fleshy, short-hispid processes of two lengths, the longer flexuous, slightly tapering, solid, 10–18 × 1–1.5 mm., the shorter narrowly conical, perforate, 4 × 1 mm.; scattered bracts present between the processes, very slenderly stalked, heads infundibuliform, c. 0.2 mm. across; wall c. 6 mm. thick; fruiting perianths numerous, proximal free region white, somewhat fleshy, "seeds" (thin, horny pericarps) ellipsoid, 10 × 6 mm., style one-third the distance up the ventral face, testa fleshy, embryo with the radicle ventral, the cotyledons parallel to the median plane of the ovary, equal; core 20–30 mm. across; peduncle 65–120 × 10 mm., short-pubescent.

Vernacular names: *Aw* or *Ka aw*, Tenasserim and peninsular Siam; *Terap* (Malay), Malaya, Sumatra and Borneo; *Teureup*, (Sundanese), *Bendo* (Javanese), Java. Uses: the seeds are eaten roasted but, although the flesh tastes sweet (fide Koorders & Valeton, 1906), the ripe fruit has a nauseous smell (fide Corner, 1940); cloth is made by aboriginal tribes from the bark; the latex is used for bird-lime.

Distribution: In evergreen forest to 1000(–4500) ft., tolerant of a short dry season, peninsular Burma and Siam, Malaya, Sumatra and islands off the west coast and in the Sunda Straits, Riouw Archipelago, Billiton, Borneo, Java, Lesser Sunda Islands (e. to Sumbawa), Palawan.

Burma. Tenasserim. South Tenasserim, Nwagun Valley, *Parkinson 1636* (K). **Siam.** Peninsular Siam. Banang Sta, Pattani, *Kerr 7389* (BM); Bang Son, *Kerr 1563* (BM); Kao Luang, near Sritamarat, *Kerr 15563* (BM); Narathiwas, Ruesaw, *Thathiamrom 2364* (CGE, ♀).

Malaya. Kedah. 58th mile Wong Baling, *Chew Wee Lek 130* (K, ♂). Perak. *King 10965* (K, SING, ♂, ♀); Grik, *Burkill & Haniff SFN 12533* (SING, ♀); 11th mile toward Jor, from Tapah, *Haniff SFN 14293* (SING); Larut, *King 3494*, Oct. 1882 (BM, K, L, ♂, ♀), *6799*, Nov. 1884 (BM, K, P); Larut, Turu, *King 6967*, Dec. 1884 (SING, ♂); Simpang, *Wray 2035* (SING, ♂, ♀); Taiping, *Wray s.n.* (SING); 10th mile Tapah-Pahang road, *Burkill & Haniff SFN 13441* (SING, ♀). Pahang. Kuala Lipis, *Burkill & Haniff SFN 15680* (K, SING, ♀); Kuala Temkelis, *Ridley 2328* (SING, ♂, ♀); Tembeling, *Henderson SFN 21899* (A, BO, SING, ♀), *Ridley s.n.*, 1891 (SING, ♀). Selangor. Batu Tija, *Ridley s.n.*, Feb. 1904 (SING). Malacca. *Maingay 1484* (GH, K, L, ♂, ♀). Johore. Patani Keohil, Batu Pahat, *Ridley s.n.*, Nov. 1900 (SING, ♀). Penang. Waterfall, *Curtis s.n.*, July 1893 (SING, ♂, ♀). Singapore. Bukit Panjang Res., *Ridley s.n.*, Feb. 1899 (SING). (Fide Corner, 1940, common in lowland forest throughout Malaya.)

Sumatra. Atjeh. Sokoluway, *Batten Pooll s.n.*, 1939 (SING). Tapanuli. Barus, *bb 31581* (BO, L); Padang Lawas, Purbasinamba, *bb 6196* (BO). West Coast. Melintang, *sine nom. et num.* (L); Ophir, Lubuk Gadang, *bb 18739* (BO); Ophir, Lubuk Gadang, Parek, *bb 19484* (BO), *19627* (BO, L); Ophir, Simpang, *bb 18722* (BO); Pajakumbuh, *sine nom. et num.* (BO, ♂); Priaman, *HB 754* (L); Sidjungdjung, Muaro, *bb 5203* (BO, L), *9049* (BO, L, U, ♀). East

COAST. Asahan, Bandar Puluh, *Yates 1899* (BO, P, ♀); Huta Padang Estate, near Kisarin, *Krukoff 203* (BO, ♂), *301* (BO), *4367* (A, BO, L, SING, ♀); P. Mendol, *bb 21459* (BO, L); Sibolangit, *Lörzing 5861* (BO, L, U, ♂, ♀). INDRAGIRI. Belimbing, *bb 28502* (BO, L); Kuala Keritang, *bb 28697* (BO, L); Kwantan, Muara Pantei, *bb 23862* (BO, L); Padang Tarab, *Koorders 10457* (BO); Pulau Pauh, *Koorders 10459* (BO). DJAMBI. Simpang, *bb 13121* (BO). BENKULEN. Kruï, G. Kemala, *bb 8769* (BO); Redjang, Tabah Penandjung, *bb 1807* (BO, L). PALEMBANG. Djankar, Pasemahlanden, *bb 8683* (BO, L); Komering Ulu, *Grashoff 603* (BO); Lematang Ilir, Semangus, *bb 32172* (BO, L); Lematang Ulu, *Lambach 1215* (BO, L, ♀); Martapura, *Bal 43* (BO); Muara Dua, *Teysmann HB 3778* (BO); Muara Dua, Kisau, *bb 9230* (BO); n.w. of Ranaumeer, Gunong Pakiwang, *Van Steenis 3887* (BO, L, SING, ♂). LAMPONGS. Menggala, *bb 8470* (BO, L, U); Seputih, Suwikis, *bb 2856* (BO); Seputih-Tulangbawang, Gunung Sugit, *Gusdorf 139* (BO, ♀); Telukbetong, Ibadjimenah, *bb 8094* (BO, L, U). SIMALUR. *Achmad 89* (BO, L, ♀), *545* (BO, L). NIAS ISLAND. *Hagerup s.n.* (C), *sine nom. et num.* (L). BATU ISLANDS. Pulau Tello, *Demang s.n.* (BO). ENGGANO. Near Bua Bua, *Lütjeharms 4417*, *4754* (A, BO, K, L, P, SING). ISLANDS IN THE SUNDA STRAITS. Krakatau group: Lang Eiland, *Docters van Leeuwen-Reijnvaan 14231* (BO); Verlaten Eiland, *Backer s.n.*, May 1908 (L), *Boedijn 2326* (BO). Pulau Sebisi, *Docters van Leeuwen-Reijnvaan 5388* (BO, ♀). BILLITON. *Teysmann s.n.* (BO), *HB 17584* (BO); Tandjungpandan, *sine nom. et num.* (BO); Tandjungpandan, Banlan, *bb 8676* (BO, L). RIOUW ARCHIP. Karimon: Simpangbanan, *bb 9967* (BO); Tandjong Pundur, *bb 6310* (BO, L).

Borneo. SARAWAK. *Beccari PB 1037* (K, ♀); Kuching, Sungei Semangoh For. Res., *Xuas S 0184* (SING, ♀). WEST BORNEO. B. Lampai, *Teysmann HB 7101* (BO, P); Pontianak, Olakolak, *bb 12634* (BO); Sanggau, Ketatai, *bb 18573* (BO). SOUTH AND SOUTHEAST BORNEO. Dusun [= Barito River] *Korthals s.n.* (L); Tanah Bumbu, Kampong Baru, *bb 13055* (BO, ♀). EAST AND NORTHEAST BORNEO. Berouw: Betemaran, *bb 19039* (A, BO, L); Betemuaer, *bb 19109* (BO, P); Domaring, *bb 18896* (BO, K). E. Kutei: Bengalon Rapak, *bb 15318* (BO, L), *15327* (BO); Rapak, *bb 14622* (BO, ♀); Samarinda, *sine nom. et num.*, 1926 (BO); Sangkulirang, Landak, *bb 14843* (BO, ♂); Sangkulirang, Rantau Bahan, *bb 15219*, *15220* (BO, L), *15223* (BO, K, L), *15227* (BO, L), *15241* (BO, K, L), *15254* (BO); T. Lelan, *bb 14689* (BO, L, ♂), *14692* (BO, ♂). W. Kutei: Kendisi, *bb 16690* (BO); Longbleh, *bb 16130* (A, BO, L), *16131* (BO, SING), *16132* (BO); Mujup, *bb 16770* (BO, K). P. LAUT. Sungei Paring, *bb 13197* (BO).

Java. *Blume s.n.* (P), *Junghuhn s.n.* (L), *Lahaie 2212* (P), *Reinwardt s.n.* (L), *Zippelius s.n.* (L). WEST JAVA. Bantam: Batuhideung, Tjimara, Gunong Merang, *Koorders 8699* (BO, L). Batavia: Bidara Tjina, *Edeling 7277* (BO, P, ♂); Depok, *Beumée 5679* (BO, ♀), *Büsgen 17* (BO, L), *Koorders 42229* (BO), *Van Steenis 5663* (BO, ♂), *Backer 35151* (BO); Djasinga, *Smith 10484* (BO, ♀); Dungus, 10 km. from Djasinga, *NIFS Ja 1973* (BO); Kebajosa, *Backer s.n.* (BO, ♀); Meester Cornelis, *Backer 35316* (BO). Buitenzorg: Kotaparis, *Bakhuizen van den Brink 1817* (U); Tjilinung, *Hallier s.n.* (BO). Preanger: Palabuanratu, Sukabumi, *Koorders 8696*, *8698* (BO, L), *11843* (BO, K, L, P, ♂, ♀), *11844* (BO, L, ♂), *11845* (BO, L, P, ♂, ♀), *11846* (A, BO, L), *33101* (BO); Garut, Pangentongan-Telagabodas, *Koorders 14123* (BO, L), *26173* (BO, L, ♂, ♀); Tjiandjur, Sukanagure, *Koorders 8697* (BO); Tjikoja, *Zollinger 1058* (BM, P, U, ♀). CENTRAL JAVA. Banjumas: Pringombo, Bandjarnagara, *Koorders 39144* (BO, K, L, P, ♂, ♀); Pringombo, Bongkelan, *Koorders 39176* (BO, ♂); Pringombo, Singomerto, *Koorders 8711* (BO, ♀), *8712* (BO, L, ♀). Djapara: *Koorders*

19 (BO); Kudus, Sumanding, *NIFS Ja 1811* (BO). Pekalongan: Margasari, *Berger 7371* (BO, ♂, ♀). *Noltée 4053* (BO, L, ♀); Subah, *Koorders 11638* (BO, ♀), *11639* (BO, L), *13358*, *13359*, *13362*, *36891*, *36959* (BO). Semarang: Gunong Andong, *Koorders 36617* (BO); Karangasem, *Koorders 8708* (BO), *8709* (BO, L), *28441* (BO); Kedungdjati, *Koorders 8700* (BO), *8701*, *8703* (BO, L), *8704*, *8705* (BO), *8707* (BO, L), *25027* (BO), *26097* (BO, L); Telomojo, *Koorders 28013* (BO, L), *36237*, *39278* (BO). Rembang: Sekar, Tambakredjo, *NIFS Ja 1592* (BO). Tegal: Kalisalak, *Koorders 8710* (BO). EAST JAVA. Besuki: Banjuwangi, Rogodjampi-Balak, *Koorders 8727* (BO); Djember, Glundengan, *NIFS Ja 2707* (A, BO, L, SING); Djember, Puger, *Koorders 8719* (BO, L); Djember, Tjuramanis, *Koorders 8720*, *8721* (BO, L), *8722* (BO, ♂), *8723* (BO, L), *8725* (BO), *8726* (BO, L), *38465*, *38557*, *39932*, *39966* (BO); Muntjar, *Becking 82* (BO); Situbondo, Pantjur-Idjen, *Koorders 8715* (BO, L), *8716* (BO), *8717* (BO, L, P), *8718* (BO, L). Kediri: Gadungan, Pare, *Koorders 23027* (BO); Klino, *NIFS Ja 2000* (BO, L), *Kalshoven 31* (BO). Madiun: Gunong Pandan, *Koorders 12381* (BO); Lawu, near Plaosan, *Elbert 302* (L); Ngebel, *Koorders 8706* (BO, L); Ngebel, Gondowido, *Koorders 29843* (BO); Ngebel, Gunong Wilis, *Koorders 38804* (BO). Malang: Gunong Baung near Lawang, *Bijhouwer 81* (BO, L); Karangputih, *Kalshoven XII* (BO). Probolinggo: Lumadjang, Gunong Sawur-waderan, *Koorders 8724* (BO, L). NUSA KAMBANGAN. *Koorders 8713*, *8714*, *20081*, *20089*, *20150* (BO, L), *22031* (BO, L, P), *24658*, *27034* (BO, L). KANGEAN ARCHIP. G. Eteng near Tambajangan, *Backer 27848* (BO). MADURA. Sampong, *Vordermans 125*, *129* (BO). P. BAWEAN. *NIFS Ja 4220* (BO, L, ♂, ♀).

Lesser Sunda Islands. BALI. Karang Asem, Besakilj, *bb 13278* (BO); Tjandikusuma, *Becking 128*, *135* (BO). LOMBOK. W. Lombok, Batukumlung, *bb 15501* (K, L). SUMBAWA. *Colfs 348* (L). **Philippine Islands.** PALAWAN. Aborlan, Iraan Mts., *Sulit PNH 12489* (A, L, ♂).

In publishing the name *Artocarpus elasticus*, Blume ascribed it to Reinwardt and gave a brief description of the male inflorescence and of pinnatifid leaves. The type is taken to be a sterile specimen in the Rijksherbarium, Leiden, bearing a single pinnatifid juvenile leaf and labelled by Reinwardt "Artocarpus elastica Rwdt." There are no specimens in the herbarium bearing this name that were determined by Blume himself. At the same time (1825) Blume described collections with entire leaves and both male and female inflorescences under the name *Artocarpus pubescens* Willd., which is a superfluous name for *A. hirsutus* from southern India.

Artocarpus elasticus is the commonest species of the genus in western Malaysia, but it is probably often under-collected, both because it is well known and because of the large size of the leaves. Thus Corner (1940) remarks that it is common throughout the lowland forests of Malaya, but from several of the states no collections have been seen in the course of this study. It is noted by Corner that *A. elasticus* may be deciduous in those areas of Malaya in the north and east that have a distinct dry season. Except for Palawan, from which a single collection has been seen, *Artocarpus elasticus* is apparently absent from the Philippines and all records in the literature must be transferred to the following species, the newly described *A. sericicarpus*.

Under the name *Artocarpus blumeana* Tréc. [sic], Schumann and Hollrung (Fl. Kais. Wilhelmsland, 39. 1889) recorded a collection, *Hollrung*

47, from Finschhafen, northeastern New Guinea, stating that the fruit was the size of an apple, with a brown rind, yellow flesh and small seeds. This collection was presumably destroyed at Berlin and no duplicate has been seen. It cannot be identified from the description and it was not mentioned by Diels in his "Die Moraceen von Papuasien" (Bot. Jahrb. **67**: 171–235. 1935).

20. **Artocarpus sericicarpus** Jarrett, sp. nov. Holotype, Luzon, *Merrill 2024* (US); isotype (K).

Gumihan Kamel in Ray, Hist. Pl. **3**, App. 52. 1704.

Artocarpus blumii auct. non Tréc., Vidal, Revis. Pl. Vasc. Filip. 254. 1886; Elmer, Leafl. Philip. Bot. **2**: 613. 1909.

Artocarpus elasticus auct. non Blume, Fern.-Villar, Noviss. App. 202. 1880; Stapf, Kew Bull. **1894**: 108. 1894; Wester, Philip. Agr. Rev. **8**: 109. *t. 8a.* 1915, Bull. Bur. For. Philip. **39**: 78. *t. 19b, 32c.* 1924; Merr. Enum. Philip. Pl. **2**: 41. 1923; Brown, Useful Pl. Philip. **1**: 463. *fig. 188.* 1941.

Differt ab *A. elastico* et *A. tamaran* inflorescentiis masculis capitulis subtuberculatis ad rugosis, floribus pilis crispis obtectis, femineisque processibus solidis longioribus (20–35 mm.), pilis longis subappressisque, obtectis, etiam ab *A. elastico* foliis supra laevibus, ab *A. tamaran* nervis lateralibus utrinque 11–16, nec 15–23.

[Arbores ad 30(–40) m. altae.] *Ramuli juniores* [6–]15 mm. diametro, rugosi, praesertim infra nodos [pubescentes vel] villosi, pilis rufis, [appressis vel] patentibus; cicatrices stipularum annulatae, 1 mm. latae, parum prominentes, conspicuae; lenticellae infra nodos circum ramulos inaequaliter dispositae. *Stipulae* 8 [6–12] cm. longae, late lanceolatae, acutae, villosae, pilis rufis, [subappressis vel] patentibus, etiam appresse pubescentes, pilis canescens. *Folia* c. 40 × 25 [20–70 × 10–50] cm., elliptica vel ovata, breviter acuminata, basi rotunda vel cuneata, laciniis lateralibus binis brevibus [adulta integra, margine integerrima, vel leviter crenata, juvenilia plus minusve pinnatifida], supra laevia, interdum scabriuscula, pilis minutis appressis, subtus pubescentia, viridia, in sicco rufibrunnea; costa nervi lateralesque subtus prominentes; nervi laterales utrinque 12 [11–16], recti; nervi transversales paralleli, subtus prominuli; areolae inter retem venularum subtus bullatae; hypodermis strato unico [vel duplico] cellis superne isodiametricis composita; glandulae subimmersae, capitibus depresso-globosis, 4-cellis; [petiolus 20–75 mm. longus].

Inflorescentiae axillis foliorum solitariae. *Ad anthesin*: *capitulum masculum* (immaturum) 35 × 15 mm. [–100 × 20 mm., unicum maturum visum], superficie subtuberculata ad rugosa, floribus numerosissimis obtecta; [perianthia tubulosa, 1.5 mm. longa, supra bilobata, lobis pilis crispis obtecta; stamina 1.8 mm. longa, filamentis latis, supra arcte contractis, cellis antherum oblongis, 0.4 mm. longis;] pedunculus 30 [matura 55–100] × 4 mm., appresse pubescens; *capitulum femineum* 4.5 × 4 cm., subglobosum, stylis simplicibus ad 1 mm. exsertis. [*Syncarpia* ad 8.5 × 5 cm (processibus exclusis), ellipsoidea vel cylindrica, fulva, in sicco brunnea, processibus crebris duarum longitudinum, carnosis obtecta; processus longiores flexuosi, teretes, solidi, 20–35 × 0.5–1 mm., pilis longis, subappressis obtecti, breviores anguste conici, perforati, 3–6 × 1 mm., appresse pubescentes; bracteae interflorales rarae, tenuissimae, capitibus infundibuliformibus, c. 0.2 mm. latis; stratum externum syncarpii c. 2 mm. crassum; "semina" (pericarpia cornea) numerosa, ellipsoidea, 10 × 6 mm., perianthiis liberis, albis, subcarnosisque inclusa; embryum radicula ventrali, cotyledonibus subaequalibus, oblique positis; axis syncarpii 15–20 mm. diametro; pedunculus 95–180 × 6 mm., appresse pubescens.]

VERNACULAR NAMES: *Terap* (Malay), Borneo; *Gomihan* or *Gumihan*, Philippines. USES: the seeds are eaten roasted and Wester (1924) states that the juicy perianths surrounding them are sweet and aromatic with a fair to good flavour.

DISTRIBUTION: In evergreen forest to 1000(–3000) ft., Borneo, Philippine Islands, Celebes, Moluccas.

Borneo. SARAWAK. Banting, *Hewitt s.n.*, Sept. 1908 (K); Kuching, *Dickson s.n.*, Oct. 1952 (SING, ♂), *Haviland 1774* (CAL, SING, ♂). EAST AND NORTHEAST BORNEO. Berouw: Domaring, *bb 18877* (BO); Inaran, *bb 12132* (BO); Sungei Pulai, *bb 19190* (BO), *19194* (BO, SING). Bulungan: Salembatu, Sungei Rumah, *bb 11289* (BO). E. Kutei: Rapak, *bb 14625* (BO, L, ♂). W. Kutei: Upper Mahakam, Bato Urah, *bb 20677* (A, BO). BRITISH NORTH BORNEO. *The Governor s.n.*, Dec. 1893 (K, leaf with drawing of fruit).

Philippines. LUZON. Tayabas: Linayangan, *Merrill 2024*, Jan.–Apr. 1903 (K, US, ♂, ♀); Lucban, *Elmer 9160* (A, BO, K, L, ♀); Mt. Binuang, *Ramos & Edano BS 28855* (US, ♀). Camarines: Nueva Caceres, *Vidal 920* (K); Tigao, *Wester s.n.*, June 1915 (A, ♀). Albay: *Curran FB 10597* (NY, US, ♀). Sorsogon: Gubat, *Vidal 3845* (K, ♀). SAMAR. *Ramos BS 17596* (BM, K, US, ♂, ♀); Wright, Loquilocon, Sitio Tinane, *Sulit PNH 6147* (A, ♂, ♀). BILIRAN. *McGregor BS 18532* (A, BO, ♀). NEGROS. Oriental, Dumaguete, Cuernos Mts., *Elmer 10307* (A, BM, BO, K, L, US, ♀). MINDANAO. Surigao: *Hutchinson 7562* (NY). Bukidnon: Mindagat, Manai, *Pelzer PNH 13561* (A, L, PNH, ♂, ♀).

Celebes. NORTH PENINSULA. Kwandang, Titidu, *bb 7496* (BO); Minahassa, Liwutung, *Koorders 19041* (BO); Minahassa, Kajuwatu, *Koorders 19039* (BO); Minahassa, Lobu, *sine nom. et num.*, Dec. 1906 (BO). CENTRAL CELEBES. Luwu, *Heyne 2883* (BO); Malili, Kawata, *NIFS Cel./V–241 no. 235* (BO, ♂, ♀), *241 no. 308* (BO, L, ♀); Malili, Tomoni, *bb 32458* (BO, L); Malili, Usu, *NIFS Cel./II–499* (A, BO, L, SING); Palopo, Baramamase, *bb 22985* (L); Poso, Kalora, *bb 28729* (BO, L); Tapalang, *Noerkas 444* (BO). SOUTHEAST PENINSULA: B. Watuwila, *Kjellberg 984* (S, ♀).[11] P. MUNA. Raha, Wasalangka, *bb 21310* (BO, K).

Moluccas. TALAUD ISLANDS. Karakelang, Gunong Duata, *Lam 2845* (L). SULA ISLANDS. North Mangoli, *bb 29789* (BO, L); Sanana, Kali Waj Gaj, *bb 28808* (BO). BURU. Balo, *bb 31353* (BO, L). **Cultivated.** JAVA. Bogor, Hort. Bot. *VII G 121* (BO), *VIII B 32* (L).

Artocarpus sericicarpus has not previously been distinguished from *A.*

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[11] This specimen was examined by Mr. E. J. H. Corner, to whom I am indebted for information concerning the embryo.

elasticus, but it differs from the latter in characters of both the male and female inflorescences, notably in the very long and slender sterile processes on the syncarp. The specific epithet is derived from the appearance produced by the long hairs covering these processes. Sterile specimens can also be identified, since, although the leaves are sometimes slightly scabrid above, they are never short-hispid, as in *A. elasticus*. Their texture is usually more thinly coriaceous.

No very satisfactory specimen was available for selection as the type and the collection chosen consists of a shoot bearing young male and female inflorescences, and a detached leaf. It shows all the diagnostic characters with the exception of the length of the mature syncarp processes.

A collection of this species was sent to the Royal Botanic Gardens, Kew, by the Governor of British North Borneo in response to an enquiry about cloth made from *timbaran* bark, and was the subject of a note by Stapf (1894). In an accompanying letter it was stated that the specimen came from a species of *tarap*, of which there were three kinds used for making bark cloth, this being the best. Stapf concluded that it was very close to and probably a variety of *Artocarpus elasticus*. The vernacular name *timbaran* has not otherwise been recorded for this species, and is perhaps more correctly applied to *A. tamaran*. However, until *Artocarpus elasticus*, *A. sericicarpus* and *A. tamaran* have been clearly separated and studied in Borneo, their uses and correct native names cannot be stated with certainty.

21. **Artocarpus tamaran** Becc. For. Borneo, 626. 1902; Renner, Bot. Jahrb. 39: 366. 1907. Holotype, Sarawak, *Beccari PB 2996* (FI); isotypes (FI, L).

Trees, height to 40 m. *Twigs* 5–10 mm. thick, rugose, puberulent, with scattered patent rufous hairs (to 5 mm. long), denser at nodes; annulate stipular scars c. 0.5 mm. broad, slightly prominent; lenticels scattered. *Stipules* 3–9 cm. long, lanceolate, acute, villous, the hairs rufous, subappressed. *Leaves* 20–35 × 11–17 cm., ovate-elliptic, varying ovate, short-acuminate, base rounded, margin entire or shallowly crenate; juvenile leaves to 100 cm. long, deeply pinnatifid, the pinnae emarginate at the base and the midrib narrowly winged by lamina, to pinnate, the rachis not winged and the pinnae pinnatifid; main veins prominent beneath, intercostals slightly so; glabrous above, main veins beneath appressed-sericeous, midrib often also with longer, patent hairs, reticulum with sparse, short, appressed hairs; lateral veins (15–)17–23 pairs, straight; intercostals parallel; green, drying pale to dark red-brown; hypodermis of 2 or 3 cell-layers present, complete, cells isodiametric in surface view; gland-hairs slightly immersed, heads depressed-globose, 4-celled; petiole 35–40 mm. long.

Inflorescences solitary in leaf-axils. *At anthesis*: *male head* (immature) 70 × 10–14 mm., cylindric, the surface tuberculate with numerous irregular, cylindric, obtuse, solid processes c. 3 × 2 mm., entirely covered by flowers, apices of processes pilose with rufous hairs c. 2 mm. long borne on surface of axis; perianths tubular, 0.6 mm. long, bilobed above, minutely pubescent; stamen (immature), filament broad, flattened, abruptly contracted above, anther-cells oblong, 0.2 mm. long; peduncle 35–55 × 3–5 mm., indumentum as twig; *female head* with simple styles exserted to 0.5 mm. *Syncarp* to 10 × 5 cm. (fide Beccari, to 14 × 8 cm. ? including processes), cylindric, drying dark brown, covered by closely set, fleshy processes of two lengths, the longer flexuous, filiform, solid, to 10 × 0.5 mm., the shorter conical, perforate, 3 × 1 mm., all rough from short, recurved hairs; wall c. 8 mm. thick; "seeds" (pericarps) numerous, ellipsoid, 6 × 4 mm.; core c. 12 mm. across; peduncle 55–100 × 6 mm. (–130 mm., fide Beccari), indumentum as twig.

·VERNACULAR NAMES: *Tarap tempunan* (Malay); *Tamaran* (fide Beccari); *Tembaran*. USES: cloth is made from the bark.

DISTRIBUTION: In evergreen forest to 1800 ft., Borneo.

Borneo. SARAWAK. Kuching, M. Mattang, Vallombrosa, *Beccari PB 2996*, Dec. 1866 (FI, K, ♂, ♀). WEST BORNEO. Bukit Lempai, *Teysmann 7104* (BO, L); Melawie, Klepuk, B. Sanggau, *bb 29070* (A, BO, L). SOUTH AND SOUTHEAST BORNEO. Pleihari, Sungei Sangga, *bb 9944* (BO, L); Tanah Bumbu, Kampong Baru, *bb 13316*, *13345* (BO, ♂, ♀). EAST AND NORTHEAST BORNEO. Balikpapan: Pemaluan, *bb 24760* (BO, L). E. Kutei: Pengadan, *bb 13024* (BO); Sg. Kerajaan, n. of Sangkulirang, *Kostermans 5853* (K, L, ♀). W. Kutei: Blu-u, *Jaheri 1498* (BO). Tidung: Sobediang, *bb 17869* (A, BO, ♀). BRITISH NORTH BORNEO. Sepilok For. Res., 15 mi. w. of Sandakan, *Wood SAN 16544* (A, L, ♂, ♀). Kabili-Sepilok For. Res., *Puasa Kepong FN 55241* (KEP). P. LAUT. Sungei Paring, *bb 13201* (BO).

Both the leaves and the inflorescences of *Artocarpus tamaran* are very distinctive. The appearance of the male head is somewhat remarkable, since the surface, which is completely covered by flowers, is produced into short, irregularly cylindric, solid projections, and the tips of these are pilose with hairs that are borne on the axis, between the flowers. The syncarp processes are smaller and more slender (to 10 × 0.5 mm.) than in either *Artocarpus elasticus* or *A. sericicarpus* and are covered by recurved hairs. The leaves have an unusually large number of lateral veins (17–23 pairs, as compared with 11–16 pairs in the two preceding species) and the form of the deeply pinnatifid juvenile leaves, with sessile pinnae, emarginate at the base, and a narrowly winged rachis, is unique in the genus.

22. **Artocarpus sumatranus** Jarrett, sp. nov. Holotype, Indragiri, *bb 22055* (BO); isotype (L).

Differt ab *A. kemando et A. maingayi* syncarpio processibus conicis obtecto, foliis subtus omnino tenuiter pubescentibus.

Arbores ad 25 m. altae. *Ramuli juniores* 2.5–3 mm. crassi, tenuiter rugosi, appresse hispidi-pubescentes; cicatrices stipularum annulatae, 0.5 mm. latae, parum prominentes, inconspicuae; lenticellae rarae. *Stipulae* 1–2 cm. longae, ovato-lanceolatae, acutae, appresse pubescentes, pilis rufis. *Folia* [6–]11–18 × [3–]5–10 cm., oblongo- vel obovato-elliptica, obtusa vel breviter obtuseque acuminata, basi rotunda vel cuneata, margine integra, supra glabra vel appresse puberulentia, subtus omnino tenuiter pubescentia, viridia, in sicco rufi-brunnea; costa nervi lateralesque subtus prominentes; nervi laterales utrinque c. 11, recti vel leviter curvati; nervi transversales paralleli, subtus prominuli; areolae, inter retem venularum, subtus parum bullatae; hypodermis strato duplico cellis superne isodiametricis composita; glandulae semi-immersae, capitibus depresso-globosis, 4-cellis; petiolus 10–30 mm. longus.

Inflorescentia axillis foliorum solitaria. [*Capitulum masculum* (immaturum) 26 × 5 mm., cylindricum, superficie rugosa, floribus numerossisimis obtecta; perianthia tubulosa, 0.6 mm. longa, clavata, supra bilobata, lobis crassis, minute pubescentia; stamina (immatura) cellis antherum ellipticis, 0.2 mm. longis; pedunculus 20 × 3 mm., appresse hispidi-pubescens.] *Syncarpium* (submaturum) 4 × 2 cm., cylindricum, in sicco rufi-brunneum, processibus crebris, carnosis, conicis, hispidi-pubescentibus, c. 1.5 × 1.5 mm., perforatis, stylis simplicibus 0.5 mm. longis exsertis, obtectum; pedunculus 35 × 3 mm., appresse hispidi-pubescens.

VERNACULAR NAME: *Pudu* (Malay).

DISTRIBUTION: In lowland evergreen forest, Sumatra (Indragiri, Lampongs).

Sumatra. INDRAGIRI. Kwala Keritang, *bb 28715* (BO, L); Selat Pandjang, Kamparmonding, *bb 22055*, Mar. 1937 (BO, L, ♀); Tempuling, *bb 10271* (BO, ♂). LAMPONGS. *Teysmann s.n.* (BO).

Artocarpus sumatranus resembles *A. kemando* and *A. maingayi* in the general size of its parts, and is distinguished from them primarily by the conical, rather than umbonate or truncate, processes on the syncarp of the holotype. Minor vegetative differences enable the single male and two sterile collections cited above to be associated with the type. The leaves are a little larger than in *A. kemando* or *A. maingayi* and, while they resemble the former in outline, they are obtuse or obtusely acuminate and thinly pubescent throughout beneath, instead of on the main veins only. The twigs are also slightly stouter. The male peduncle is longer than in either of the two following species, and the indumentum of the peduncles differs in being appressed, instead of patent (but *cf.* the anomalous collections discussed under *A. kemando*).

23. **Artocarpus kemando** Miq. Fl. Ind. Bat. Suppl. 418. 1861; Becc. For. Borneo, 628. 1902; Renner, Bot. Jahrb. **39**: 366. 1907; Ridley, Fl. Malay Penin. **5**: 335. 1925; Merr. Pl. Elmer. Born. 46. 1929; Burkill, Dict. 256. 1935; Corner, Gard. Bull. Singapore **10**: 282. 1939, Wayside Trees, 656. 1940. Holotype, Sumatra, *Teysmann HB 4515* (L); isotypes (BO, P, U).

Artocarpus brunneifolia S. Moore, Jour. Bot. **63**, Suppl. 112. 1925. Holotype, Sumatra, *Forbes 3046* (BM); isotypes (BO, GH, L, P).

Evergreen trees, height to 35 m. *Twigs* 2–2.5 mm. thick, finely rugose, shortly subappressed or appressed hispid-pubescent, hairs rufous; annulate stipular scars c. 0.5 mm. broad, inconspicuous; lenticels few, scattered. *Stipules* 0.7–2 cm. long, lanceolate, acute, rufous appressed-pubescent. *Leaves* 5–15 × 2–6 cm., elliptic-oblong, varying elliptic, acute to acuminate, base rounded or cuneate, margin entire; juvenile leaves elongate; main veins prominent beneath; glabrous above, main veins beneath appressed-pubescent, surface between glabrous or nearly so; lateral veins 9–13 pairs, straight or slightly curved; intercostals parallel; deep green, drying red-brown or pale red-brown; hypodermis of 1–3 cell-layers present, cells isodiametric in surface view; gland-hairs superficial to half immersed, heads depressed-globose, 4-celled; petiole 10–20 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* 20–40 × 3–5 mm., cylindric, the surface rugose, covered by flowers; perianths deeply bilobed, 0.4 mm. long, short-pubescent; stamen 0.45 mm. long, filament cylindric, anther-cells ellipsoid, 0.2 mm. long; peduncle 7–13 × 2 mm., pubescent with short, patent hairs; *female head* with simple styles exserted to 0.5 mm. *Syncarp* to 4 × 2.5 cm., ellipsoid, drying brown, fleshy, covered by contiguous, low, umbonate processes, c. 2 mm. across, or the surface becoming nearly smooth and areolate, patent-pubescent with short, inflated hairs; wall c. 1 mm. thick; fruiting perianths several, proximal free region thin-walled, not fleshy, "seeds" (horny pericarps) subglobose, 8 × 5 mm., style sub-basal, testa fleshy, embryo subreniform, the long axis horizontal, concave below over the basal hilum with the radicle ventral, the cotyledons parallel to the median plane of the ovary, equal or one slightly shorter; core c. 5 mm. across; peduncle 15–40 × 3 mm., indumentum as male.

VERNACULAR NAMES: *Pudu* or *Kudu* (Malay), Malaya, Sumatra, Borneo.

DISTRIBUTION: In evergreen forest, often on swampy ground, to 500 (–1500) ft., southern Malaya, southeastern Sumatra, Banka, Billiton, Lingga Archipelago, Borneo.

Malaya. PAHANG. Temerloh, *Hamid CF 5171* (K, SING, ♂). JOHORE. Kangka Sedili Ketchil, *Corner s.n.*, June 1934 (SING); Mawai, S. Berassau, *Corner s.n.*, Feb. 1935 (SING); Mawai, S. Kayu, *Corner s.n.*, Feb. 1935 (SING). SINGAPORE. Bukit Timah, *Langlassé 288, 303* (P), *Ridley 6432* (BM, SING, ♂, ♀); Jurong, 15th mile, *Corner s.n.*, Mar. 1933 (SING); Mandai road, *Kiah SFN 37716* (A, BM, BO, K, PNH, SING, ♀), *s.n.*, Aug. 1940 (SING, ♀); Seletar Forest, Nee Soon, *Sinclair SFN 40322* (L, SING); Reservoir Jungle, *Corner SFN 37000* (A, BM, BO, K, SING, ♂, ♀); Sungei Toas, *Goodenough 3378* (SING, ♀).

Sumatra. INDRAGIRI. Muara Serangge, *bb 30028* (BO, L, ♂); Pagarumbei, Tjenako River, *bb 25789* (A, BO, L); Sungei Akar, *bb 28629* (BO). DJAMBI. Muara Pidjuan, *bb 12275* (BO). PALEMBANG. *NIFS T 1191* (BO, L, U, ♂); Banjuasin and Kubustreken, *Grashoff 768* (BO); Banjuasin, Bajunglintjir, *NIFS T 755* (BO, L, SING, U, ♂, ♀), *1193* (BO, K, L, U, ♀); Lematang Ilir, Gunong Megang, *NIFS T 360* (BO, L, ♂, ♀), *837* (BO, K, L, U, ♂, ♀), *1205* (BO); Muara Mengkulem, R. Rawas, *Forbes 3046*, 1880 (BM, BO, GH, L, P, ♂, ♀). LAMPONGS. Kebang, *Teysmann HB 4515* (BO, L, P, U, ♂). BANKA. Blinju, *Grashoff 106* (BO, L, ♂); Toboali, *Teysmann HB 7244* (BO, L). BILLITON. *Teysmann HB 16727* (BO);

Tandjungpandan, *Teysmann s.n.* (BO); Tandjungpandan, Banlan, *bb 7268* (BO); Was, *Rossum 492* (BO, K, L, ♀). LINGGA ARCHIP. P. Sinkep, Ulu Santil, *bb 2002* (BO).

Borneo. SARAWAK. *Beccari PB 935* (K, P, ♀); near Kuching, *Beccari PB 2666* (C, K, P, ♀); Sungei Semengoh For. Res., Kuching, *Muas S 191* (SING). WEST BORNEO. Gunong Sangiang, *Romburgh 35* (BO, ♂); Melawie, Tjatil B. Tengkujung, *bb 26350* (BO, L); Melian, Dawak, *bb 12402* (BO); Sungei Landak, *Teysmann HB 11255* (BO, K, P, ♀), *11311* (BO, ♂); Sungei Tjabang, *Romburgh 16* (BO). SOUTH AND SOUTHEAST BORNEO. Beneden Dajak, Danau Rawah, *bb 13477* (BO); Beneden Dajak, near Peda Ketapi, *Meegan V* (BO); Muara Teweh, Nihan Dajak, *bb 10055* (BO); Pleihari, Djilatan, *bb 9900* (BO); Puruktjahu, Kalapeh, *bb 11082* (BO); Sampit, Natai Nangka, *bb 14072* (BO, ♂, ♀). EAST AND NORTHEAST BORNEO. Bulungan: Mara, *bb 10785* (BO). E. Kutei: Sg. Bambangan, s.e. of Samarinda, *Kostermans 6068* (A, L, ♀); Sg. Tiram, *bb 35033* (L); Tandjong Bangko region, near mouth of Mahakam River, *Kostermans 7190* (K, L, ♀). W. Kutei: Blu-u, *Jaheri 1499* (BO); Bukit Lajang, *bb 16242, 16254, 16260* (A, BO, L); near L. Djanean, *Endert 5065* (K, L, ♀); Longbleh, *bb 16154* (A, BO, L); Mujup, *bb 16731, 16762* (A, BO, L); Sebulu, *bb 15802, 15803* (BO); Tandjong Isui, *Endert 1952* (L). BRITISH NORTH BORNEO. Sabah For. District, Keningau, Agudon, *Angian 7721* (SARF, ♀); Tambunan, *Herb. For. Dept. B.N.B. 5252* (SING, ♀); Elphinstone Prov., Tawao, *Elmer 21511, 21780* (A, BM, BO, C, GH, K, L, P, SING, U, ♀).

Although it has been generally recognized that *Artocarpus kemando* and *A. maingayi* are closely related to each other, they have usually been treated as distinct species, Beccari (1902), reduced *A. maingayi*, from King's description, to synonymy under *A. kemando*. However, since King had not seen the latter species, he had been unable to differentiate *A. maingayi* from it clearly.

Corner, in 1939, listed the differences between the species in the shape of the leaves, the length and indumentum of the peduncles, and the surface markings and indumentum of the syncarps (given above in the key to the species). The puberulent upper surface of the immature leaves in *A. maingayi* is also a useful distinguishing character, since the hairs are often conspicuous against the dark red-brown dried leaves. This character, together with the leaf shape, usually enables even sterile collections to be assigned to one or the other of the species with certainty. Both Ridley (1925) and Corner (1940) suggested that *Artocarpus maingayi* could perhaps be treated as a variety of *A. kemando*, but it is felt that they are sufficiently distinct from each other to justify their maintenance at specific rank. The distributional areas of the two species are complementary, overlapping only in Johore; *A. maingayi* is found to the west and north, and *A. kemando* to the south and east, within western Malaysia (excluding Java).

Two anomalous collections, which do not agree in their characters with either species, must be noted here. The first of these is *Forbes 3046* from Palembang, Sumatra, which is cited above. This collection was described by S. Moore in 1925 as a new species, *Artocarpus brunneifolia*, which he distinguished from *A. maingayi* by the larger, glabrous leaves and the longer, glabrous peduncles. Apart from the velutinous syncarp, the male perianths and the stipules, the specimen is nearly glabrous. The leaves resemble those of *A. kemando* in shape, but are rather large (to 19 × 7 cm.). The inflorescences are immature, but their measurements are within the range of variation of *A. kemando*, and the umbonate processes on the young syncarp agree with *A. kemando*, rather than with *A. sumatranus* or *A. maingayi*. The collection is probably from a juvenile shoot of *Artocarpus kemando*.

The second specimen is *Burkill & Haniff SFN 13843*, Grik, Perak, Malaya (SING, ♀). This was cited by Ridley (1925) as *Artocarpus kemando*, but the characters are somewhat intermediate between this species and *A. maingayi*. The young syncarp has the velutinous surface of *A. maingayi*, but the processes are umbonate, as in *A. kemando*, and the peduncle is 12 mm. long. The obovate-elliptic, short-acuminate leaves, which measure 7.5–12 × 3.5–5 cm. and are appressed-puberulent beneath, are not typical of either species, and the peduncle also differs from both in being appressed-pubescent.

24. **Artocarpus maingayi** King in Hook. f. Fl. Brit. Ind. **5**: 542. 1888, et in Ann. Bot. Gard. Calcutta **2**: 11. *t. 8A*. 1889; Renner, Bot. Jahrb. **39**: 366. 1907; Ridley, Fl. Malay Penin. **3**: 354. 1924; Corner, Gard. Bull. Singapore **10**: 282. 1939, Wayside Trees, 657. 1940. Syntypes, Malaya, Perak, *King 3595* (CAL, not seen), *6963* (CAL, not seen; duplicates examined, BM, K, L, P, SING), *Scortechini s.n.* (not seen; duplicate examined, K), Malacca, *Maingay 1481* (CAL, not seen).

Evergreen trees, height to 40 m. *Twigs* c. 2 mm. thick, finely rugose, shortly subappressed or appressed hispid-pubescent, hairs rufous; annulate stipular scars c. 0.5 mm. broad, inconspicuous; lenticels few, scattered. *Stipules* 0.7–2 cm. long, lanceolate, acute, rufous appressed-pubescent. *Leaves* 5–18 × 2.5–7.5 cm., obovate-elliptic, varying elliptic, shortly and obtusely acuminate to shallowly retuse, base rounded or cuneate, margin entire; main veins prominent beneath; glabrous above (young leaves appressed-puberulent), main veins beneath appressed-pubescent, surface between glabrous or nearly so; lateral veins 9–13 pairs, straight or slightly curved; intercostals parallel, irregular; deep green, drying red-brown (hairs on upper surface of young leaf conspicuous); hypodermis of 1–3 cell-layers present, cells isodiametric in surface view; gland-hairs superficial to half immersed, heads depressed-globose, 4-celled; petiole 10–20 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* 30–55 × 5–6 mm., cylindric, the surface rugose, covered by flowers; perianths deeply bilobed, 0.4 mm. long, short-pubescent; stamen 0.45 mm. long, filament cylindric, anther-cells ellipsoid, 0.2 mm. long; peduncle c. 5 × 2 mm., velutinous; *female head* with simple styles exserted to 0.5 mm. *Syncarp* to 4.5 × 2 cm., subellipsoid, drying brown, fleshy, tesselate with very low, truncate processes c. 2 mm. across, velutinous with inflated hairs; scattered bracts present between the processes, heads infundibuliform, c. 0.2 mm. across; peduncle 3–8 × 4 mm., velutinous.

DISTRIBUTION: In evergreen forest to 500 ft., western and southern Malaya, Sumatra (Atjeh, Tapanuli, West and East Coast), Simalur.

Malaya. PERAK. [*Scortechini*] *s.n.* (K, ♀); Larut, *King 6963*, Dec. 1884 (BM, K, L, P, SING, ♀). SELANGOR. *Murdoch 76* (BM); Kuala Lumpur, Carcosa, *Yeob CF 5702* (SING, ♀); Kuala Lumpur, Public Gardens, *Burkill SFN 6335* (SING, ♂), *Foxworthy CF 2359*, *Green s.n.*, Nov. 1941 (SING, ♀), *Hamid CF 4893* (K, SING, ♂, ♀), *Mat Soh CF 13826* (SING, ♀); Kuala Lumpur, Weld Hills Reserve, *Hamid CF 573* (SING, ♂, ♀), *4575* (K, SING). NEGRI SEMBILAN. Tampin, *Burkill SFN 3209* (K, SING, ♂, ♀). MALACCA. Sungei Udang, *Alvins 31* (SING). JOHORE. Ma'okil For. Res., Kluang, *Wyatt Kepong FN 71305* (K, ♂); Mawai-Jemalaung road, Sungei Kayu Ara, *Corner s.n.*, May 1935 (SING).

Sumatra. ATJEH. Gajolanden, Pendeng to Gadjah, *Van Steenis 9313* (L, ♀). TAPANULI. Barus, Pankalan Tapus, *bb 28400*, *29536* (A, BO, L, SING); Sibolga, Lapian, *bb 3809* (BO, L). WEST COAST. Ophir, Aer Bangis, *bb 19850* (A, BO, L); Ophir, Gadang, *bb 19477* (A, BO, L, SING); Painan, Duku, *bb 3107* (BO, L, SING, ♀), *3139* (BO, L). EAST COAST. Asahan, Simpang Toba, *bb 10438* (BO); Bengkalis, Sungei Missigit, *Beguin 572* (BO, L). SIMALUR. *Achmad 48* (BO, L, ♂, ♀), *1256* (BO, L, ♀); Lampang Aer, *bb 3036* (BO, L); Landschap Tapah, Defajan, *Achmad 1453* (BO, L, ♂, ♀), *1522* (BO, K, L, SING, ♀).

The three following species, *Artocarpus hirsutus*, *A. nobilis* and *A. sepicanus*, are placed at the end of section *Artocarpus* as being anomalous in their characters. In the discussion of the classification of the section (p. 132 above) it is pointed out that certain characters of these species, namely, the echinate syncarp in *A. hirsutus* and the presence of well-developed interfloral bracts in *A. nobilis* and *A. sepicanus*, are intermediate to those of sect. *Duricarpus*. Additional material, which has recently become available, shows that all three species also resemble sect. *Duricarpus* in the subapical position of the style.

25. **Artocarpus hirsutus** Lamarck, Encycl. Méth. **3**: 210. 1789, "*hirsuta*"; Roxb. Fl. Ind. **3**: 521. 1832; Wight, Ic. Ind. Or. **6**: *t. 1957.* 1853; Dalz. & Gibson, Bombay Fl. 244. 1861; Beddome, Fl. Sylvat. *t. 308.* 1873; King in Hook. f. Fl. Brit. Ind. **5**: 541. 1888; King, Ann. Bot. Gard. Calcutta **2**: 9. *t. 5.* 1889; Watt, Dict. Econ. Prod. Ind. **1**: 329. 1889; Dalgado, Fl. Goa, 179. 1898; Talbot, Trees Bombay ed. 2. 332. 1902, For. Fl. Bombay **2**: 527. *fig. 532.* 1908; Cooke, Fl. Bombay **2**: 656. 1907; Renner, Bot. Jahrb. **39**: 365. 1907; Bourdillon, For. Trees Travancore, 368. 1908; Troup, Silvicult. Ind. Trees **3**: 876. *fig. 323.* 1921; Fischer in Gamble, Fl. Madras **3**: 1369. 1928.

Ansjeli Rheede, Hort. Ind. Malab. **3**: 25. *t. 32.* 1682.

Castanea Malabarica Angelina dicta Ray, Hist. Pl. **2**: 1384. 1688.

Artocarpus pubescens Willd. Sp. Pl. ed. 4. **4**: 189. 1805, nomen illegitimum; Persoon, Syn. Pl. **2**: 531. 1807; Sprengel, Syst. Veg. ed. 16. **3**: 804. 1826; Tréc. Ann. Sci. Nat. Bot. III. **8**: 122. 1847.

Ficus malabarica Miq. Hooker Lond. Jour. Bot. **7**: 457. 1848, receptaculis exclusis, quae sunt *Ficus palmata* Forskål, 1775; King, Ann. Bot. Gard. Calcutta **1**: 182. 1888. Holotype, Madras, *Wight 873* (U).

Evergreen trees, height to c. 70 m., bark grey. *Twigs* 4–7 mm. thick, rugose, appressed-hispid, hairs yellow; annulate stipular scars c. 0.5 mm. across, not prominent; lenticels scattered. *Stipules* 1.5–2.5 cm. long, ovate-lanceolate, acute, densely appressed-hispid, hairs yellow. *Leaves* 10–25 × 5–15 cm., elliptic, rhomboid or ovate, short-acuminate, base rounded to cuneate, margin entire; juvenile leaves at least to 50 × 35 cm., pinnatifid, margin dentate towards apex; main veins prominent beneath, intercostals scarcely so; glabrous above or with scattered hairs on main veins, these appressed-pubescent beneath; lateral veins 10–13 pairs, straight; intercostals parallel; dark green, drying red-brown to blue-grey above, pale red-brown beneath; hypodermis absent; gland-hairs slightly immersed, heads depressed-globose, c. 6-celled; petiole 10–20 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* 70–160 × 5–7 mm. narrowly cylindric, smooth, covered by flowers; perianths tubular, 1.5 mm. long, bilobed above, sparsely pubescent; stamen 2.2 mm. long, filament slender, cylindric, anther-cells oblong, 0.3 mm. long; peduncle 20–40 × 2.5–4 mm., sub-appressed hispid-pubescent; *female head* with simple styles exserted to c. 1 mm. *Syncarp* to at least 5 × 4 cm. (the size of a lemon, fide Beddome, 1873), short-cylindric to ellipsoid, varying subglobose, yellow to orange, drying red-brown, echinate from closely set, rigid, cylindric, acute, hispid processes, 5–8 × 1 mm.; peduncle 45–65 × 4 mm., subappressed hispid-pubescent.

VERNACULAR NAMES: *Anjili* (Tamil), *Hebhalsina* (Kanarese), *Ran-* or *Pat-phunnas* (Malayalim). USES: the wood is very valuable for boat and house building and the species is planted as a timber tree.

DISTRIBUTION: From sea level to 4000 ft. in the evergreen forests of the Western Ghats, India.

India. Peninsular India, *Wight 2174* (K); Canara and Mysore, *Law s.n.* (K); Malabar and Concan, *Hooker f. & Thomson s.n.* (CAL, U), *Stocks, Law, etc. s.n.* (BM, GH, L, P, U, ♂, ♀); Malabar, *Buchanan s.n.* (BM, ♂, ♀), *Luck s.n.* (K), *Wight 948* (U); S. Malabar, Dhoni, *Ali 27* (CGE, ♂), *Jape 27* (K), *Tiga 53* (CGE, ♂, ♀); S. Malabar, Kalladikos, *Fischer 2620* (K, ♂, ♀); Ndipu [?], *Buchanan s.n.*, Feb. 1801 (BM, ♂). TRAVANCORE-COCHIN. Cooli Thora, *Lawson 266* (DD, K, ♂, ♀). MADRAS. S. Canara, *Beddome 7520* (BM); e. of Goa boundary, Manchikeri, *Fernandes 1585* (A, ♀); Madura, Sirumalais, *Bourne 1813* (K); near Mangalore, *Hohenacker 455* (P), *Wight 2715* (C, GH, K, P, ♂, ♀); Mercara, *Wall 455* (U); Nilgiris, *Johnson s.n.*, Dec. 1850 (K, ♂); Nilgiris, Gudalier, *Gamble 15496* (K); Nilgiris, Nadiwatam, *Gamble 18262* (K); Tenkasi, Courtallen, *Wight 873* (U). MYSORE. Bababoodun Hills, *Law s.n.* (K, ♂, ♀). BOMBAY. *Law s.n.* (K, ♂, ♀); Concan, *Law s.n.* (K); Concan, Sanklu [= Sangli], *Stocks, Law & Dalzell s.n.* (K, ♂, ♀); Kala Nuddi, *Ritchie 1377* (GH, K).

Lamarck's description of *Artocarpus hirsutus* was based on Rheede's account, under the vernacular name *Ansjeli*, which may be identified with certainty as referring to this species.

Beddome stated (1873) that the florets on the male head were intermixed with numerous chaffy scales, but he apparently was referring to the rather long hairs found on the surface of the receptacle between the flowers, which are all that are shown in the analyses on his plate. King (1889) also mentioned chaffy scales, but the linear "receptacular scales" that he included in his illustration appear to be aborted florets. A careful examination has been made of the male inflorescences, and neither interfloral bracts nor sterile flowers — apart from a few of the latter that failed to develop fully — have been found.

In considering the characters of *Artocarpus hirsutus* (p. 132 above), with a view to placing it in the most "natural" position within subgenus *Artocarpus*, it is stated that the internal structure of the mature syncarp is not known. Since the publication of this section of the paper a collection has become available with what are probably the fruiting perianths of this species, containing mature pericarps. This collection, *Fernandes 1585*, which is cited above, consists of a sheet bearing some sterile shoots of *Artocarpus hirsutus* and three packets. The first packet contains fragments of the syncarp wall of *A. hirsutus* and a few fruiting perianths, with a note, "skin & seeds of wild Jackfruit." The second contains numerous mature, indurated endocarps which are sufficiently different in detail (shape and appearance of testa) to be referable without doubt to a different species. There is a note, "seeds of wild Jackfruit 10 inch × 5 inch = 80 seeds were counted." From the field label the endocarps appear to be from a fallen fruit. The only other species of *Artocarpus* found wild in the area is *Artocarpus* (subg. *Pseudojaca*) *gomezianus* (represented by a subspecies to be described in the following paper) and, although only submature syncarps have been seen of this entity, the characters of the "seeds" are in fairly good agreement with those of the endocarps on *Fernandes 1585*. The dimensions given of the fruit are also apparently erroneous and may refer to the jackfruit, since some seeds of this are preserved in the third packet.

The identity of this fruiting material cannot yet be regarded as fully established, but, in the absence of any other information, a description of the fruiting perianths and the enclosed structures is given: proximal free region thick-walled (? fleshy — somewhat decayed), "seeds" (pericarps with an indurated endocarp not separated from the thin exocarp), ovoid, 15 × 8 mm., style subapical, testa thick, reddish-purple, indurated, embryo with the radicle apical, the cotyledons equal, longitudinal, at an angle of c. 45° to the median plane of the ovary. If these perianths are correctly assigned to *Artocarpus hirsutus*, as seems likely, the characters of the embryo suggest that the species should be assigned to a new series in sect. *Duricarpus*. The species would agree with the other members of the section in most of the characters of the syncarp, but would differ in the shape of the male head and in the absence of interfloral bracts from the inflorescences.

26. **Artocarpus nobilis** Thwaites, Enum. Pl. Zeylan. *262*. 1861; Beddome, Fl. Sylvat. *t. 309*. 1873; Trimen, Cat. Pl. Ceylon, 85. 1885; King in Hook. f. Fl. Brit. Ind. **5**: *542*; King, Ann. Bot. Gard. Calcutta **2**: 12. *t. 10*. 1889; Watt, Dict. Econ. Prod. Ind. **1**: 333. 1889; Trimen, Handb. Fl. Ceylon **4**: 98. 1898; Willis, Cat. Pl. Ceylon, 84.

1911; Macmillan, Trop. Pl. & Gard. ed. 4. 250. 1935; Abeyes. & Rosayro, Checklist Ceylon, 49. 1939. Holotype, Ceylon, *Thwaites CP 2818* (PDA, not seen); isotypes (BM, C, GH, K, P).

Artocarpus pubescens auct. non Willd., Moon, Cat. Pl. Ceylon, 61. 1821.

Evergreen trees, height to 20 m. *Twigs* 10–12 mm. thick, rugose, shortly appressed-hispid; annulate stipular scars c. 1 mm. broad, not or slightly prominent; lenticels mostly in a ring below scar. *Stipules* 3–12 cm. long, oblong-lanceolate, shortly and densely appressed-hispid, hairs yellow. *Leaves* 14–32 × 8–23 cm., ovate, short-acuminate, base broadly rounded to broadly cuneate, margin inrolled, crenate or crenate-sinuate between the lateral veins; juvenile leaves pinnatifid; main veins prominent beneath, intercostals slightly so; young leaves slightly scabrid on both surfaces from minute appressed hairs, becoming smooth; lateral veins 10–13 pairs, straight; intercostals parallel; green, drying red-brown, paler beneath; hypodermis absent; gland-hairs sunken, heads flattened, 8-celled; petiole 18–25 mm. long.

Inflorescences solitary or paired in leaf-axils. *At anthesis*: *male head* 70–130 × 15 mm., cylindric, smooth, covered by flowers and bracts; perianths tubular, 1.3 mm. long, shortly bilobed above, minutely pubescent; stamen 1.8 mm. long, filament slender, cylindric, anther-cells globose, 0.2 mm. long; bracts rather stoutly stalked, heads peltate, to 0.6 mm. across, ciliate; peduncle 30–70 × 3 mm., indumentum as twig; *female head* with the surface nearly covered by peltate heads of bracts, to 0.5 mm. across, and simple styles exserted to 0.7 mm. between them. *Syncarp* to 20 × 10 cm., cylindric, drying black, covered by closely set, rigid, short-cylindric, obtuse, puberulent processes, 1 × 1–1.5 mm.; numerous peltate bracts persistent between processes; wall c. 2 mm. thick; fruiting perianths numerous, proximal free region thin-walled, not fleshy, "seeds" (pergamentaceous pericarps) obovoid, 8 × 7 mm., style subapical, testa horny, embryo with the radicle ventral, the cotyledons parallel to the median plane of the ovary, equal; core c. 12 mm. across; peduncle 110–150 × 6–8 mm., indumentum as twig.

VERNACULAR NAMES: *Del* or *Bedi-del* (Sinhalese). USES: the timber is valuable and the seeds are eaten roasted.

DISTRIBUTION: Endemic in evergreen forest up to c. 2000 ft. in the wetter parts of Ceylon.

Ceylon. *Koenig s.n.* (BM, C), *Oltmans 109*, *Rouin s.n.* (L), *Thwaites 2818* (BM, C, GH, K, P, ♂, ♀), *sine nom. 15* (L); Kandy, Hillcrest, *Worthington 6749* (CGE, ♂, ♀). (Fide Thwaites, 1861, not uncommon in the southern and central regions of the island.)

Artocarpus nobilis is the only species of the genus in which the margin of the adult leaf is more or less regularly crenate, although a shallowly crenate margin is found in some specimens, probably taken from juvenile shoots or from the lower branches of mature trees, of several other species. Koenig's specimens bear an apparently unpublished epithet under *Sitodium.*

27. **Artocarpus sepicanus** Diels, Bot. Jahrb. 67: 176. 1935, "*sepicana*." Holotype, northeastern New Guinea, *Ledermann 10628* (B).

Trees, height to 40 m., bark yellow-brown, peeling off in flakes. *Twigs* 3–5 mm. thick, scarcely to acutely rugose, glabrous; annulate stipular scars c. 0.5 mm. broad, not or slightly prominent; lenticels scattered. *Stipules* 1–3 cm. long, ovate, acute, glabrous. *Leaves* 8–30 × 4–12 cm., ovate-elliptic, ovate- or obovate-oblong or elliptic, short-acuminate, base usually oblique and half cordate, varying subequal and shallowly cordate, glabrous, margin entire or shallowly crenate; juvenile leaves to 40 × 16 cm., margin shallowly and regularly crenate; main veins prominent beneath, intercostals slightly so; lateral veins 9–16 pairs, straight; intercostals parallel; mid-green with pale yellow main veins, drying pale brown or the upper surface greyish; hypodermis absent; gland-hairs superficial, heads globose, 6–8-celled; petiole 10–25 mm. long.

Inflorescences solitary in leaf-axils. *Male head* (nearly at anthesis) c. 20–30 × 5–7 mm., cylindric, smooth, covered by perianths and bracts; perianths 2 (or 3)-fid to half their length, 0.8 mm. long, minutely pubescent; stamen, filament cylindric, anther-cells oblong, 0.4 mm. long; bracts rather stoutly stalked, heads peltate, to 0.8 mm. across, short-ciliate; peduncle c. 15–30 × 1–1.5 mm., glabrous. *Female head* (at anthesis) with bifid styles exserted to 1.5 mm. *Syncarp* (submature) to 4.5 × 1.5 cm., cylindric, green, drying light brown, the surface areolate with closely set, fleshy, very short, truncate, velutinous processes, to 0.5 × 2 mm., polygonal in surface view, (?) becoming nearly smooth; numerous bracts persistent between processes, heads peltate, to 1 mm. across; peduncle c. 25–45 × 2.5 mm., glabrous.

DISTRIBUTION: In evergreen forest to 600 ft., endemic to New Guinea.

New Guinea. VOGELKOP. Bomberai: K. Wermudena, *bb 22493* (BO, L). Manokwari: Momi, *bb 33418* (BO, K, L); Oransbari, *Brouwer BW 2513* (L); Warnapi, 15 km. from Ransiki, *Kostermans 409* (BO, L). DUTCH NORTH NEW GUINEA. Hollandia: *Schram BW 2761* (K, L, ♂, ♀); Berap, Nimburan, *bb 28906* (BO, L, ♂); Mamberamogebiet, Pioneerbivak, *bb 31101* (BO, L); Tami, *Brouwer BW 771, 782* (L). DUTCH SOUTH NEW GUINEA. Mimika, Aria, Uta, *bb 32861* (L). PAPUA. Central Division: Port Moresby, Mt. Lawas Timber Reserve, Rubulogo Creek, *Jackson NGF 4520* (K, L, SING). MANDATED TERRITORY OF NEW GUINEA. Madang District: Ramu Valley c. 5 miles se. Faita airstrip, *Saunders 181* (L). Morobe District: Lae, *NGF 694* (L, ♂). Sepik District: Malu, *Ledermann 10628*, Jan. 1913 (B, ♀); Sepik River, near Yellow River, *Womersley NGF 3785, 3871* (A, BO, K, L, SING, ♂).

The material of *Artocarpus sepicanus* which is at present available is inadequate for a complete description of the inflorescences. The internal structure of the submature syncarp of *Schram BW 7261* has been examined since the introductory portion of this paper was published and may be described as follows: wall c. 1 mm. thick; proximal region of perianths thin-walled, not fleshy, free only near the base, partly matured ovaries ellipsoid, laterally compressed, to 4 mm. long including the short stalk, pergamentaceous but somewhat indurated above the hilum, style subapical, hilum about halfway down the ventral face, testa (empty) membranaceous, with the conspicuous micropyle at the apex of the ovary, and the chalaza at the base; core c. 5 mm. across. The rather wide separation of the subapical style and the ventral hilum is unusual in *Artocarpus* but is found to a marked degree in the mature ovary of *Prainea papuana*.

Although several of the collections cited are sterile, they can be identified by the characteristic foliage. The leaves are somewhat similar to those of *A. teysmannii*, which also occurs in western New Guinea, but may be distinguished by the narrower outline, the less smooth appearance, and the oblique or shallowly cordate base.

ARTIFICIAL KEYS TO THE SPECIES OF ARTOCARPUS SUBGENUS ARTOCARPUS

Key to Specimens bearing Male Inflorescences

1. Head with the surface largely covered by the peltate heads of numerous bracts.
    2. Head cylindric, length/breadth = 4–10.
        3. Head c. 2–3 × 0.5–0.7 cm. .... 27. *A. sepicanus.*
        3. Head 7–13 × 1.5 cm. .... 26. *A. nobilis.*
    2. Head globose to clavate or short-cylindric, length/breadth = 1–3.5(–4).
        4. Twigs and leaves glabrous.
            5. Leaves pinnate. .... 1. *A. anisophyllus.*
            5. Leaves simple. .... 2. *A. lanceifolius.*
        4. Twigs and leaves (at least on the main veins beneath) hispid or hispid-pubescent.
            6. Peduncle to 0.6 cm. .... 7. *A. rigidus.*
            6. Peduncle 0.8–7.5 cm.
                7. Peduncle and twigs with patent hairs.
                    8. Head 1.5–3 × 1.5–2 cm.; peduncle 1.2–3 cm. .... 6. *A. hispidus.*
                    8. Head 4–9 × 2.5–3.5 cm.; peduncle 2.5–7 cm. .... 5. *A. odoratissimus.*
                7. Peduncle and twigs with appressed hairs.
                    9. Leaves smooth above, hispid-pubescent on the main veins only beneath; perianths 1 mm. long, deeply 2(or 3)-lobed; peduncle 0.8–5 × 0.3 cm. .... 3. *A. melinoxylus.*
                    9. Leaves scabrid above, hispid-pubescent throughout beneath; perianths 2 mm. long, shortly bilobed; peduncle 6–7.5 × c. 0.15 cm. .... 4. *A. chaplasha.*
1. Head with bracts few or entirely lacking, cylindric, varying ellipsoid or clavate, length/breadth = (1.5–)4–20.
    10. Surface of head smooth.
        11. Numerous filiform or clavate processes present between flowers and projecting 1–2 mm. from surface.
            12. Head 0.5–1 cm. across; adult leaves entire. 17. *A. teysmannii.*
            12. Head c. 2 cm. across; adult leaves deeply pinnatifid. .... 13. *A. multifidus.*

11. Projecting processes absent or a few scarcely emergent.

13. Lateral veins of leaf 6–10 pairs, curved.

14. Peduncle and twigs glabrous; head with a basal annulus formed by the enlargement of the peduncle into a flange to 3 mm. wide; base of leaf decurrent onto petiole. ...... 15. *A. heterophyllus.*

14. Peduncle and twigs pilose with patent, flexuous, rufous hairs c. 3 mm. long, varying glabrous; head without a basal annulus; base of leaf abrupt. ...... 14. *A. integer.*

13. Lateral veins of leaf 10–25 pairs, straight.

15. Peduncle densely appressed-hispid; head 7–16 × 0.5–0.7 cm. ...... 25. *A. hirsutus.*

15. Peduncle not as above.

16. Peduncle and twigs pungent with patent, rigid, rufous, acicular hairs, c. 2 mm. long. ...... 10. *A. horridus.*

16. Peduncle and twigs not as above.

17. Peduncle with subpatent, recurved hairs, hooked at the tips; head 2–2.5 × 0.5 cm. .. 16. *A. lowii.*

17. Peduncle not as above.

18. Head c. 0.7 cm. across; anthers 0.3–0.5 mm. long. ...... 9. *A. treculianus.*

18. Head more than 1 cm. across; anthers 0.6–1.2 mm. long.

19. Anthers 1.2 mm. long; adult leaves deeply pinnatifid, lobes 12–20 pairs. ...... 12. *A. pinnatisectus.*

19. Anthers 0.6–0.8 mm. long; adult leaves entire to pinnatifid, lobes to 5(–9) pairs.

20. Scattered bracts usually present (appearing as tufts of hairs on the surface); perianth lobes with deflexed, inflated hairs; leaves pubescent beneath with straight or slightly undulate hairs. .. 8. *A. blancoi.*

20. Bracts absent; perianth lobes sparsely pubescent to glabrous; leaves (in the Philippines) subglabrous beneath, except the main veins, or pubescent, frequently with uncinate hairs. ...... 11. *A. communis.*

10. Surface of head variously rugose.

21. Head 6–20 × 1–2.5 cm.; peduncle 3.5–10 cm.; twigs 0.5–2 cm. thick.

22. Head tuberculate with obtuse processes c. 3 × 2 mm., the apices pilose, hairs rufous, c. 2 mm. long. ...... 21. *A. tamaran.*

22. Head rugose-sulcate to subtuberculate, not pilose.

23. Head subtuberculate, perianths with crisped hairs. ...... 20. *A. sericicarpus.*

23. Head rugose-sulcate; perianths without crisped hairs.

24. Head 6.5–10.5 × 1 cm., shallowly sulcate; leaves smooth above, or nearly so. ...... 18. *A. scortechinii.*

        24. Head 6–20 × 1.5–2.5 cm., deeply sulcate; leaves scabrid above. . . . . 19. *A. elasticus.*
  21. Head 2–5.5 × 0.3–0.6 cm.; peduncle 0.5–2 cm.; twigs 0.2–0.3 cm. thick.
    25. Peduncle c. 2 cm., hairs appressed; leaves subappressed-pubescent throughout beneath. . . . . 22. *A. sumatranus.*
    25. Peduncle to 1.3 cm., hairs patent; leaves usually appressed-pubescent on main veins only beneath.
      26. Peduncle c. 0.5 cm., velutinous; leaves obovate-elliptic varying elliptic, shortly and obtusely acuminate to retuse, young leaves appressed-puberulent above. 24. *A. maingayi.*
      26. Peduncle 0.7–1.3 cm., pubescent; leaves elliptic-oblong varying elliptic, acute to acuminate, glabrous above. . . . . 23. *A. kemando.*

KEY TO SPECIMENS BEARING FEMALE INFLORESCENCES [12]

1. Processes covering the syncarp markedly dimorphic, the longer ones solid, flexuous, the shorter perforate, with styles exserted at anthesis.
  2. Solid processes few, to 4 mm. long; syncarp to c. 8.5 × 2.5 cm. . . . . 17. *A. teysmannii.*
  2. Solid processes numerous, longer.
    3. Adult leaves deeply pinnatifid; solid processes c. 15 × 1 mm., rough from stout, recurved hairs, the longer ones crisped. . . 13. *A. multifidus.*
    3. Adult leaves entire.
      4. Leaves shortly appressed-hispid above; solid processes 10–18 × 1–1.5 mm., shortly patent-hispid. . . . . 19. *A. elasticus.*
      4. Leaves smooth or nearly so above.
        5. Lateral veins 11–16 pairs; solid processes 20–35 × 0.5–1 mm., subappressed-pubescent, hairs c. 2 mm. long. 20. *A. sericicarpus.*
        5. Lateral veins 15–23 pairs; solid processes c. 10 × 0.5 mm., rough from short, recurved hairs. . . 21. *A. tamaran.*
1. Processes (or areolae) covering the syncarp all alike, perforate, with styles exserted at anthesis.
  6. Syncarp 15–100 × 10–50 cm., fruiting perianths thick-walled, fleshy; cauliflorous; adult leaves entire.
    7. Syncarp with a basal annulus formed by the enlargement of the top of the peduncle into a flange to 5 mm. wide (sometimes obscure); peduncle and twigs glabrous; base of leaf decurrent onto petiole. . . . . 15. *A. heterophyllus.*
    7. Syncarp without a basal annulus; peduncle and twigs pilose with patent, rufous hairs c. 3 mm. long, varying glabrous; base of leaf abrupt. . . . . 14. *A. integer.*
  6. Syncarp smaller, or fruiting perianths thin-walled or lacking (seeds not developed); not cauliflorous.
    8. Syncarp cylindric, to 20 × 10 cm., the surface covered with short-cylindric, obtuse, indurated processes, 1 × 1–1.5 mm., numerous peltate bracts persistent between them, the heads to 0.5 mm. across. . . . . 26. *A. nobilis.*

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[12] The measurements given are those of the mature syncarp but the key has been drawn up, as far as is practicable, so that it can be used for female inflorescences at any stage from anthesis to maturity.

8. Syncarp not as above.

9. Syncarp globose to short-cylindric, length/breadth = 1–1.5, the surface armoured with indurated processes; pericarp with the style apical; embryo symmetrical, the radicle apical.

10. Processes broadly cylindric, 1–4 × 1–3 mm., surface of the syncarp ± tesselate.

11. Processes pubescent; twigs and leaves glabrous. .... 2. *A. lanceifolius.*

11. Processes hispid; twigs and leaves (at least on the main veins beneath) hispid or hispid-pubescent.

12. Processes with usually patent, slightly crisped hairs; leaves smooth above, hispid-pubescent on the main veins only beneath; male peduncle 0.8–5 × 0.3 cm. .... 3. *A. melinoxylus.*

12. Processes with appressed hairs; leaves scabrid above, hispid-pubescent throughout beneath; male peduncle 6–7.5 × c. 0.15 cm. .... 4. *A. chaplasha.*

10. Processes narrowly cylindric or tapering, 5–13 × 1–1.5 mm., surface of the syncarp ± echinate.

13. Processes glabrous; adult leaves pinnate. .... 1. *A. anisophyllus.*

13. Processes hispid; adult leaves entire.

14. Processes 8–13 × 1 mm., apices clavate. .... 5. *A. odoratissimus.*

14. Processes 5–9 × 1–1.5 mm., apices acute to obtuse.

15. Peduncle 4.5–6.5 cm.; male head narrowly cylindric, 7–16 × 0.5–0.7 cm. .... 25. *A. hirsutus.*

15. Peduncle to 3.5 cm.; male head globose to obovoid, 1.3–3 × 1.3–2 cm.

16. Peduncle and twigs with patent hairs; leaves elliptic to obovate-elliptic, scabrid above, base cuneate; male peduncle 1.2–3 cm. .... 6. *A. hispidus.*

16. Peduncle and twigs with ± appressed hairs; leaves not as above (smooth above and/or base rounded); male peduncle to 0.6 cm. .... 7. *A. rigidus.*

9. Syncarp cylindric or ellipsoid, rarely subglobose, length/breadth = 1–4, the surface covered by fleshy processes or merely areolate; pericarp with the style lateral to sub-basal (apical in *A. sepicanus*); embryo often asymmetrical, the radical ventral to sub-basal.

17. Syncarp more than 10 cm. across, covered by attenuate or conical processes to 15 mm. long, varying to low facets or areolae, cultivars often seedless. .... 11. *A. communis.*

17. Syncarp less than 10 cm. across.

18. Twigs to 3 mm. thick, hispid-pubescent; syncarp to 5 × 3 cm.

19. Syncarp with conical processes; peduncle appressed-hispid-pubescent. .... 22. *A. sumatranus.*

19. Syncarp with umbonate or truncate processes, or the surface merely areolate.

20. Syncarp patent-pubescent, with low, umbonate

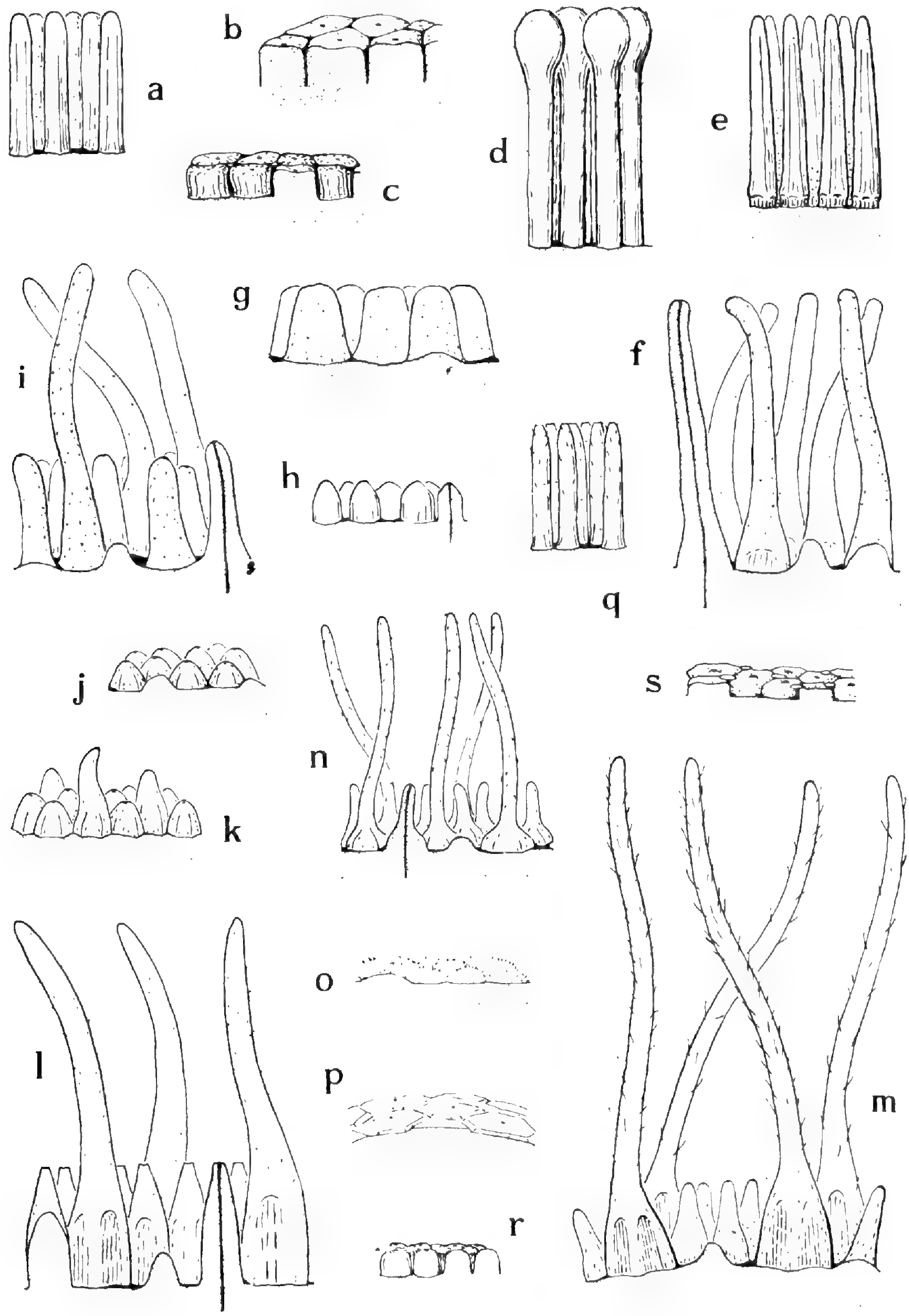

FIG. 16. The surface of the syncarp in *Artocarpus* subg. *Artocarpus*. a, *A. anisophyllus*; b, *A. lanceifolius*; c, *A. melinoxylus*; d, *A. odoratissimus*; e, *A. rigidus*; f, *A. blancoi*; g, *A. treculianus*; h, *A. horridus*; i, *A. multifidus*; j, *A. lowii*; k, *A. teysmannii*; l, *A. elasticus*; m, *A. sericicarpus*; n, *A. tamaran*; o, *A. kemando*; p, *A. maingayi*; q, *A. hirsutus*; r, *A. nobilis*; s, *A. sepicanus* (all approx. × 2½).

processes or the surface merely areolate; peduncle 1.5–4 cm., patent-pubescent. . . . . 23. *A. kemando.*

20. Syncarp velutinous, tesselate with very low, truncate processes; peduncle to 0.8 cm., velutinous. . . . . 24. *A. maingayi.*

18. Twigs stouter, or glabrous to puberulent.

21. Syncarp processes with inflated hairs, usually rough from their deflexed tips, and/or the twigs with rigid, patent, acicular hairs.

22. Leaves deeply pinnatifid, with 12–20 pairs of lateral lobes; syncarp at least 15 × 5 cm., styles simple. . . . . 12. *A. pinnatisectus.*

22. Leaves entire or pinnatifid, with up to 5(–9) pairs of lateral lobes; syncarp smaller, styles bifid.

23. Peduncle and twigs pungent with rigid, patent, acicular hairs, c. 2 mm. long; syncarp processes c. 3 × 1.5–3 mm., varying glabrous. . . . . 10. *A. horridus.*

23. Peduncle and twigs villous to glabrous; syncarp processes never glabrous.

24. Processes 2.5–4 × 2.5–3 mm., bracts absent. . . . . 9. *A. treculianus.*

24. Processes 8–15 × 1.5 mm., scattered bracts usually present. 8. *A. blancoi.*

21. Syncarp processes (or areolae) without inflated hairs; twigs without acicular hairs.

25. Twigs 8–15 mm. thick; syncarp to at least 8.5 × 5.5 cm., covered by short-cylindric, obtuse or truncate, hispid-pubescent processes c. 3 × 2 mm. . . . . 18. *A. scortechinii.*

25. Twigs to 6 mm. thick; syncarp smaller, surface not as above.

26. Syncarp with numerous peltate bracts, the heads to 1 mm. across, the surface areolate with very short, truncate, velutinous processes, (?) becoming nearly smooth. . . . . 27. *A. sepicanus.*

26. Syncarp without peltate bracts.

27. Syncarp processes conical, or with the apices depressed at maturity and the surface hence areolate; peduncle 3.5–5.5 cm., with scattered, subpatent, recurved hairs, hooked at the tips; leaves elliptic, lateral veins 11–16 pairs. . . . . 16. *A. lowii.*

27. Syncarp processes conical at maturity; peduncle 3–10 cm., without patent hairs; leaves ovate to ovate-elliptic, lateral veins 6–12 pairs. . . . . 17. *A. teysmannii.*

THE GENERA OF OLEACEAE IN THE SOUTHEASTERN UNITED STATES

KENNETH A. WILSON AND CARROLL E. WOOD, JR.

THE OLEACEAE generally have been regarded as a natural family, but there seems to be no such agreement about their position within the sympetalous dicotyledons. Usually, however, the family is treated either as the sole member of the order Oleales or as constituting suborder Oleineae of the Gentianales (Contortae), aberrant within the order especially in the reduction of the stamens to two. The former view has been held by Wettstein, Rendle, and recently by Benson (who would, in addition, divide the Gentianales), the latter by Bentham and Hooker, Engler, Engler and Diels, Engler and Gilg, and (most recently) Cronquist, among others. Hutchinson has taken a more extreme position, splitting the Gentianales into three orders and aligning the Oleaceae with the Loganiaceae in his Loganiales. These varying viewpoints reflect both the perplexing similarities and the uncertainties of the interrelationships of the Oleaceae, Loganiaceae (including Buddlejaceae), Gentianaceae (including Menyanthaceae), Apocynaceae and Asclepiadaceae, the families usually grouped together here.

Although the questions of the ordinal position of the Oleaceae and of the interrelationships of many of the sympetalous families obviously require further consideration, our purpose here, beyond merely noting these problems, is to present data from a different level in the form of treatments of the genera of the Oleaceae as they occur in the southeastern United States, thus making some of the information concerning this interesting family more readily and immediately available. These treatments are a part of a biologically oriented generic flora which is being prepared for the southeastern United States as a joint effort of the Arnold Arboretum and the Gray Herbarium made possible through the interest and support of George R. Cooley and through a grant from the National Science Foundation. This paper follows the format and scheme set forth in the preceding papers and outlined in the first publication in the series.[1] As in the previously published papers, the descriptions are based upon the species of each genus which occur within the area bounded by and including North Carolina and Tennessee, on the north, and Arkansas and Louisiana, on the west; additional characters and supplementary information based upon other species are placed in brackets when included in the description. The abbreviations used in the citation of periodicals follow the general principles set forth by Lazella Schwarten and H. W. Rickett (Bull. Torrey Bot. Club **76**: 277–300. 1958). References which are included but which have not

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[1] The previous papers in this series were published in Jour. Arnold Arb. **39**: 296–346. 1958 (woody Ranales); **40**: 94–112. 1959 (Nymphaeaceae and Ceratophyllaceae), 161–171 (Empetraceae and Diapensiaceae), 268–288 (Primulales).

been checked are followed by an asterisk (*). Annotations, when included, follow each reference and are inclosed by brackets. We are much indebted to many of our friends and colleagues in connection with all of this work on the flora of the southeastern United States. In connection with the Oleaceae, in particular, we are grateful to George R. Cooley for material of *Osmanthus* from the sand-pine scrub of central Florida.

OLEACEAE (OLIVE FAMILY)

Trees or shrubs, sometimes climbing, with opposite, seldom alternate, simple or pinnately compound leaves, without stipules. Flowers regular, bisexual, rarely unisexual (the plants then dioecious or polygamous). Calyx 4(rarely more)-lobed, rarely wanting. Corolla 4(rarely more)-lobed, petals rarely almost free or wanting; aestivation imbricate or valvate, rarely contorted. Stamens 2 (rarely 3 or 4), epipetalous, alternate with the corolla lobes, the anthers dehiscing longitudinally, the pollen usually 3(4)-colpate. Pistil solitary, of 2 carpels, the style 1 or wanting, the stigma 2-lobed or simple, the ovary superior, 2-loculed, each locule with 2 (rarely 1–4) pendulous and anatropous, or ascending and amphitropous, ovules. Fruit a berry, drupe, capsule or samara. Seed with a straight embryo, the endosperm oily or wanting.

A family of 22–30 genera and over 400 species of the temperate and tropical regions of the world, but centered primarily in Asia and Malaysia. In our area it is represented by seven genera, three of which (*Syringa, Ligustrum, Jasminum*) were introduced as ornamentals but have since become established in our flora.

The family is distinguished by the usually four-parted perianth, the two epipetalous stamens, the two-loculed superior ovary, and the usually opposite, exstipulate leaves. On the basis of the position of the ovule and seed and the nature of the fruit, the family is divided into two subfamilies and three tribes. More recent cytological and morphological studies have resulted in a reclassification of the genera of the two subfamilies into seven tribes (cf. Johnson). Cytologically, the family may be divided into two groups: (1) genera with base chromosome-numbers of 11, 13, and 14; and (2) genera with base chromosome-numbers of 23 and 24. The 23-chromosome group corresponds largely to those genera placed in the subfamily Oleoideae and presumably represents a natural group. It has been postulated that the members of this group had a common origin from an allopolyploid ancestor. On the other hand, the genera with 11, 13, or 14 chromosomes form a heterogeneous assemblage corresponding roughly to the subfamily Jasminoideae, but including also *Forsythia* and *Fontanesia*, of the Oleoideae. The family is in need of very thorough cytological and morphological study of the species in order to establish clearer and more natural generic lines and subfamily groupings.

The family is best represented in our area in cultivation, where, in addition to species belonging to our native or naturalized genera, it also includes species of *Fontanesia, Abeliophyllum, Forsythia, Phillyrea*, and *Osmarea* (*Phillyrea* × *Osmanthus*).

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KEY TO THE GENERA OF OLEACEAE

A. Flowers apetalous.
  B. Leaves pinnate; fruit a samara. .... 1. *Fraxinus*.
  B. Leaves simple; fruit drupaceous. .... 4. *Forestiera*.
A. Flowers with a distinct corolla.
  C. Corolla with elongate, nearly separate petals (united only at the base), white; fruit drupaceous. .... 5. *Chionanthus*.
  C. Corolla evidently sympetalous, with a distinct tube.
    D. Flowers unisexual or bisexual, the plants dioecious or polygamous; fruit a drupe. .... 3. *Osmanthus*.
    D. Flowers bisexual.
      E. Fruit a capsule, persistent; flowers usually lilac to purple, rarely white. .... 2. *Syringa*.
      E. Fruit a berry persisting only a few months; flowers white or yellow.
        F. Corolla less than 1 cm. long, white, 4-lobed; fruit a 2-loculed berry with membranous to stony endocarp, not 2-lobed. .... 6. *Ligustrum*.
        F. Corolla more than 1 cm. long, white or yellow, 4–9-lobed; fruit a 2-lobed berry (1 lobe sometimes aborting). .... 7. *Jasminum*.

Subfam. OLEOIDEAE Knobl.

Tribe FRAXINEAE Endl.

1. Fraxinus L. Sp. Pl. 2: 1057. 1753; Gen. Pl. ed. 5. 477. 1754.

Deciduous trees, rarely shrubs; leaves opposite, pinnately compound [or rarely simple]. Plants dioecious, polygamo-dioecious, or monoecious.

Inflorescences axillary on the branches of the preceding year, clustered or in panicles. Flowers apetalous [or petals 2–6], the calyx small, 4-parted, or wanting. Staminate flowers with 2 (rarely 3 or 4) stamens, the anthers oblong or linear, 4-loculed, dehiscing longitudinally. Pistillate flowers with 0–2 abortive stamens, the pistil with a single style, the stigma 2-lobed, the ovary with 2 pendulous ovules in each locule. Flowers perfect in *F. quadrangulata*. Fruit a 1(2)-seeded, flattened or terete samara. TYPE SPECIES: *Fraxinus excelsior* L. (*Fraxinus*, the ancient Latin name of the ash.) — ASH.

A genus of about 65 species in two sections and seven subsections, chiefly of the temperate regions of the Northern Hemisphere, centered primarily in North America, eastern Asia, and the Mediterranean region, but also extending southward into the tropics in the West Indies, Mexico, and Malaysia. The 12 species (recognized by Miller) of the United States and Canada, fall into sect. FRAXINUS, with the exception of *Fraxinus cuspidata* Torrey, of the southwestern United States, which is a member of sect. ORNUS (a group of about 26 species, chiefly of eastern Asia, with inflorescences terminal on leafy shoots). The seven species of our area belong to two subsections of sect. FRAXINUS.

Section FRAXINUS (§ *Fraxinaster* DC.), with axillary inflorescences on the branches of the preceding year, includes five subsections, four of which occur in the United States and two in our area.

Subsection FRAXINUS (subsect. *Bumelioides* Endl.), with flowers bearing a deciduous calyx, has about 15 species centered in the Mediterranean region, extending westward to central Asia. One species (*F. nigra* Marsh.) occurs in northeastern North America and in northeastern Asia (var. *mandschurica* (Rupr.) Lingelsh.). A single species, *F. quadrangulata* Michx., the blue ash, with 4-angled twigs, enters our region, ranging from Ontario, Michigan and Wisconsin, to Alabama, Arkansas and Oklahoma, in dry or moist, rich woods.

Subsection MELIOIDES Endl., with asepalous flowers, includes about 13 species of Central America, Mexico, the United States and Canada — five of which occur in our area — and two of central Asia. Our species of this subsection fall into two complexes distinguished primarily by the presence of papillae on the lower epidermis of the leaflets ("white ash complex") or by the absence of these papillae ("red ash complex"). Specific lines within the genus are difficult to define because of both genetic and ecological variation, as well as the difficulties resulting from hybridization and polyploidy. The distinctions between the various species have been based on the number, size, shape, margin, and pubescence of the leaflets; the shape of the leaf scars and of the terminal and lateral buds; and the size and shape of the samaras.

Fraxinus americana L. ($2n = 46, 92, 138$), the white ash, which occurs in rich woods from Minnesota to Quebec, to Nova Scotia, New England, Florida and Texas, is very variable in its leaf shape. Tests of various populations of this species indicate that it is composed of at least three ecotypes which differ primarily in their resistance to cold damage but also in the pubescence of the leaves. The "southern" ecotype, which ranges from Maryland to southern Indiana and southward, has pubescent leaves with reddish petioles and midribs, and suffers severely from cold damage. Both the "northern" and "intermediate" ecotypes are more resistant to winter-killing and have leaves which are somewhat less pubescent.

Fraxinus pennsylvanica (including *F. Darlingtonii* Britton, *F. Michauxii* Britton, and *F. Smallii* Britton) ($2n = 46$), the red ash, which occurs in low woods and on stream banks from Quebec to Saskatchewan, south to Florida and Texas, is also variable in the shape and texture of the leaf, and in the shape of the samaras. Progeny tests indicate that named varieties based on pubescence do not merit taxonomic recognition since pubescent seedlings may be obtained from either pubescent or glabrous parents. Three ecotypes similar to those of *F. americana* have also been described for this species (Wright). *Fraxinus pennsylvanica* differs from *F. americana* in the papillose condition of the lower epidermis of the leaflets, in the shape of the leaf scars, in the shape of the terminal and lateral buds, and in the diameter of the samaras. The two ashes are also ecologically distinct, *F. pennsylvanica* occurring in low elevations often in the vicinity of lakes and streams, and *F. americana* occurring in higher elevations; only occasionally do the two come in contact.

The status of *Fraxinus biltmoreana* Beadle, the Biltmore ash, is in need of further investigation. It has been interpreted both as a result of the rare hybridization of *F. pennsylvanica* and *F. americana*, and as a pubescent variety of the latter (var. *biltmoreana* (Beadle) J. Wright ex Fern.).

Fraxinus caroliniana Mill. (including *F. pauciflora* Nutt.), the water ash, is a shrubby tree of the swamps and lowlands of the coastal plain from Florida to Texas, northward to Virginia. Although a number of variants based on leaf pubescence and samara shape have been named, and at least one (*F. pauciflora* Nutt.) has been given specific rank, it would appear that this species is merely extremely variable.

Fraxinus tomentosa Michx. f. (*F. profunda* Bush) ($2n = 138$), the pumpkin ash, of bottom lands from Florida to Louisiana, northward to New York, Ohio, Indiana, southern Illinois, and Missouri, is a species of very questionable status. It is not clearly differentiated from *F. pennsylvanica*, and is identifiable only by average measurements of a group of characters including the length and width of the leaflets, length and width of the samaras, and length of the stomata, styles and ovaries, all of which are greater in *F. tomentosa* than in *F. pennsylvanica*. Breeding experiments are needed in *F. tomentosa* to determine whether it is an autopolyploid of *F. pennsylvanica* or is of hybrid origin.

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Tribe SYRINGEAE G. Don

2. **Syringa** L. Sp. Pl. 1: 9. 1753; Gen. Pl. ed. 5. 9. 1758.

Deciduous shrubs or small trees; leaves opposite, simple. Inflorescences terminal or lateral panicles. Flowers bisexual. Calyx campanulate, 4-toothed. Corolla salverform, 4-lobed. Stamens 2, included or exserted. Pistil with a single style, the stigma 2-lobed, the ovary with 2 pendulous ovules in each locule. Fruit a loculicidal capsule with 2 seeds in each locule. TYPE SPECIES: *Syringa vulgaris* L. (The name from the Greek *syrinx*, a pipe, originally applied to the genus *Philadelphus*[1] from the use of its branches for pipes, later transferred to this genus.) — LILAC.

A genus of about 28 species in two subgenera centered in western China, ranging east and north to Korea and northern Japan, and west and south to Tibet, Afghanistan, and the northwestern Himalaya. Two species occur in Europe in the Balkan peninsula (*S. vulgaris* and *S. Josikaea* Jacq.). The genus is represented in our flora by *S. vulgaris* which escapes sparingly from cultivation or persists in old plantings.

More than 20 species of *Syringa* are grown as ornamentals in gardens throughout the temperate world. By far the most popular species is *S. vulgaris*, represented by over 500 cultivars which have been developed by selection, cross-pollination of garden forms, or by the propagation of sports. Many of the older cultivars have already disappeared from gardens, but several hundred are still popular today.

Species of subg. SYRINGA do not hybridize with those of subg. LIGUSTRINA (Rupr.) K. Koch. Moreover, within subg. SYRINGA no hybrids have been obtained from crosses between species of different series, with the notable exception of ser. *Pinnatifoliae* Rehder, closely allied to ser. *Syringa* (ser. *Vulgares* Rehder). Both series were maintained, nevertheless, on morphological grounds in spite of the genetic compatibility between the two. Within each series there is a considerable amount of genetic compatibility, and many hybrids have been developed, often of great horticultural value, although many are sterile or lack vigor. More than 14 hybrids and their numerous cultivars, mostly in ser. *Syringa*, are in cultivation.

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[1] It is of interest that in many areas *Philadelphus* is known by the common name "Syringa."

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Tribe OLEINEAE Endl.

3. **Osmanthus** Lour. Fl. Cochinchin. **1**: 28. 1790.

Evergreen shrubs or small trees; leaves opposite, simple, entire. Inflorescences axillary or terminal, cymes or panicles. Flowers bisexual or unisexual in various combinations, the plants dioecious, [monoecious, polygamous, or bearing only bisexual flowers]. Calyx 4-parted. Corolla imbricate, 4-parted, usually with a short tube. Stamens 2 (rarely 4), included. Pistil with a single style, the stigma capitate, entire (or 2-lobed), the ovary with 2 pendulous, anatropous ovules in each locule. Fruit a 1-seeded drupe. (Including *Cartrema* Raf., *Amarolea* Small.) TYPE SPECIES: *O. fragrans* (Thunb.) Lour. (The name from the Greek *osme*, fragrance, and *anthos*, flower, in reference to the fragrant flowers.) — WILD OLIVE, DEVILWOOD.

A genus of more than 30 species in at least four sections, primarily of eastern and southeastern Asia, but extending into Polynesia, with two to four species in North America and one or two species native to our area.

Osmanthus americanus (L.) Gray, with dark purple, ellipsoid, ovoid or subglobose fruits with stones pointed at both ends or only at the base, occurs in a variety of habitats (rich woods, hammocks, wooded bluffs, sand scrubs) from Florida to Louisiana, north to southeastern Virginia, and also in Mexico. The leaves are variable in texture and shape, the fruit in shape and size, and the inflorescence in length and compactness.

At least three variants of *O. americanus* have been described from peninsular Florida. *Osmanthus megacarpus* (Small) Small ex Little, from the sand hills of Highlands County at the southern end of the Lake Region, has very much larger, globose fruit, but the range in the fruit-size overlaps that of *O. americanus*. Purported differences in the stone are of no significance, since similar shapes occur in *O. americanus*; the two are otherwise very similar. On these bases the large-fruited plant has been treated as *O. americanus* var. *megacarpus* (Small) P. S. Green. *Osmanthus floridanus* Chapm., from "sandy pine barrens, Manatee, South Florida," was said to differ from *O. americanus* in having yellowish-green fruit and pubescent inflorescences. An additional possible species was postulated by Small in a plant from the northeastern coastal region with small, globose fruit, and a stone scarcely pointed at the base. The total variation is striking, particularly in Florida, but whether species based primarily on such differences in the fruit are valid is very problematic. A study, especially in the field, of population variations in leaves, fruits, and inflorescences, correlated with habitat differences, is much needed.

Osmanthus is equally puzzling in Mexico where *O. americanus* var. *americanus* occurs in Oaxaca and Veracruz, and a small-leaved plant with compact inflorescences, var. *microphyllus* P. S. Green, is known from two collections from Nuevo León. *Osmanthus mexicanus* Lundell, with elliptic to oblanceolate, acuminate leaves, is known only from the type collection from Chiapas and appears to fall within the range of variation of *O. americanus*.

The American species of *Osmanthus* belong to sect. LEIOLEA (Spach) P. S. Green (inflorescence paniculate, corollas small and of thin texture) which otherwise includes about seven species of tropical and subtropical eastern Asia. The American species have also been treated as a separate genus, *Cartrema* Raf. (*Amarolea* Small), particularly on the basis of the more elaborately branched inflorescence. *Osmanthus americanus* is a hexaploid ($2n = 138$), while four other species (Asiatic and none belonging to this section) are diploids ($2n = 46$). The problem of the generic status of the American species deserves further study, taking into account all of the other species of *Osmanthus* and those of closely related genera, including *Linociera, Notelaea, Olea, Phillyrea,* and *Steganthus* (cf. Green).

The remaining three sections are Asiatic. Section OSMANTHUS is represented in our area only in cultivation, most notably by the very fragrant *O. heterophyllus* (G. Don) P. S. Green (*O. ilicifolius* (Hassk.) Mouillef.), $2n = 46$, and *O. fragrans* (Thunb.) Lour., $2n = 46$, the latter not hardy much to the north. *Osmanthus* × *Fortunei* Carr. is a hybrid of these two species. The species of the Pacific area present a particularly perplexing problem in the structure of their flowers and inflorescences. These may represent either a separate section or may constitute an independent genus (*Gymnelaea* (Endl.) Spach; cf. L. A. S. Johnson).

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4. **Forestiera** Poir. Encycl. Méth. Suppl. **1:** 32. 1810; **2:** 664. 1811 [1812].

Deciduous or rarely evergreen shrubs; leaves opposite simple, entire or serrate, short-petioled. Plants dioecious or polygamo-dioecious. Inflorescences axillary on the branches of the preceding year, the flowers clustered or in short racemes. Flowers apetalous, calyx minute, 4-parted or irregularly toothed, fugacious, or occasionally wanting. Staminate flowers mostly sessile, stamens 1–4, anthers oblong, 4-loculed, opening longitudinally, pistil wanting or rudimentary. Pistillate flowers on short, 1–3-flowered peduncles; abortive stamens 0–4; pistil with a slender style, the stigma simple or 2-lobed, the ovary with 2 pendulous ovules in each locule. Fruit a 1(rarely 2)-seeded black or dark-blue drupe. (*Adelia* P. Browne, nom. rejic., not L., nom. cons. [Euphorbiaceae]; *Borya* Willd., not Labill.) TYPE SPECIES: *Forestiera cassinoides* (Willd.) Poir. (*Borya cassinoides* Willd. = *Adelia cassinoides* (Willd.) O. Ktze.). (The name in honor of Charles Le Forestier, physician and naturalist during the early 1800's.)

A genus of perhaps 20 species ranging from Brazil northward through Mexico and the West Indies to the United States. The plants occurring in our area have been interpreted as representing three to six species.

The differences in interpretation of the species of this genus point to the lack of understanding of the biology of the group. The species have been distinguished on the basis of the time of flowering (i.e., before or after the leaves expand), the shape of the leaves, the shape of the fruit, the cutting of the leaf margin, the presence or absence of pubescence, and the persistence of the leaves. Additional information, particularly that based on field observation, is essential in this genus, and data on ecological variation, as well as any evidence of hybridization or introgression, should be accumulated.

The two most widely distributed species occurring in our area are *Forestiera acuminata* (Michx.) Poir., which ranges from Florida to Texas, northward to South Carolina, Tennessee, Illinois, Missouri, and Kansas on river banks, in swamps and in hammocks, and *F. ligustrina* (Michx.) Poir., ranging from Florida to Texas, Georgia, Tennessee, and Kentucky, on rocky soils, sand dunes and in pinelands. *Forestiera segregata* (Jacq.) Krug & Urban (including *F. porulosa* (Michx.) Poir.) occurs in hammocks, marshes and low pinelands and ranges from the West Indies northward to Florida and Georgia (cf. Johnston).

Forestiera acuminata and *F. neo-mexicana* Gray have both been reported to have a diploid chromosome number of 46.

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5. **Chionanthus** L. Sp. Pl. 1: 8. 1753; Gen. Pl. ed. 5. 9. 1754.

Deciduous shrubs or low trees; leaves opposite, simple, entire, petioled. Inflorescences loose, drooping panicles, from the axillary buds near the end of the year-old branches. Plants polygamo-dioecious. Calyx 4(rarely 5)-parted. Petals white, narrow, linear, united at the base. Stamens 2 (rarely 3 or 4), short, on the base of the corolla, the anthers apiculate, 4-loculed. Pistil with a short style, the stigma 2-lobed, the ovary with 2 ovules in each locule. Fruit a 1(seldom 2)-seeded dark-blue, ovoid drupe. TYPE SPECIES: *Chionanthus virginicus* L. (The name from the Greek *chion*, snow, and *anthos*, flower, in allusion to the abundant white flowers.) — FRINGE-TREE, OLD-MAN'S-BEARD.

A genus of three or four species, two in eastern North America and one or two in eastern Asia. Both American species are native in our area, and *Chionanthus retusus* Lindl. & Paxt. (China, Korea, Japan) may be found in cultivation. *Chionanthus virginicus* L. ($2n = 46$), a tall shrub or tree to 10 m. in height, the flowers with acuminate anthers and petals 2–3 cm. long, occurs in swampy or damp woods, or on stream banks, or in much drier, rocky soils with *Pinus*, *Quercus* and *Carya*, ranging from Florida to Texas, northward to New Jersey, Pennsylvania, West Virginia, southern Ohio, southern Missouri, and Oklahoma. It is also widely cultivated. *Chionanthus pygmaeus* Small, a small shrub to 40 cm. in height spreading by underground stems, the flowers with blunt-tipped anthers and petals about 1 cm. long, is an endemic of the sand-scrub in the lake region of central Florida.

Differences in the pubescence and shape of the leaves, the size of the flowers and the length of the petals are apparent between the more northern plants of *Chionanthus virginicus* and those of peninsular Florida. The significance of the variation in this species is as yet obscure.

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6. **Ligustrum** L. Sp. Pl. 1: 7. 1753; Gen. Pl. ed. 5. 8. 1754.

Deciduous or evergreen shrubs or small trees; leaves opposite, simple, entire. Inflorescences terminal panicles. Flowers white, bisexual. Calyx campanulate, 4(or irregularly)-toothed. Corolla funnelform, 4-lobed, the lobes as long as the tube or much shorter. Stamens 2, inserted on the tube of the corolla, included or exserted. Pistil with a single style, the stigma 2-lobed, the ovary with 2 pendulous, anatropous ovules in each locule. Fruit a 1–4-seeded berry with membranous to stony endocarp; [fruit dehiscent in *L. sempervirens*]. Type species: *L. vulgare* L. (*Ligustrum*, the classical name of *L. vulgare*.) — Privet.

A genus of about 30 species in three sections, chiefly of eastern Asia and Malaysia to Australia, one species (*L. vulgare* L.) in Europe and North Africa. A number of species are widely cultivated as ornamental shrubs for their foliage and attractive small, white flowers. The species represented in our flora are all escapes from cultivation; others in cultivation may also be expected to escape.

The most widely cultivated and best-known species is *Ligustrum vulgare* L. ($2n = 46$), sect. Ligustrum (sect. *Baccatae* Mansf.) (endocarp membranous, seeds 2–4), which has become widely naturalized in thickets and open woods throughout much of eastern North America.

Section Sarcocarpion (Franch.) Mansf. (endocarp dehiscent, seed 1) consists of a single species, *L. sempervirens* (Franch.) Linglesh. from western China, which is now sparingly cultivated and probably not at all represented in our area.

All other species of the genus belong to sect. Subdrupacea Mansf. ("Subdrupaceae") and at least three have become established in our area. *Ligustrum ovalifolium* Hassk. is extensively naturalized along roadsides and in disturbed areas on the coastal plain and in the piedmont from Virginia southward. Plants identified as *Ligustrum sinense* Lour. have become established in North Carolina, South Carolina, Alabama, and Louisiana, where they may grow in large stands which, when in flower, saturate the area with an unpleasant, penetrating odor. Some question exists with respect to the taxonomy and nomenclature of this plant, but the solution must await a study of the Chinese species of the genus. Reports of *Ligustrum amurense* Carr. in southeastern Virginia apparently are based on fruiting material only; these specimens seem to be identical with our *L. sinense*, but flowering material is needed to verify this identification. *Ligustrum lucidum* Ait. ($2n = 46$), and *L. obtusifolium* Sieb. & Zucc. ($2n = 46$) have been reported in scattered localities from eastern Pennsylvania, Virginia, or North Carolina southward. *Ligustrum Quihoui* Carr., which is cultivated in the Southeast, has been reported as an escape in northern Virginia and may well occur elsewhere. Conscientious collecting is very much needed to determine the present distribution and future spread of these Asiatic species. Key characters are based primarily on flowering specimens, but fruiting specimens should also be collected whenever possible.

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Subfam. JASMINOIDEAE Knobl.

Tribe JASMINEAE R. Br.

7. **Jasminum** L. Sp. Pl. 1: 7. 1753; Gen. Pl. ed. 5. 7. 1754.

Deciduous or evergreen, erect or climbing shrubs; leaves opposite or alternate, simple or pinnately compound. Inflorescences terminal or axillary on year-old branches, cymose (flowers rarely solitary). Flowers bisexual. Calyx campanulate or funnelform, 4–9-lobed, the lobes of varying length. Corolla yellow or white, [pink or red,] salverform, 4–9-lobed, the tube cylindrical. Stamens 2, included. Pistil with a single style, the stigma 2-lobed, the ovary 2-loculed, each locule with 1–4 amphitropous and ascending, or seldom anatropous and pendulous, ovules. Fruit a 2-lobed berry, each locule with 1 or 2 seeds, 1 of the 2 carpels often failing to develop. TYPE SPECIES: *J. officinale* L. (*Jasminum*, the latinized Arabic name.) — JASMINE.

A genus of about 200 species in four sections, chiefly tropical and subtropical, occurring in eastern and southern Asia, Malaysia, Africa, and Australia, with a single species (*J. lanceolatum* Ruiz & Pav.) in tropical America (Peru). Many species are widely cultivated as garden ornamentals, and several have escaped from cultivation and have become naturalized in tropical and subtropical areas. Although poorly represented in herbaria, at least four species are known to be established in the flora of our area.

Section ALTERNIFOLIA DC. (leaves alternate, simple or compound or both) is represented in our area only in cultivation by *J. humile* L. ($2n = 26$), from eastern Asia, and perhaps others.

Section TRIFOLIOLATA DC. (leaves opposite, trifoliolate) includes *J. Mesnyi* Hance ($2n = 24, 26$), from western China, an evergreen, rambling shrub with bright yellow, often double, flowers and a foliaceous calyx, which has been reported to have escaped cultivation in Georgia. *Jasminum azoricum* L., from the Canary Islands, an evergreen climber with white flowers, has become established in Key West. In addition to these, *J. nudiflorum* Lindl. ($2n = 52$), from China, a shrub with arching branches and one of the hardiest species, is widely grown for its bright yellow flowers which appear in earliest spring.

Section UNIFOLIOLATA DC. (leaves opposite, simple) is represented by *J. Sambac* (L.) Ait. ($2n = 26, 39$) and *J. amplexicaule* Wallich ex Don (= *J. undulatum* Kerr.), both of which have become established in woods and thickets in Florida. At least *J. gracillimum* Hook. ($2n = 26$) and *J. multiflorum* (Burm. f.) Andr. ($2n = 26, 39$) are also in cultivation.

Section JASMINUM (§ *Pinnatifolia* DC.) (leaves opposite, five-foliolate or more) includes *J. officinale* L. forma *grandiflorum* (L.) Kobuski ($2n = 26$), a deciduous shrub with large, white flowers, which is known both in cultivation and as an escape in pinelands and thickets in southern Florida.

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A REVISED KEY TO THE CHINESE SPECIES OF JASMINUM

Clarence E. Kobuski

Recently, while identifying a series of Chinese specimens of the genus *Jasminum*, I realized that a dozen or more taxa had been added since my earlier synopsis (Jour. Arnold Arb. **12**: 145. 1932) of the genus in China. In this first paper no new species were described. However, nearly half of the names already published were reduced to synonymy.

Since then three papers have been published by me, all of them devoted to the descriptions of new taxa or changes in nomenclature. These papers are: (1) "A new *Jasminum* from Hainan," published in Sunyatsenia **3**: 110. 1936; (2) "New and noteworthy species of Asiatic *Jasminum*," in Jour. Arnold Arb. **20**: 64. 1939; and (3) "Further notes on *Jasminum*," also in Jour. Arnold Arb. **20**: 403. 1939. Twenty taxa were described as new or changed in status in these three publications.

Other papers were published on *Jasminum* in China during this period; one, which was overlooked by me at the time, was by Hayata, Ic. Pl. Formosa, **9**: 70. 1920. In this paper a new species, *J. shimadai*, was described from Formosa. At first I was surprised that I had overlooked this paper but finally realized that in 1932, when I wrote the synopsis, Formosa was not considered as part of China but was associated with Japan. The Japanese botanists working on the flora of the island at that time related their works with the Japanese rather than the Chinese flora. The description and illustration by Hayata show that this taxon is a synonym of the very variable and widely distributed *J. lanceolarium* Roxb.

In 1933, Gagnepain, in his paper "Oleacées nouvelles d'Indochine" (Bull. Soc. Bot. France, **80**: 70, 74. 1933) oddly enough included two new Chinese species, *J. fuchsiaefolium* and *J. pinfaensis*. In his description of the former the author noted that the corolla was unknown and the fruit immature which makes it difficult to include in a key. The latter species, *J. pinfaense*, although not seen by me, is surely new and has been incorporated in the key using the description for characters.

Finally, Handel-Mazzetti, Symb. Sin. 7 ^{2}: 1012. 1936, described a new form, *J. lanceolarium* f. *unifoliolatum*, a surprising association, since *J. lanceolarium* belongs to the series *Trifoliolata* and the described form undoubtedly belongs to the series *Unifoliolata*. The very brief description consists of only two words, "*Folio unifoliolata*." I could understand the placing of this taxon with *J. lanceolarium* were there both trifoliolate and unifoliolate leaves present such as are found in *J. forrestianum*, but Handel-Mazzetti merely states that the specimen had four pairs of unifoliolate leaves. Probably, the specimen either belongs to an already described species in the unifoliolate series or represents a new species. No material is available to me at this time.

At the suggestion of some of my colleagues I have revised my earlier key to include most of the new additions. Probably other species have since been described by Chinese botanists but their works to a great extent are not available at present for comparison and study.

Further to assist workers in this group a list of accepted taxa and synonyms is given following the key.

KEY TO THE SERIES

A. Leaves alternately arranged. . . . 1. *Alternifolia.*
A. Leaves opposite in arrangement.
  B. Leaves compound.
    C. Leaves trifoliolate. . . . 2. *Trifoliolata.*
    C. Leaves five-foliolate or more. . . . 3. *Pinnatifolia.*
  B. Leaves simple. . . . 4. *Unifoliolata.*

Series 1. ALTERNIFOLIA DC.

A. Calyx-teeth subulate-setaceous, longer than calyx-tube.
  B. Leaves and plant glabrous. . . . *J. floridum.*
  B. Leaves puberulous. . . . *J. giraldii.*
A. Calyx-lobes diminutive or obtuse, shorter than calyx-tube.
  B. Leaves both simple and ternate; leaflets 5–8 cm. long; inflorescence 30–50-flowered, the corymbs 7–12 cm. across.
    C. Calyx-lobes and pedicels glabrous. . . . *J. diversifolium* var. *glabricymosum.*
    C. Calyx-lobes and pedicels villous. . . . *J. diversifolium* var. *subhumile.*
  B. Leaves ternate or pinnate; leaflets 1.5–3.5 cm. long; inflorescence 3–8-flowered. . . . *J. humile.*

Series 2. TRIFOLIOLATA DC.

A. Calyx-lobes foliaceous.
  B. Leaves persistent, coriaceous, present at time of flowering. . . . *J. mesnyi.*
  B. Leaves deciduous; flowers appearing before leaves.
    C. Plants erect or scandent; simply branched.
      D. Leaves uniformly green. . . . *J. nudiflorum.*
      D. Leaves variegated or some entirely yellow. . . . *J. nudiflorum* f. *aureum.*
    C. Plants pulvinate; intricately ramose. . . . *J. nudiflorum* var. *pulvinatum.*
A. Calyx-lobes quite vestigial or subulate when present.
  B. Leaves palmately trinerved.
    C. Leaves and branchlets glabrous. . . . *J. urophyllum.*
    C. Leaves and branchlets puberulent. . . . *J. urophyllum* var. *wilsonii.*
  B. Leaves pinnately veined.
    C. Leaves and branchlets glabrous.
      D. Terminal leaflet same size or only slightly larger than the lateral leaflets, the veining obscure. . . . *J. lanceolarium.*
      D. Terminal leaflet more than twice as large as the lateral leaflets, the veining pronounced, especially on the lower surface. . . . *J. forrestianum.*

C. Leaves and branchlets pubescent.
D. Calyx-lobes vestigial; leaves and branchlets puberulent. *J. lanceolarium* var. *puberulum.*
D. Calyx-lobes subulate-setaceous; leaves and branchlets pilose.
E. Corolla-tube up to 4 cm. long; lateral leaflets petiolulate, smaller than the terminal leaflet but up to 6 cm. long. *J. sinense.*
E. Corolla-tube ca. 2 cm. long; lateral leaflets sessile, ca. 1 cm. long, about one-tenth the length of the terminal leaflet. *J. anisophyllum.*

Series 3. PINNATIFOLIA DC.

A. Calyx-lobes subulate-setaceous, 5–8 mm. long.
B. Flowers white. *J. officinale.*
B. Flowers pink. *J. stephanense.*
A. Calyx-lobes usually obtuse or, if subulate, not more than 1 mm. long.
B. Leaflets distinctly trinerved. *J. polyanthum.*
B. Leaflets five-nerved. *J. dispermum.*

Series 4. UNIFOLIOLATA DC.

A. Calyx-lobes diminutive, obtuse, not subulate-setaceous.
B. Corolla * 35 mm. long (in toto), the tube 25 mm. long; leaves 10–26 cm. long, 6–10 cm. wide.
C. Inflorescence a subsessile, axillary cyme, with ca. 10 flowers. *J. coffeinum.*
C. Inflorescence an axillary panicle or raceme (sometimes terminal), many-flowered.
D. Veins at an acute angle, arching gracefully upward; inflorescence an axillary or terminal raceme. *J. wangii.*
D. Veins at an obtuse angle, nearly perpendicular to midrib, rather straight, arching only slightly; inflorescence an axillary panicle. *J. robustifolium.*
B. Corolla ca. 25 mm. or less in length; leaves seldom over 4 cm. wide, usually considerably less.
C. Inflorescence terminal, a many-flowered, diffuse cyme up to 10 cm. wide; corolla-tube and lobes (linear) nearly equal. *J. seguinii.*
C. Inflorescence terminal and axillary, the flowers usually in close clusters; corolla-tube considerably longer than the lobes (acute).
D. Leaves usually 9–16 cm. long, 3–4 cm. wide, lanceolate or oblong-lanceolate; Western China (Yunnan). *J. duclouxii.*
D. Leaves 3.5–8.5 cm. long, 1.5–4 cm. wide, ovate; Eastern China (Kwangtung). *J. microcalyx.*
A. Calyx-lobes subulate-setaceous.
B. Calyx-tube glabrous.
C. Leaves coriaceous.
D. Calyx-lobes ciliate; leaves pale whitish green. *J. rehderianum.*
D. Calyx-lobes eciliate; leaves verdant, not whitish.
E. Calyx-lobes not exceeding 2 mm. in length. *J. cinnamomifolium.*
E. Calyx-lobes much longer, 6–8 mm. long.

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* Corolla in *J. robustifolium* unknown.

F. Leaves small, ovate, 4 cm. or less long, ca. 1.5 cm. wide. .... *J. trineuron.*
F. Leaves much longer, 7–10 cm. long, ca. 1.5 cm. wide. .... *J. laurifolium.*
C. Leaves not coriaceous.
D. Flowers red; fruit yellow. .... *J. beesianum.*
D. Flowers white; fruit black. .... *J. nervosum.*
B. Calyx-tube pubescent.
C. Leaves and branchlets flavescent; leaves 2–4 cm. long, chartaceous, appearing nearly triangular. .... *J. nintooides.*
C. Leaves glabrous or pubescent, not flavescent, seldom less than 6 cm. long (occasionally 4–7 cm. in *J. multiflorum*).
D. Inflorescence a 3-flowered cyme subtended by two pairs of bracts with the upper pair considerably longer than the lower; flowers subsessile or nearly so; calyx white or yellowish white in flower. .... *J. albicalyx.*
D. Inflorescence not conspicuously bracteate, even though cymose; calyx green, not white in flower.
E. Corolla conspicuously double, the corolla-tube short, ca. 5 mm. long; leaves with sharply raised primary veins, especially on lower surface. .... *J. sambac.*
E. Corolla simple, with 5 lobes (occasionally 6), the corolla-tube usually 10 mm. or more in length; primary veins usually not conspicuous.
F. Leaves thin, membranaceous; calyx densely pilose with long, whitish pubescence. .... *J. pilosicalyx.*
F. Leaves not particularly thin, some coriaceous; calyx pubescence not long, whitish, pilose.
G. Stem leaves cordate at the base. .... *J. multiflorum.*
G. Stem leaves cuneate or truncate at the base.
H. Leaves distinctly cuneate at the base. *J. coarctatum.*
H. Leaves truncate or obtuse at the base, not cuneate.
I. Corolla-tube ca. 1 cm. long; leaves elliptic-oblong, 11 × 3.5 cm., very acuminate at the apex, the veins inconspicuous on the upper surface. .... *J. pinfaense.*
I. Corolla-tube up to 3 cm. long; leaves ovate, seldom over 6–7 cm. long, obtuse to broadly acute at the apex, the veins conspicuously depressed on the upper surface. .... *J. amplexicaule.*

FINDING LIST FOR THE TAXA

Accepted names are printed in bold-face type, synonyms in italics.

J. affine Lindl. = **J. officinale**
J. albicalyx Kob.
J. amplexicaule Buch.-Ham.
J. anastomosans Wall. = **J. nervosum**
J. angulare Bunge = **J. nudiflorum**
J. angustifolium Ker. = **J. laurifolium**
J. angustifolium var. *β laurifolium* Ker = **J. laurifolium**
J. anisophyllum Kob.
J. arboreum Ham., not Schultes = **J. diversifolium**
J. argyi Lévl. = **J. floridum**

J. beesianum Forrest & Diels
J. beesianum × *officinale* f. *grandiflorum* = **J. × stephanense**
J. bicorollatum Noronha = **J. sambac**
J. blinii Lévl. = **J. polyanthum**
J. bodinieri Lévl. = **J. sinense**
J. chrysanthemum Roxb. = **J. humile** var. **revolutum**
J. cinnamomifolium Kob.
J. coarctatum Roxb.
J. coffeinum Hand.-Mazz.
J. delafieldii Lévl. = **J. polyanthum**
J. delavayi Franchet = **J. beesianum**
J. discolor Franchet = **J. lanceolarium**
J. dispermum Wall.
J. diversifolium Kob.
J. diversifolium var. **glabricymosum** (W. W. Sm.) Kob.
J. diversifolium var. **subhumile** (W. W. Sm.) Kob.
J. duclouxii (Lévl.) Rehd.
J. dumicola W. W. Sm. = **J. duclouxii**
J. dunnianum Lévl. = **J. lanceolarium** var. **puberulum**
J. esquirolii Lévl. = **J. multiflorum**
J. floridum Bunge
J. floridum var. *spinescens* Diels = **J. floridum**
J. forrestianum Kob.
J. fragrans Salisbury = **J. sambac**
J. fuchsiaefolium Gagn.
J. giraldii Diels
J. grandiflorum L. = **J. officinale** f. **grandiflorum**
J. heterophyllum Roxb. = **J. diversifolium**
J. heterophyllum var. *glabricymosum* W. W. Sm. = **J. diversifolium** var. **glabricymosum**
J. heterophyllum var. *subhumile* W. W. Sm. = **J. diversifolium** var. **subhumile**
J. humile L.
J. humile var. **glabrum** (DC.) Kob.
J. humile var. **siderophyllum** (Lévl.) Kob.
J. inodorum Jacq. = **J. humile**
J. inornatum Hemsley = **J. microcalyx**
J. lanceolarium Roxb.
J. lanceolarium var. **puberulum** Hemsley
J. laurifolium Roxb.
J. macrophyllum Hort. = **J. diversifolium**
J. mairei Lévl. = **J. humile** var. **siderophyllum**
J. mairei var. *siderophyllum* Lévl. = **J. humile** var. **siderophyllum**
J. mesnyi Hance
J. microcalyx Hance
J. multiflorum (Burm. f.) Andrews
J. nervosum Lour.
J. nintooides Rehd.
J. nudiflorum Lindl.
J. nudiflorum f. **aureum** Dippel
J. nudiflorum var. **pulvinatum** (W. W. Sm.) Kob.
J. nudiflorum var. *variegatum* Mouillefert = **J. nudiflorum** f. **aureum**
J. odoratum Noronha = **J. sambac**
J. officinale L.
J. officinale f. **grandiflorum** (L.) Kob.
J. pachyphyllum Hemsley = **J. lanceolarium**
J. paniculatum Roxb. = **J. lanceolarium**
J. pentaneurum Hand.-Mazz.
J. pilosicalyx Kob.
J. pinfaense Gagn.
J. polyanthum Franchet
J. prainii Lévl., syn. nov. = **J. laurifolium** Roxb.
J. primulinum Hemsley = **J. mesnyi**
J. pubescens Willd. = **J. multiflorum**
J. pubigerum D. Don *β glabrum* DC. = **J. humile** var. **glabrum**
J. pulvinatum W. W. Sm. = **J. nudiflorum** var. **pulvinatum**
J. quadrifolium Buch.-Ham. = **J. sambac**
J. quinquinerve Lambert = **J. dispermum**
J. rehderianum Kob.
J. reticulatum Wall. = **J. coarctatum**
J. revolutum Sims = **J. humile** var. **revolutum**
J. robustifolium Kob.
J. sambac (L.) Aiton
J. sambuc Wight = **J. sambac**
J. schneideri Lévl. = **J. duclouxii**
J. seguinii Lévl.
J. shimadae Hayata = **J. lanceolarium**
J. sieboldianum Blume = **J. nudiflorum**
J. sinense Hemsley
J. × stephanense Lemoine & Son

J. subhumile W. W. Sm. = **J. diversifolium** var. **subhumile**
J. subulatum Lindl. = **J. floridum**
J. taliense W. W. Sm. = **J. seguinii**
J. trineuron Kob.
J. tsinlingense Lingelsheim = **J. giraldii**
J. undulatum Ker-Gawler, not Willd. = **J. amplexicaule**
J. urophyllum Hemsley
J. urophyllum var. *henryi* Rehd. = **J. urophyllum** var. **wilsonii**
J. urophyllum var. **wilsonii** Rehd.
J. valbrayi Lévl. = **J. beesianum**
J. viminale Salisbury = **J. officinale**
J. violascens Lingelsheim = **J. beesianum**
J. vulgatum Lamarck = **J. officinale**
J. wallichianum Lindl. = **J. humile** var. **glabrum**
J. wangii Kob.
J. wardii Adamson = **J. beesianum**
J. zambac Roxb. = **J. sambac**
Lonicera cavaleriei Lévl. = **J. sinense**
L. rehderi Lévl. = **J. sinense**
Melodinus duclouxii Lévl. = **J. duclouxii**
Mogorium pubescens Lamarck = **J. multiflorum**
M. sambac Lamarck = **J. sambac**
M. undulatum Lamarck = **J. sambac**
Nyctanthes multiflora Burm. f. = **J. multiflorum**
N. pubescens Retzius = **J. multiflorum**
N. sambac L. = **J. sambac**
N. undulatum L. = **J. sambac**

THE GENERA OF PLUMBAGINACEAE OF THE SOUTHEASTERN UNITED STATES [1]

R. B. CHANNELL AND C. E. WOOD, JR.

IN A PRECEDING PAPER in this series (The genera of the Primulales of the southeastern United States, Jour. Arnold Arb. **40**: 268–288. 1959), the Plumbaginaceae were excluded from the order Primulales. However, various authors have associated this family and order (especially through the Primulaceae), on the basis of the pentamerous floral symmetry, sympetalous corolla, obdiplostemony, and unilocular ovary with a single, basal, anatropous ovule. Other authors have treated the Plumbaginaceae as a separate, but related, order, the Plumbaginales. In contrast, Hallier allied the family with the Caryophyllales (Centrospermae), and a recent study by Friedrich (Phyton Austria **6**: 220–263. 1956) led to a similar conclusion. Considering evidence from anatomy, floral morphology, palynology, embryology, and cytology (as well as from ecology and geographical distribution), Friedrich placed the Plumbaginaceae in the Caryophyllales as a separate suborder, Plumbaginineae, perhaps derived from near the Phytolaccaceae (which with Achatocarpaceae, Gyrostemonaceae, Tetragoniaceae, Nyctaginaceae, Molluginaceae, and Ficoidaceae constitute his suborder Phytolaccineae). In such a position the Plumbaginaceae are aberrant in the sympetalous corolla, anatropous ovule and straight embryo. The suggestion of Cronquist (Bull. Jard. Bot. Bruxelles **27**: 22, 23. 1957) that the family be retained in a separate order Plumbaginales, related to but more advanced than the Caryophyllales, seems to be both flexible and reasonable to follow at the present time.

PLUMBAGINACEAE (LEADWORT FAMILY)

Perennial [rarely annual] herbs or subshrubs [sometimes lianas] of polygonaceous habit, ours with alternate, simple, entire, exstipulate leaves. Flowers complete, actinomorphic, 5-merous, hypogynous, bracteate, often heterostylous, variously disposed, ours racemose to paniculate or in modified cymes. Calyx synsepalous, plicate, prominently 5–10-ribbed [-angled or -winged], the lobes membranous or scarious, showy, persistent. Corolla sympetalous or of nearly or quite distinct clawed petals, marcescent, the

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[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium made possible through the support of George R. Cooley and the National Science Foundation. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. **40**: 94–112, 161–171, 268–288. 1959, and in the present issue. We are indebted to Dr. G. H. M. Lawrence and Dr. L. H. Shinners for their kind help in connection with the nomenclature of *Plumbago capensis*.

lobes contorted and imbricate. Stamens opposite the lobes of the corolla, epipetalous at the base of the corolla or hypogynous, introrse, the anthers 2-loculed, longitudinally dehiscent, the pollen grains often dimorphic. Gynoecium 5-carpellate; styles 1 or 5, linear; stigmas 5, linear [or capitate]; ovary 1, unilocular, usually 5-lobed or -ribbed, the single anatropous, 2-integumented ovule pendulous from a funicle arising from the base of the locule. Fruit an achene, utricle or capsule, wholly or partly enclosed by the persistent calyx. Seed with a straight embryo and firm crystalline-granular endosperm. Embryo sac tetrasporic, 8-nucleate of several distinctive types. (Armeriaceae.)

A family of ten genera and approximately 325 species, chiefly of semi-arid, saline and calcareous situations, of wide geographical distribution, mostly of the Old World, especially the Mediterranean and Central Asiatic regions; a number of species cultivated as ornamentals.

The Plumbaginaceae are distinguished from other sympetalous groups by the combination of obdiplostemony, five styles or style-branches, and unilocular ovary with a solitary basal ovule.

The occurrence over the herbage of two types of epidermal glands which secret mucilage and/or calcium salts is a characteristic feature of the family. Chalk glands are universally present on or depressed below the surface of the leaves and stem, and commonly exude water and calcium salts, the latter finally being dispersed over the surface of the plant by rain. Elevated capitate glands which secrete mucilage occur in various members of the family, but apparently are of more restricted distribution, usually being confined to the leaf-axils and the upper surface of the leaf-bases.

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KEY TO THE GENERA OF PLUMBAGINACEAE

Leaves cauline; flowers short-pedicelled, borne singly at the nodes in spike-like racemes; corolla tubular-salverform, at least twice as long as the calyx; style 1, slender, with 5 stigmas. . . . . 1. *Plumbago.*

Leaves radical; flowers sessile, borne singly or 2 or 3 together in secund spikes, these in panicles or corymbs; corolla of distinct or nearly distinct, long-clawed lobes; styles 5, distinct throughout, filiform, each with a linear-clavate stigma. . . . . 2. *Limonium.*

Tribe PLUMBAGINEAE Spach

1. **Plumbago** L. Sp. Pl. 1: 151. 1753; Gen. Pl. ed. 5. 75. 1754.

Leafy herbs or subshrubs of *Polygonum*-like habit, inhabiting hammocks and waste places, the stems somewhat woody and often greatly elongate, the flowers borne in elongate spike-like racemes or panicles at the ends of the branches and in the upper leaf axils. Flowers solitary at the nodes on short pedicels, each subtended by a bract and two lateral bracteoles; at least some species heterostylous. Calyx tubular, truncate at the base, the 5 ribs beset with prominent capitate-glandular trichomes, the somewhat inequilateral triangular lobes short, the sinuses hyaline. Corolla salverform, long-exserted, the lobes broad. Stamens with long, slender filaments free from the corolla; pollen monomorphic, deeply tricolpate with an ornamentation of coarse, blunt spines. Style 1, slender, terminated by a tuft of 5 linear-clavate stigmas; ovary pestle-shaped, the neck tapering into the style. Capsule included, beaked, dehiscent into 5 thick-textured rigid valves, these sometimes coherent at the base and apex; seed linear-oblong, somewhat pointed. Embryo sac of the "Plumbago" type, lacking synergid and antipodal cells. TYPE SPECIES: *P. europaea* L. (The name from Latin, *plumbum*, lead, perhaps alluding to the occurrence of epidermal "chalk" glands, their calcareous exudate imparting a lead-gray color to the herbage.) — LEADWORTS.

A pantropical genus of approximately 20 species, only *Plumbago europaea* and possibly *P. capensis* Thunb. found outside tropical and subtropical regions; one species native in our area, two or more cultivated, one naturalized.

Plumbago scandens L. is an erect, decumbent or climbing, somewhat woody plant, confined in our area to the southern portion of peninsular Florida where it grows in shady hammocks, as well as on shell mounds in open situations. It has a wide distribution through the West Indies to Argentina, Bolivia, and Peru, and also occurs from Texas and Arizona southward through Mexico and Central America. The calyx, 8–9 mm. long at anthesis, bears prominent capitate-glandular trichomes along the ribs from tip to base, but is otherwise glabrous; the tube of the white or purplish corolla is 1.5–2 cm. long.

A second species, an erect, often diffusely branched, cultivated shrub, a native of South Africa, has become naturalized along roadsides and in waste places in some areas of southern Florida. The azure-blue (or white) corollas have tubes 2.5–4 cm. long, and the calyces, 10–12 mm. long at anthesis, are pubescent, in addition to bearing the characteristic gland-tipped trichomes along the distal two-thirds of each rib. Although it has long been known as *Plumbago capensis* Thunb. (1794), the correct name for this plant eventually may prove to be *P. auriculata* Lam. (Encycl. 2: 270. 1786), which was included by Boissier in the synonymy of *P. capensis* in DC. Prodr. 12: 693. 1848. Lamarck's description may apply to this plant, but the critical characters of corolla and calyx, without which certain identification is impossible, are not mentioned. *Plumbago auriculata* was adopted by Merrill (Fl. Manila, 361. 1912) without discussion and apparently only on the basis of Boissier's disposition of the name. He has been followed by several other authors, but it seems best to retain Thunberg's very widely known name unless the holotype of *P. auriculata* can be located and shown to be the plant in question. *Plumbago capensis* is sufficiently hardy to be cultivated on much of the southeastern Coastal Plain, especially near the coast. Chromosome numbers of $2n = 14$ and 16 have been reported for this species. The red-flowered *P. indica* Thunb., a native of southern Asia, is also cultivated in the southeastern United States. Heterostyly has been reported in both of these species.

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Tribe STATICEAE Bartl.

2. **Limonium** Miller, Gard. Dict. Abr. ed. 4. 1754, nom. cons.

Acaulescent herbs of *Rumex*-like habit, with tough, thickened caudices, petioled radical leaves and naked scapes forming ample panicles or corymbs, the ultimate branches bearing the singly disposed flowers or few-flowered spikelets as secund spikes. Flowers sessile or nearly so, subtended by 3 (or more) ensheathing bracts (the inner the longer); [flowers often heterostylous]. Calyx tubular-funnelform, prominently 5-ribbed, the 5 lobes scarious-hyaline in texture, often with smaller intervening lobes or dentate-erose sinuses. Corolla blue or lavender, the 5 lobes nearly or quite distinct, long-clawed. Stamens with long, slender filaments, epipetalous at the base of the corolla claws or nearly hypogynous; pollen tricolpate, monomorphic [or often dimorphic], ornamented with polygonal areoles surrounded by rods with swollen ends arranged in complete rows. Styles 5, rarely 3, separate, linear-filiform, as long as the filaments; stigmas 5, often dimorphic, ours monomorphic, linear-clavate, papillate; ovary short, cuneate-clavate, truncate. Fruit indehiscent, oblong-clavate, prominently 5-angled, truncate, included or exserted from the persistent calyx, usually capped by the marcescent corolla and the 5 style bases. Seed oblong-ovate, the embryo straight, in mealy endosperm. Embryo sac of the "Fritillaria" type. (*Statice* L., 1753, partim, emend. Willd. 1809, nom. rejic.) TYPE SPECIES: *L. vulgare* Mill. (The name derived from *leimonion*, the ancient Greek name, presumably from *leimon*, a marsh.) — SEA-LAVENDER, MARSH-ROSEMARY, CANKER-ROOTS, STATICE.

Approximately 150 species in 16 sections, the genus occurring on all continents; four species in our area, all of sect. LIMONIUM, subsect. LIMONIUM, and in need of re-evaluation.

Limonium angustatum (Gray) Small (not *L. carolinianum* var. *angustatum* sensu Blake), with linear-lanceolate leaves ending in cusps 2 mm. long, is known only from the Florida Keys. *Limonium obtusilobum* Blake, distinguished by the glabrous calyx with obtuse lobes 0.4–0.8 mm. long, is widespread, but apparently uncommon, in Florida. *Limonium carolinianum* (Walt.) Britt. var. *carolinianum*, having quite glabrous calyx tubes with lobes 0.5–0.7 mm. long, is distributed in salt marshes along the coast from

Mississippi to Florida, north to southeastern New Hampshire; var. *compactum* Shinners occurs on the coast of Texas. *Limonium Nashii* Small, characterized by pubescent calyx tubes with lobes 1–1.7 mm. long, occurs from Louisiana to Florida, north to Newfoundland and the Gulf of St. Lawrence. The latter two species apparently intergrade.

Most species of *Limonium* are dimorphic in respect to pollen structure and stigma morphology. Such dimorphic types are self-sterile but cross-compatible. In *L. vulgare* heterostyly of the conventional kind is also known. Monomorphic, self-compatible species with a single pollen- and stigma-type are known in a number of sections. Such monomorphism is regarded by Baker as a secondary development within the genus. The European and South American members of subsect. LIMONIUM are all dimorphic, with one exception, *L. humile* Mill., of Ireland and Britain; all of the North American species, including ours, are monomorphic. Both *L. mexicanum* Blake, of Baja California, and *L. californicum* (Boiss.) Heller, are diploid ($2n = 18$), whereas, on the basis of inferences drawn from pollen measurements, the plants along the Gulf of Mexico and the Atlantic coast are tetraploids.

Balanced chromosome numbers of 12, 14, 16, 18, 28, 36 and 64 ($x = 6, 7, 8, 9$) have been reported for various species of *Limonium*. Plants with somatic numbers of 27, 32, 33, 34, 35 and 37 are either known to be or are suspected of being apomictic, a condition not yet demonstrated in any of the species in subsect. LIMONIUM.

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VANDERBILT UNIVERSITY
AND
THE ARNOLD ARBORETUM

STUDIES ON THE STIPULES OF SIX SPECIES OF VITACEAE

J. J. SHAH

MAJUMDAR (1955, 1956), AND HIS STUDENTS (Mitra and Majumdar, 1952; Majumdar and Pal, 1958) have recently reviewed the work on stipules, and hence no detailed survey of the literature is made here. So far as the writer is aware, the origin and development of stipules of the Vitaceae have not been studied. Even in some of the recent studies on stipules, the earliest stages of stipule initiation and vascularization have not been fully described. Lubbock (1899) described the stipules of the Vine as large and appearing some time before the leaves covering the whole bud. Sinnott and Bailey (1914) reported 3-, 5-, or 7-lacunar nodes in the Vitaceae and stated that the two stipules are broad-based, each opposite a pair of traces. Arshad (1955) studied the nodal anatomy of six species of *Vitis*. Surprisingly, Lawrence (1951) describes the stipules of the Vitaceae as "petiolar."

MATERIALS AND METHODS

The present contribution deals with four species of *Cissus* and two species of *Cayratia*. The species studied are *Cissus quadrangularis* Linn., *C. rotundifolia* Vahl, *C. amazonica* Linden, and a species of *Cissus* which, after an examination of some of the fresh material available on the University campus, I think should probably be considered as a variety of *C. quadrangularis*, together with *Cayratia carnosa* Gagnep. and *C. auriculata* Gamble. The material of *Cissus amazonica* was obtained from the Royal Botanic Gardens, Kew, England. The other materials were collected from the Botanic Garden, M. T. B. College, Surat; the University Botanic Garden, M. S. University, Baroda; and the campus of Annamalai University, Annamalainagar, India. Dr. R. D. Adatia, of Bombay, also kindly supplied some materials, especially of *Cayratia auriculata*. Documenting specimens are in the Herbarium of the M. S. University of Baroda.

Apical buds were fixed in formalin-acetic-alcohol and by usual methods of dehydration and infiltration were embedded in Merck paraffin or Fisher tissuemat. Transverse and longitudinal sections 8–12 μ thick were cut either parallel to or at right angles to the flat surface of the bud. These were stained with safranin and fast green or safranin and anilin blue combinations. Serial hand-cut sections of the mature stem were also examined. The clearing of apical buds and mature nodal portions was done by keeping the materials in 5–10% sodium or potassium hydroxide at room temperature in the oven at 50–60° C. The material was thoroughly washed in water, and, as suggested by Foster (1955), chloral hydrate was also sometimes used. Dilute acetic acid was used to correct too great transparency of the material (Cavers, 1947). The cleared material was then stained with safranin. The material of *Cissus* species gave excellent results. Camera-lucida diagrams were drawn with a Leitz prism-type drawing apparatus.

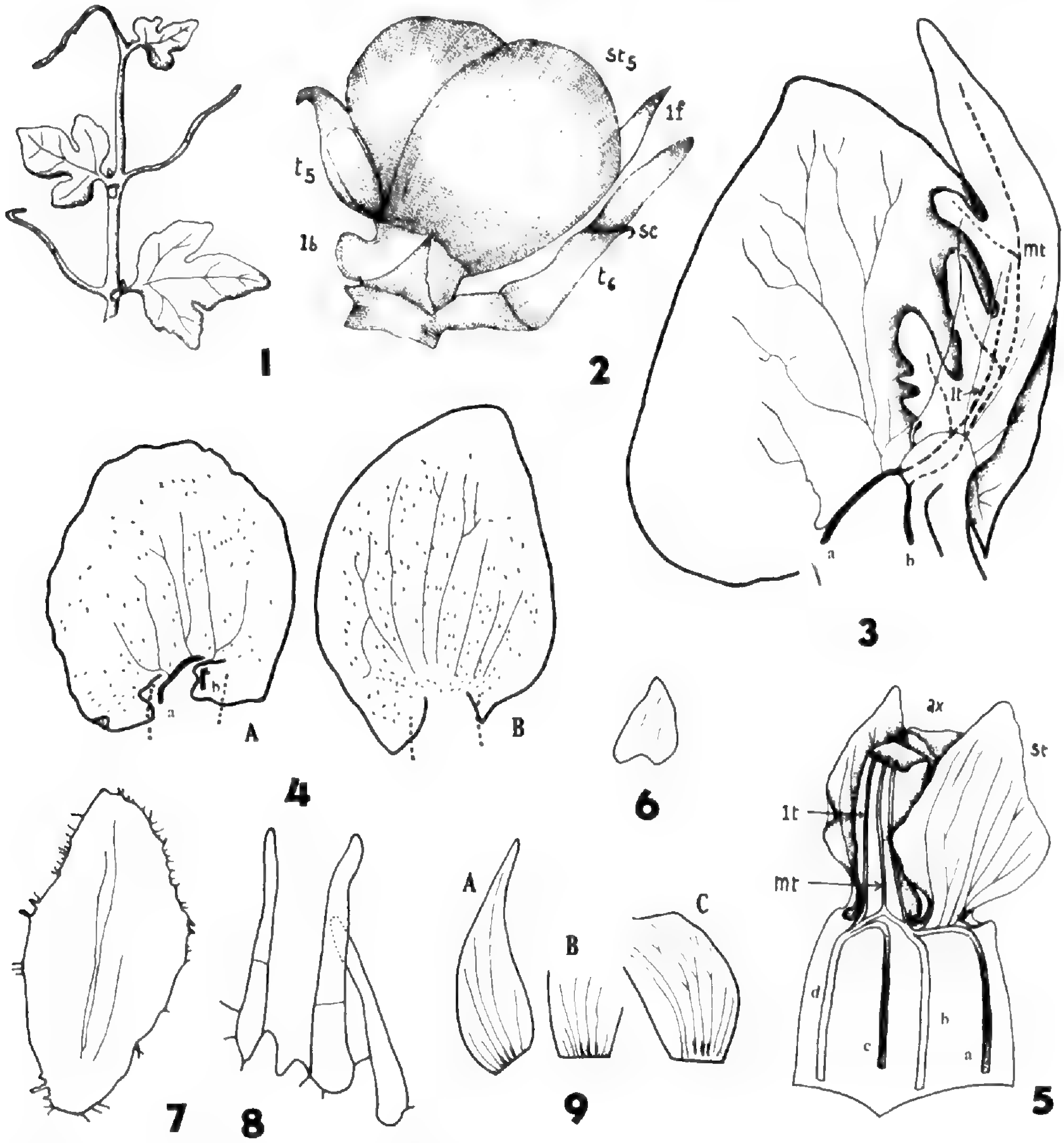
OBSERVATIONS

General morphology. All the species referred to above are tendril climbers. In all the species of *Cissus* the stipules are prominent, free and lateral. They appear to arise from the stem on either side of the base of the leaf (Figs. 1, 2, 5). In young buds, because of their early development and maturity, the stipules are very conspicuous and fully cover the young primordia of leaves and tendrils (Fig. 2). The stipules, except those of *C. amazonica*, are cordate or ear-shaped, broad and auricled (Figs. 2, 3, 4, 5). Each stipule has at its base two auricular lobes, usually situated below the node and partly covering the internode (Fig. 2).

The stipules of *Cissus amazonica* are large, ovate-falcate, acuminate and hairy (Fig. 9). The stipules of *Cayratia carnosa* are comparatively small, triangular or ovate and hairy (Figs. 6, 7), while those of *Cayratia auriculata* are ear-shaped, as in the three other species of *Cissus*. The basal region of the old stipules of both *Cayratia carnosa* and *Cissus amazonica* sometimes becomes dark and cushion-like. The number of vascular strands present depends upon the age of the stipules (Figs. 3–5, 9A–9C). The vascular strands traverse the stipules almost vertically, and most of them are independent of one another, branching being scarce (Figs. 3–6, 9A–9C). The venation is not always uniform in the stipules of the same species (Figs. 4A, 4B). The stipular scars are cauline.

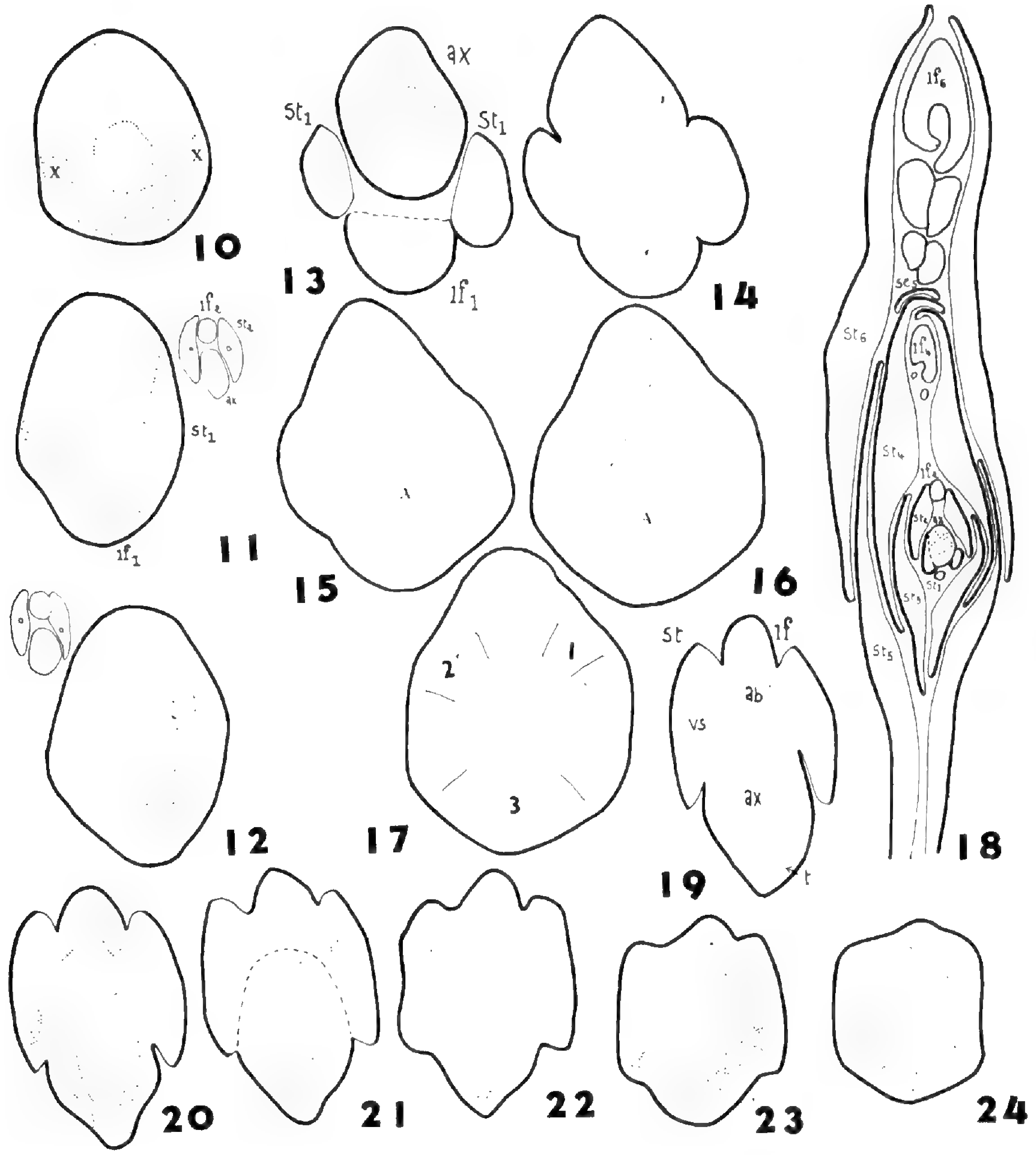
Origin of stipules. The detailed study of the origin of the stipules was concentrated mainly on the *Cissus* sp., *Cissus quadrangularis* and *Cayratia carnosa*, though important stages were ascertained in other species. In *Cissus amazonica* full investigations could not be pursued due to lack of sufficient material. Since most of the stages are similar in the first two species, only the stages observed in the first one will be described fully. Figure 18 illustrates the general arrangement of the stipules and leaves at the shoot apex of the *Cissus* sp. The tangential extensions of the stipule-pairs on either side of the shoot apex and the overlapping of stipular margins on one side only, to form a sort of equitant vernation, are evident. The following table will indicate the relative growth of the leaf and the stipule at the shoot apex. Measurements are in microns.

Node		1	2	3	4	5
Stipule	height	399	848	1441	2288	2627
	width	90	170	210	339	429
Leaf height		174	363	725	1695	5085



FIGS. 1–3, *Cissus* sp.: 1, Habit sketch; 2, Apical tip (numerals indicate the number of primordia from the apex), × 7; 3, Vascular supply of a young leaf and its stipules from a cleared preparation, × 15. FIGS. 4–5, *Cissus quadrangularis*: 4A, B, Two stipules with different venation, × 9; 5, Vascular supply of the leaf and its stipules from a cleared preparation. FIGS. 6–8, *Cayratia carnosa*: 6, 7, Old and young stipules, × 3 and 9, respectively; 8, Hairs of a stipular margin, × 130. FIG. 9, *Cissus amazonica*: A, B, C, Stipules with different venation-patterns, × 2. Abbreviations: ax = axis; lb = basal lobe of the stipule; lf = leaf; lt = lateral leaf trace; mt = median leaf trace; sc = scale of the tendril; st = stipule; t = tendril.

The organization of the shoot apex and the various stages of leaf and tendril development of various species of *Cissus* and *Cayratia* have already been described (Shah, 1956). In *Cissus* and *Cayratia* there are respectively two and three tunica layers. In both genera the initiation of the stipular primordium is first discernible when the shoot apex expands at one of its sectors to form the leaf-buttress (foliar foundation of Majumdar, 1942). The latter is identified as a crescent-shaped area surrounding the rest of the apex (FIGS. 10, 25). Towards its two lateral ends, or flanks, T_2 and inner corpus cells in *Cissus* divide periclinally and anticlinally forming two small protrusions, the earliest visible stipular primordia. FIGURES 30 and 31 illustrate the comparable histogenic development in *Cayratia*. On the lateral sides of the apex just above the young foliar primordium two regions of stipular initiation (st′) are evident (FIG. 30). In these sections the regions of stipular initiation and the leaf appear to be separated clearly,



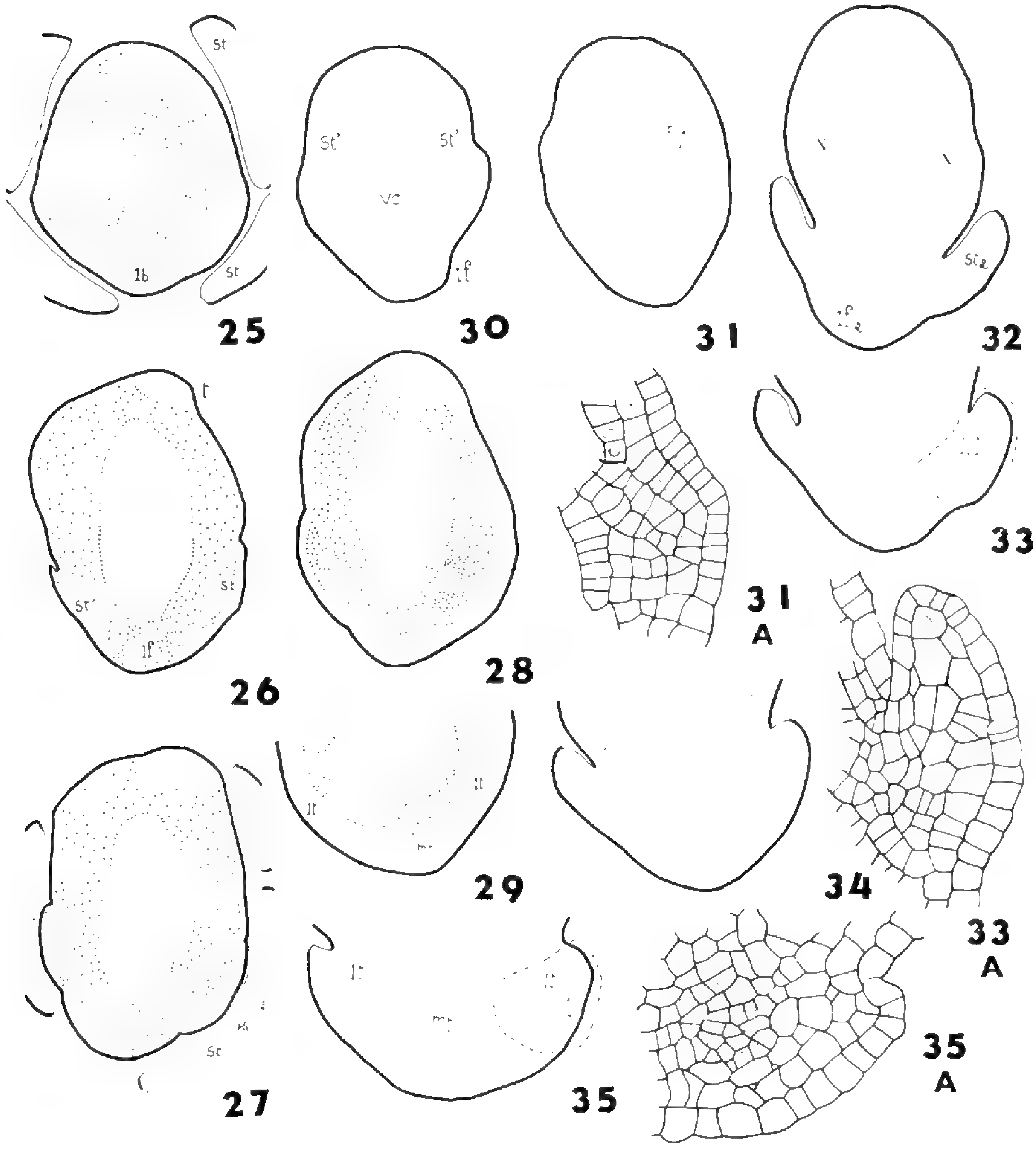
FIGS. 10–18, *Cissus* sp.: 10, Transection of shoot apex at leaf-buttress stage (X = meristematic activity), × 130; 11, 12, Transection of shoot apex at first visible node, 60 and 72 microns below apex, × 130 (inset figs. × 26); 13–17, Serial transections of shoot apex, 40, 50, 70, 90, and 100 microns, respectively, below the apex (height of right and left stipules 30 and 20 microns), A = region that is less stained, × 130; 18, Transection of shoot apex showing general arrangement of stipules and leaves (numerals indicating the respective number of the primordium from the shoot apex), × 22. FIGS. 19–24, *Cissus rotundifolia*: Serial transections of shoot apex at second visible node (Figs. 20–24 respectively from 18, 27, 36, 54 and 81 microns below Fig. 19), all × 70.

though in subsequent stages the stipules appear closely associated with the leaf (FIGS. 26, 27, 32). In fact, the shoot apex at this stage shows three meristematic areas, the two lateral ones belonging to the stipules and the median one to the leaf (FIGS. 26–27, 30–31). At this stage no procambium for the stipule trace could be observed. Cross (1937) reported similar findings in *Morus*, but did not specifically mention that the stipular primordia arose from the leaf buttress. In *Liriodendron* the median portion of the leaf buttress enlarges to become the leaf primordium and its flanks become the stipular primordia (Millington and Gunckel, 1950; Pray, 1955). In *Glycine* (Sun, 1957) the stipular primordia are clearly associated both with the base of the leaf primordium and with the flanks of the shoot apex. However, the stipule is initiated when the leaf primordium is about 70 μ high in *Morus* (Cross, 1937), 60–80 μ high in *Glycine* (Sun, 1957) and in *Opuntia* (Boke, 1944) the stipule is initiated before the leaf is 100 μ long. FIGURES 11 and 12 show an advanced stage in *Cissus*. The right stipule is well developed and its free part is 12 μ high while the left one has no free projection. The two stipules, when observed in conjunction with the apex, show their further horizontal extension almost up to the other side of the apex (FIG. 11), indicating that more apical cells are taking part in the development of the stipule. It can just as well be suggested that the stipule primordia which have originated from the leaf buttress have incorporated into themselves some additional apical tissues. Sussex (1955) also reports that in potato the leaf primordium during its subsequent growth after its initiation encroaches laterally and distally over the apical surface, incorporating into itself the surounding tissues. This obviously means that at least some tissue of the leaf buttress is also used up.

Vascularization. Majumdar (1956, p. 10) while discussing the morphology of the stipules makes the categorical statement that the stipule is "*an outgrowth of the leaf-base caused by the stimulating influence of a branch or branches sent out by the laterals*" of the foliar trace (italics his). However, Majumdar and Pal later (1958) report a case in *Dentella* where the scarious interpetiolar stipules are without any vascular supply. In *Morus*, leaf traces are differentiated after the formation of the stipular primordia (Cross, 1937). Boke (1944) reported no procambium in the young stipule of *Opuntia*. Millington and Gunckel (1950) could not determine with certainty whether or not the procambial traces differentiated prior to formation of the stipular primordia. So far as can be judged from the figures and microphotographs, the stipular primordia of *Glycine* (Sun, 1957) do not show any procambium.

It has been mentioned above that both in *Cissus* and *Cayratia*, the procambium of a stipular trace is not observed at the initiation and subsequent development of the stipule. In FIGURE 11 the right stipule in *Cissus* sp. is 12 μ high, and in FIGURE 12 (12μ below FIG. 11) the residual meristem is recognized by its dense staining and characteristic orientation of cells. The residual meristem at the region of insertion of the leaf primordium is more densely stained. FIGURES 13–17 show an advanced stage.

The stipule primordia are well developed in height and width, the right and left stipules being respectively 30 μ and 20 μ in height. The stipular and foliar primordia in conjunction with the shoot apex appear uniformly stained except the central core region of the apex. About 100 μ below the shoot apex, the vascular meristem is observed as illustrated in Fig. 17. At regions 1, 2 and 3 (Fig. 17) the cells (mostly procambium) appear compactly arranged. Farther below this, four procambium strands, each at one angle and linked with the other by residual meristem are observed. Figures 3 and 5 illustrate the nature of the vascular supply of the leaf



Figs. 25–35, *Cayratia carnosa*: 25, Transection of shoot apex at leaf-buttress (lb, densely stippled) stage, × 130; 26–29, Serial transections of shoot tip at 120, 130, 150 and 170 microns below the apex; 30–35A, Serial transections of shoot tip (Figs. 31–35 from 20, 60, 70, 80, 110 microns respectively below Fig. 30), × 130, except Figs. 31a, 33a, 35a, × 295; vc = vacuolated region; other explanations in the text.

and its stipules. Of the four trace strands (a, b, c, and d in FIG. 5) of the leaf, each of two strands (a and c), subsequently referred to as the girdle traces (Eames and MacDaniels, 1947), makes a semicircular curving or girdling from one side of the axis to the other side where the leaf is inserted. Each unites with the other strand (a with b, c with d, FIG. 5) which is near the leaf base and almost vertically oriented in the axis. All four unite to form the median trace (mt) of the leaf. At a later stage the girdle trace, as it curves to meet the other strand, gives out branches to the stipule. One of the stipular traces, as also the laterals of the leaf, arises from the fused portion of the two vascular strands (FIGS. 3, 5). Since almost all the stipular traces are vertically oriented (FIGS. 4, 6, 9), their origin could be observed accurately in the transverse and surface planes. FIGURE 37 shows the curving of the girdle trace without any stipular trace and FIG. 38 shows how the first stipular trace is differentiated from the girdle trace.

Similar observations are obtained in *Cayratia carnosa* where the node is trilacunar. *Cissus rotundifolia* (FIG. 24) and *Cissus amazonica* have pentalacunar, the *Cissus* species and *Cissus quadrangularis* tetralacunar, and *Cayratia auriculata* 7-lacunar nodes. FIGURES 30–32 show the earliest observed stages of stipule initiation in *Cayratia carnosa*. Regions marked "X" in FIG. 32 show some divisions of residual meristem cells which represent the incipient lateral procambial strands of the foliar primordium. Longitudinal sections also reveal that procambium is absent in the early leaf primordium. Even at a later stage the stipular primordium is without its procambium (FIGS. 26–29). The median trace in FIG. 29 is difficult to distinguish from the adjacent residual meristem cells but the lateral traces are discrete and densely stained. The stipular primordia also arise opposite them. These observations indicate that their initiation is due to the stimulus of the lateral leaf traces. This confirms the view of Sinnott and Bailey (1914) that the lateral traces exert a stimulating influence which results in the formation of the stipule. It does not support Majumdar's recent contention (1956) mentioned above. Arshad (1955) also reports that the origin of stipules in some species of Vitaceae is intimately connected with the branches of the lateral bundles of the leaf trace.

That the differentiation of the stipular trace occurs subsequently to the stipule development is also confirmed by the observation that sometimes only one of the early developed members of the stipular pair shows a procambial strand. FIGURES 32–35 show the vascular relationships of the second stipule from the shoot apex of *Cayratia*. Ten μ above the level of FIG. 33 a group of slightly obliquely cut and procambium-like cells was observed, an indication of the beginning of differentiation of the stipular trace. The lateral leaf traces are very well developed (FIGS. 35, 35A).

FIGURES 39–44 and 45–48 show further development of the vascular system of the stipule and its relation to the foliar girdle trace in *Cissus* and *Cayratia*. The stipule shows two procambial traces (FIG. 39). In the right stipule the traces are obliquely cut as they are about to be united with the girdle trace. In the left one the girdle trace is observed actually traversing the stipular tissue which is in conjunction with the axial tissue. In *Cayratia* (FIGS. 45–48) the free part of the stipule shows only one trace but farther below there are two traces. FIGURE 47 indicates that the horizontal extensions of the two lateral foliar traces actually traverse the stipular tissue. FIGURE 35 clearly indicates that the three leaf traces are in the foliar and stipular tissue conjoint with the axis (note the marginal meristem of the stipule in FIG. 35A). The three ridges over the three traces of the axis (FIG. 48) indicate the position of leaf and its

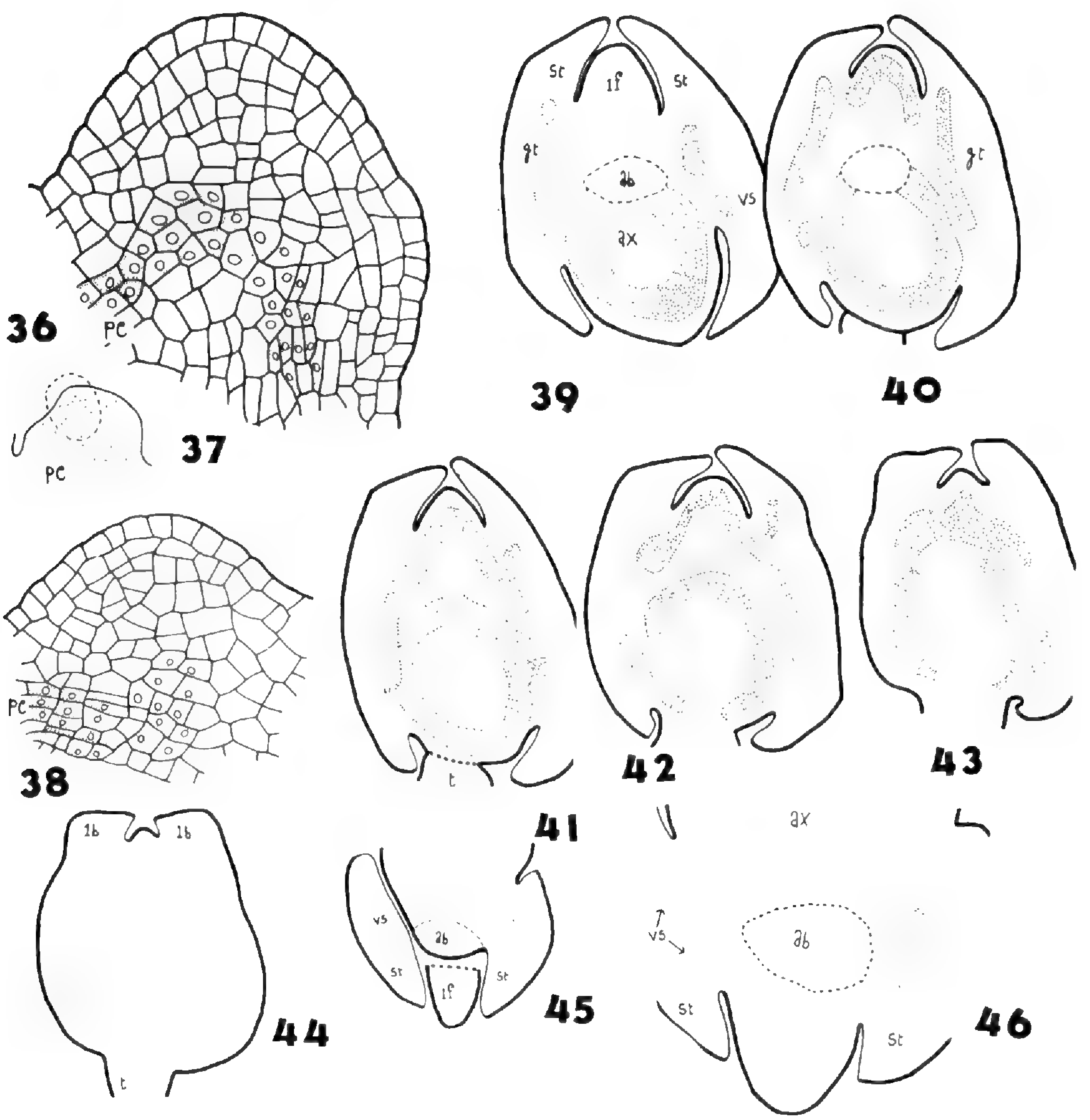


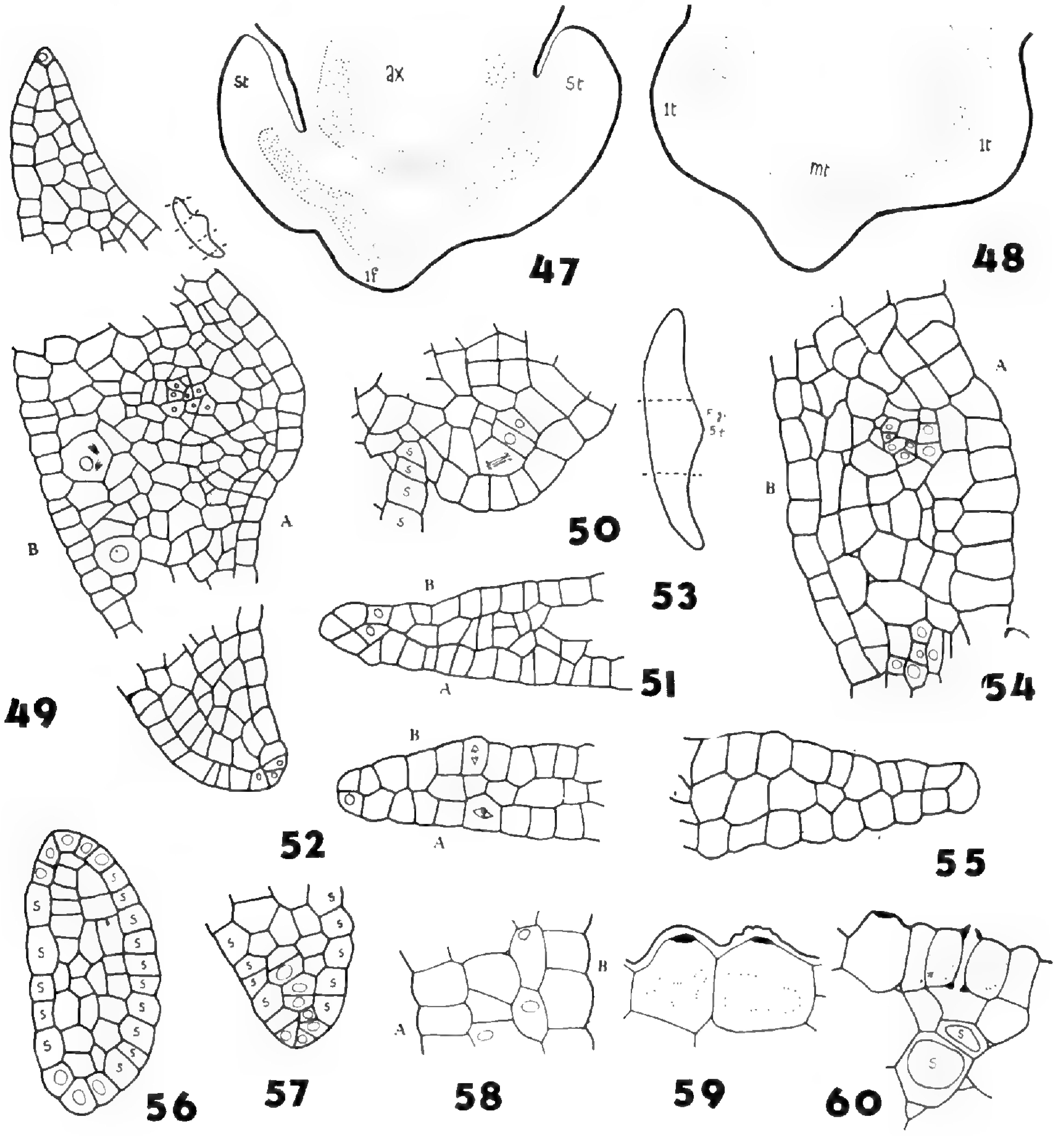
FIG. 36, *Cissus* sp.: Entire stipule with girdle-trace procambium, × 295. FIGS. 37, 38, *Cissus rotundifolia*: 37, Entire stipule with differentiation of stipule-trace procambium from the girdle-trace, × 70; 38, Part of Fig. 37 enlarged, × 295. FIGS. 39–44, *Cissus* sp.: Serial transections at the third visible node from shoot apex (Figs. 40–44 at 20, 30, 40, 70, and 110 microns respectively below Fig. 39); densely stained vascular meristem closely stippled, × 70. FIGS. 45, 46, *Cayratia carnosa*: Serial transections of an older node (Fig. 46 at 30 microns below Fig. 45), × 70, 130, respectively. Abbreviations: ab = axillary bud, ax = axis, gt = girdle trace, lb = stipular lobe, pc = procambium, vs = vertical vascular strands of the stipule.

stipules, and FIGURES 19–24 show comparable observations in *Cissus rotundifolia*.

The above observation is an important one, indicating as it does that there is a close morpho-histogenic relationship between the leaf and its stipules. It also confirms the earlier observation that the stipules originate from the flanks of the leaf buttress under the stimulus of the lateral leaf traces. The foliar and stipular tissues confluent with the axis have been derived from the leaf buttress and it is this tissue that the leaf traces traverse after their departure from the axis. The stipular traces arise in that part of the stipule which should be considered as an emergent and free one. Majumdar (1958) in his recent morphological explanation of the stipules of the Rubiaceae explains that the "collar" on which the "free part of the stipule is erected" is a product of union of two or more foliar buttresses at the shoot apex and is confluent with the axis. According to him the division of the leaf trace bundles and all vascular adjustments for the supply of the stipules and the petioles take place in the "collar," while the free limbs of the leaves and their stipules are erected on the "collar" under the influence of their respective trace bundles. As already noted, the present study does not confirm this observation.

Development of the stipule. The general development of the stipule is similar to that of *Morus* (Cross, 1937). The stipule develops rapidly in length and width. The young stipule near its base appears in transverse section to be thickened in the middle, bordered on either side by a pair of thin tangential extensions of meristematic cells (FIGS. 18, 52, 56, 57). Their edges constitute the marginal meristem of which the activity contributes to the lateral growth of the primordium. The marginal growth appears to be rapid on the side distal to the foliage leaf, as a result of which the proximal end of the stipule appears rounded. In *Cayratia* some of the abaxial and adaxial protodermal cells show dark staining contents and the marginal initials and their immediate derivatives appear meristematic (FIGS. 56, 57). The nature of the marginal meristem activity varies. The wedge-shaped marginal initial forms by anticlinal divisions a biseriate wing of adaxial and abaxial layers (FIGS. 52, 55). In FIGURE 52 the submarginal initial is away from the marginal initial and is in line with the abaxial layer (B). The mitotic figure in one of the cells of the abaxial (B) protoderm indicates that this also contributes to the formation of ground meristem. Sometimes the abaxial cell of a biseriate wing (FIG. 51) divides to form an inner cell, isolated from the ground meristem. Cross (1936) and Foster (1937) have reported similar divisions in the bud scales of *Morus* and *Rhododendron*. The activity of the marginal meristem of the two wings may not be uniform. The formation of the auricular lobe of the stipule is observed in the first or second stipule of the *Cissus* species. The frequent divisions in the subprotodermal layers at the base of the stipule produce an auricular prolongation (FIG. 50).

The process of maturation begins in the middle region of the stipule, later extending into lateral wings. The adaxial and abaxial subprotodermal layers contribute to the central core. Fig. 49 illustrates the first stipule of the *Cissus* species. The stippled cells near the procambium are meristematic. The growth in thickness in the middle region is due to the frequent periclinal divisions in the adaxial subsurface layers. Figs. 53 and 54 show comparable stages of *Cayratia*. The abaxial epidermis has a rapid



Figs. 47, 48, *Cayratia carnosa*: In continuation from Fig. 46, 40 and 120 microns below Fig. 46, × 130. Figs. 49–52, *Cissus* sp.: 49, Transection of young stipule near its base (note single procambium strand, marginally stippled cells near it densely stained, marginal meristem and raphide sac), × 300 (insert × 28); 50, Formation of auricular lobe of the stipule, × 350; 51, 52, Marginal meristem, × 350. Figs. 53–57, *Cayratia carnosa*: 53, Transection of young stipule, × 70; 54, Middle region of Fig. 53, magnified (note two procambium strands), × 295; 55–57, Marginal meristem, × 295; 56, Transection young stipule entire (note marginal meristem), × 295. Figs. 58–60, *Cissus rotundifolia*: 58, Transection of young stipule (completely stippled cells staining blue due to some contents), × 350; 59, 60, Transection of stipule epidermis with stoma, × 350. Abbreviations: A, B = adaxial and abaxial sides; s = deeply stained cells due to some contents.

development and is more thickened in its outer wall (FIGS. 58, 59). It also shows cuticular corrugations which appear tooth-like in transverse section. It is considered to be a sensory epidermis since the epidermis of the tendril also shows similar characteristics. Epidermal corrugations could not be observed in *Cayratia*. FIGURE 60 illustrates a typical stoma in the stipule of *Cissus*. The mesophyll in the mature stipule is not differentiated into palisade and spongy parenchyma. Raphide sacs are present in abundance (FIG. 4) in the mesophyll; the development of these is discernible in very young stipules.

DISCUSSION

The question of the region of origin of the stipules appears to be more or less settled. The present investigation and those of others (Millington and Gunckel, 1950; Pray, 1955; Sun, 1957; Majumdar and Pal, 1958) have proved conclusively that the stipules originate from the flanks of the leaf buttress. The views of Parkin (1948) that the free lateral stipules were cauline and, of Cross (1937) that they originated from leaf-stem transition region (which is a diverged cauline tissue at the node) do not find any support. Sun (1957) also adds that, although stipules of *Glycine* appear to arise directly from the shoot apex, the region of their origin may best be interpreted as an extension of the base of the leaf.

Majumdar (Mitra and Majumdar, 1952; Majumdar, 1955, 1956; Majumdar and Pal, 1958) considers the leaf-buttress as "an integral part of the leaf, and *its real base*" (italics by Majumdar, 1955) on which the foliar and stipular primordia are "erected" under the stimulus of their respective traces. Hence he considers stipules to be leaf-base divergences (not of base of the leaf). Explaining the cause of the origin of stipules, he mentions (1955, 1956) that it is the branch or branches of the lateral leaf traces that form the stipule. The present investigation has shown that the origin of stipules in *Cissus* and *Cayratia* is due to the stimulus of the lateral leaf traces and the subsequent development of the stipule is accompanied by the vascular branches arising from them. This confirms the view of Sinnott and Bailey (1914) that there is some sort of morphogenetic connection between lateral leaf traces and stipules. The broad-based nature of the stipule in the Vitaceae may be explained as due to the girdling of a lateral leaf trace, for the extent of the latter closely parallels the sideward extension of the stipule (see FIG. 5). Arshad (1955) explains the girdling of the lateral leaf trace as due to the incorporation of the leaf-base in the axis.

Whether the leaf-buttress is the real leaf-base and constitutes the axial component of the axis (Mitra and Majumdar, 1952) is a debatable question. Gifford (1954) mentions that "no clear delimitation can be made between the leaf buttress and the upright part of the leaf primordium" and also mentions that the leaf-buttress is not sharply delimited from the shoot apex, an expression of the intrinsic unity of leaf and stem. Majumdar (1955, 1956, 1958) also has not taken into consideration the recent work on shoot apices by French investigators like Plentofol and Buvat who describe the leaf initiation as the "raising of a localized portion of the 'anneau' by periclinal divisions in superficial layers (except the outer one) as well as in deeper layers" (in Gifford, 1954). The derivation and delimitation of the mantle and the axial core from two different zones of apical meristem (Mitra and Majumdar, 1952) are not supported by recent researches (Wetmore and Wardlaw, 1951; Gifford, 1954; Wardlaw, 1957). The entire apical meristem is interpreted as potentially capable of producing leaf primordia and the phyton concept in the interpretation the shoot has failed to stand the test of experimentation (Wetmore and Wardlaw, 1951). At all stages of development, leaves are appendages borne on an axis (Wetmore and Wardlaw, 1951). Recently Webster and Steeves (1958) reported the occurrence of truly leafless shoots in *Pteridium* and this fact, as they rightly remark, must be kept in mind in formulating any generalizations about leaf-stem relationships. It is conclusively proved, at least in some cases, that the organogenic destiny of a morphological organ such as a leaf is not at all determined at the leaf-buttress stage of its initiation (Wetmore and Wardlaw, 1951; Cutter, 1958). In fact, at this stage it has the alternative potentiality of different morphological expressions. Hence, to accept the interpretation of Majumdar and his students that the leaf-buttress is the real leaf-base and forms the mantle of the axis would be taking for granted those conceptions and features "which stand most in need of investigations by every method at our command" (Wardlaw, 1950).

Also of interest in this discussion are the observations of Boke (1944, 1951, 1952) on the Cactaceae which, according to him, provide one of the best examples substantiating Saunder's leaf-skin theory (1922), which Majumdar and his students (Mitra and Majumdar, 1952; Majumdar and Pal, 1958) support in part. In Cactaceae, according to Boke, there appears to be a progressive development of the leaf-base at the expense of the leaf itself, but no reference to its origin from the leaf-buttress is made. In fact, the existence of the latter is hardly referred to in connection with the initiation of the leaf (Boke, 1951).

Colomb (1887) defined stipules as appendages inserted on the stem at the base of the leaf and from which all the bundles arise exclusively from corresponding foliar bundles. Lubbock (1899) considered them to be normally more or less leaf-like structures at the base of, or just below, and one on each side of the leaf stalk. Sinnott and Bailey (1914) regarded the stipules as morphologically integral portions of the leaf, a generalized concept put forward by Eichler as early as 1861. Millington and Gunckel (1950) interpreted the stipules of *Liriodendron* as the "products of leaf base rather than of stem." Majumdar's concept (1956, 1958) of stipules is already discussed above. On the basis of ontogeny and vascularization the stipules of *Cissus* and *Cayratia* should be considered as the integral parts of the leaf, having their origin from the flanks of the leaf buttress.

I venture to put forward a new concept to explain the presence of stipules. The origin and subsequent development of stipules is closely associated with that of leaves having a characteristic nodal structure (Sinnott and Bailey, 1914), i.e., trilacunar or multilacunar. However, the development of the stipule is different from that of the leaf and is similar in many respects to that of the bud scale (Cross, 1937; Sun, 1957). It is well known that the determination of a growth center (see Wardlaw (1957) for the concept of growth center) of the leaf and its early development at the shoot apex are associated with the presence of a single procambial trace; but if the two or more lateral leaf traces differentiate earlier than or simultaneously with the median one, two more lateral growth centers will be established, in addition to the median one for the leaf, at the site of foliar initiation (i.e., the leaf-buttress). Each center has in its initial stages common physiological potentialities of producing an outgrowth of a localized region of the apex. This results in the development of three meristematic regions at the shoot apex. Owing to subsequent changes in the organogenic potentialities between the two lateral and the median regions, the former follow a histogenic development similar in most respects to that of the bud scale to form the stipule, and the median region because of its characteristic histogenic development becomes a leaf primordium (for better appreciation of this concept refer to Cutter's discussion on foliar determination (1958)). How far this explanation will stand the test of experimental research is yet to be seen.

SUMMARY

The origin and development of stipules of six species of the Vitaceae, four of *Cissus* and two of *Cayratia*, have been investigated. The stipules are ear-shaped or triangular, and free lateral. The stipular primordia arise from the flanks of the leaf-buttress. Their initiation is more or less simultaneous with that of the leaf and is closely associated with the lateral leaf traces. The trace procambium in the stipular primordium develops at a later stage. The vertical vascular strands arise from the lateral leaf traces during their girdling round the axis. The subsequent development of the stipule is studied and, in most respects, resembles that of the bud scale. It is concluded that early development of the stipule is due to the stimulus of lateral leaf traces. The origin and morphology of the stipules are discussed with reference to modern researches and a new concept to explain the presence of stipules is put forward.

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ANNAMALAI UNIVERSITY
ANNAMALAINAGAR, INDIA

THE GENERA OF THEACEAE OF THE SOUTHEASTERN UNITED STATES[1]

Carroll E. Wood, Jr.

THEACEAE (Camellia Family)

Shrubs or trees with simple, alternate, exstipulate leaves. Flowers complete, showy, borne singly in the axils of the leaves. Sepals 5(6), imbricate (quincuncial: 2 outside, 2 inside, 1 in-and-out), the calyx with 1–4 often caducous bracteoles. Petals 5(6–8), white, imbricate, the outermost usually smallest and somewhat cupped, united at the base. Stamens numerous, adnate to the petals. Gynoecium of 5 partly or wholly united carpels, the ovary superior, the locules 5; ovules 4–10 per locule, the placentation axile. Fruit a dehiscent capsule. (Ternstroemiaceae.) Type genus: *Thea* L. = *Camellia* L.

About 500 species in some 30 genera, primarily in the tropics of both hemispheres. Represented with us by four distinct species in three genera of the tribe Camelieae DC. Generic and specific distinctions are often difficult in the family and the number of species and genera may be considerably fewer than indicated. The family as a whole is characterized by an abundance of sclereids, often of considerable size, in nearly all organs. Anatomical features have been used in conjunction with morphological characteristics in the separation and alignment of genera, but in most instances far too few representatives have been examined to warrant the weight sometimes given this evidence. Representatives of the exotic genera *Camellia* (including *Thea*), *Eurya* Thunb., *Cleyera* Thunb., and *Ternstroemia* L. f. are in cultivation in our area. Except for *Camellia* ($2n$ = 30, 45, 60, 90), little is known of chromosomes, embryology, or genetics. The family is notable for extreme endemism, on the one hand, and polymorphic, often ill-defined species, on the other.

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[1] Prepared for a biologically oriented generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium made possible through the support of George R. Cooley and the National Science Foundation. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39:** 296–346. 1958). Other published portions of these studies will be found in Jour. Arnold Arb. **40:** 94–112, 161–171, 268–288. 1959, and in the present issue. In connection with this family, I am especially grateful to Dr. C. E. Kobuski for his kind and generous advice. Fresh specimens used in illustrating the fruit of ***Franklinia*** and ***Gordonia*** were provided through the kindness of Mrs. J. Norman Henry from plants cultivated at the Henry Foundation, Gladwyne, Pennsylvania; flowering specimens of ***Gordonia*** were collected by Dr. R. B. Channell and Dr. H. F. L. Rock, in Bladen County, N. C.

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KEY TO THE GENERA OF THEACEAE

A. Seeds with a pronounced oblong wing at the upper end; capsule ovoid, loculicidally dehiscent, with a persistent central axis; sepals suborbicular, persistent at least into young fruit; foliage coriaceous, evergreen; bases of stamen-filaments united to form conspicuous fleshy pads. . . . 1. *Gordonia.*

A. Seeds wingless or with only a narrow membranaceous margin; foliage membranaceous, deciduous; bases of filaments not united to form conspicuous pads.

  B. Capsule globose, dehiscing loculicidally from above and septicidally from below, with a persistent central axis; sepals suborbicular, dehiscent at or soon after anthesis; capsule maturing a year after flowering. 2. *Franklinia.*

  B. Capsule dehiscing loculicidally from above only, a central axis absent; sepals ovate to oblong-ovate, persistent into fruit; capsule maturing within a single season. . . . . 3. *Stewartia.*

1. **Gordonia** Ellis, Roy. Soc. London Phil. Trans. **60**: 520. *pl. 11.* 1771, nom. cons.

Shrub or tree to about 25 m. tall and 50(–65) cm. in diameter, with persistent, glabrous, lanceolate to oblong-lanceolate to elliptic leaves. Flowers long-peduncled, with 4 bracteoles below the calyx deciduous before anthesis. Sepals 5, deciduous in late fruit. Both sepals and petals silky-pubescent on the outer surface. Stamens in 5 groups coherent at the bases to form 5 thick, fleshy pads adnate to the base of the corolla and coherent with each other to form a deeply 5-lobed ring. Ovary ovoid, pubescent, gradually contracted into a stout, persistent style, 5-loculed, the ovules 4–8 in each locule, the style elongate, erect, the stigma 5-lobed. Capsule subligneous, ovoid, acute at the apex, 1.5–2 cm. long, dehiscing loculicidally, with a persistent, angled central axis. Seeds compressed, the woody testa prolonged upwards into an oblong wing. (*Lasianthus* Adans. 1763, nom. rejic.) TYPE SPECIES: *G. Lasianthus* (L.) Ellis. (The name in honor of James Gordon, 1728–1791, a nurseryman at Mile-End, near London, "to whom the science of botany is highly indebted, and whose merit is universally known for his great knowledge in the cultivation of exotic plants.") — LOBLOLLY BAY, BAY, BLACK LAUREL, HOLLY BAY, SWAMP LAUREL, TAN BAY.

Primarily a genus of tropical and subtropical Asia, with about 30 species, all evergreen. Represented with us only by *G. Lasianthus*, a well marked species which occurs on the Coastal Plain from eastern North Carolina, south to the region of Lake Okeechobee, Florida, and west along the Gulf of Mexico to Mississippi, always in acid, peaty soils of nonalluvial branch- and creek-swamps, pocosins, hammocks, bays, sand-hill bogs, etc. Flowering from July and August, the plant is a handsome tree, sometimes cultivated. It is hardy as far north as Philadelphia. The bark and wood are rich in tannin; the wood is close-grained and easily worked but is not very durable. In late summer the younger leaves are almost characteristically insect-chewed.

The Asiatic species of the genus, with bracteoles varying from two to many and with a gradual transition of sepals into petals, are sometimes segregated as *Polyspora* Sweet ex G. Don. The Old and New World plants seem to differ in various anatomical aspects, but very few of the Old World species have been studied. Our species clearly seems to be closely related to the Old World Gordonias and to represent a survivor of once more widely dispersed types. Fossil Gordonias are reported from Europe and the western United States.

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2. **Franklinia** Marshall, Arbustrum Americanum 48. 1785.

Shrub or tree to about 10 m. tall, with membranaceous, deciduous

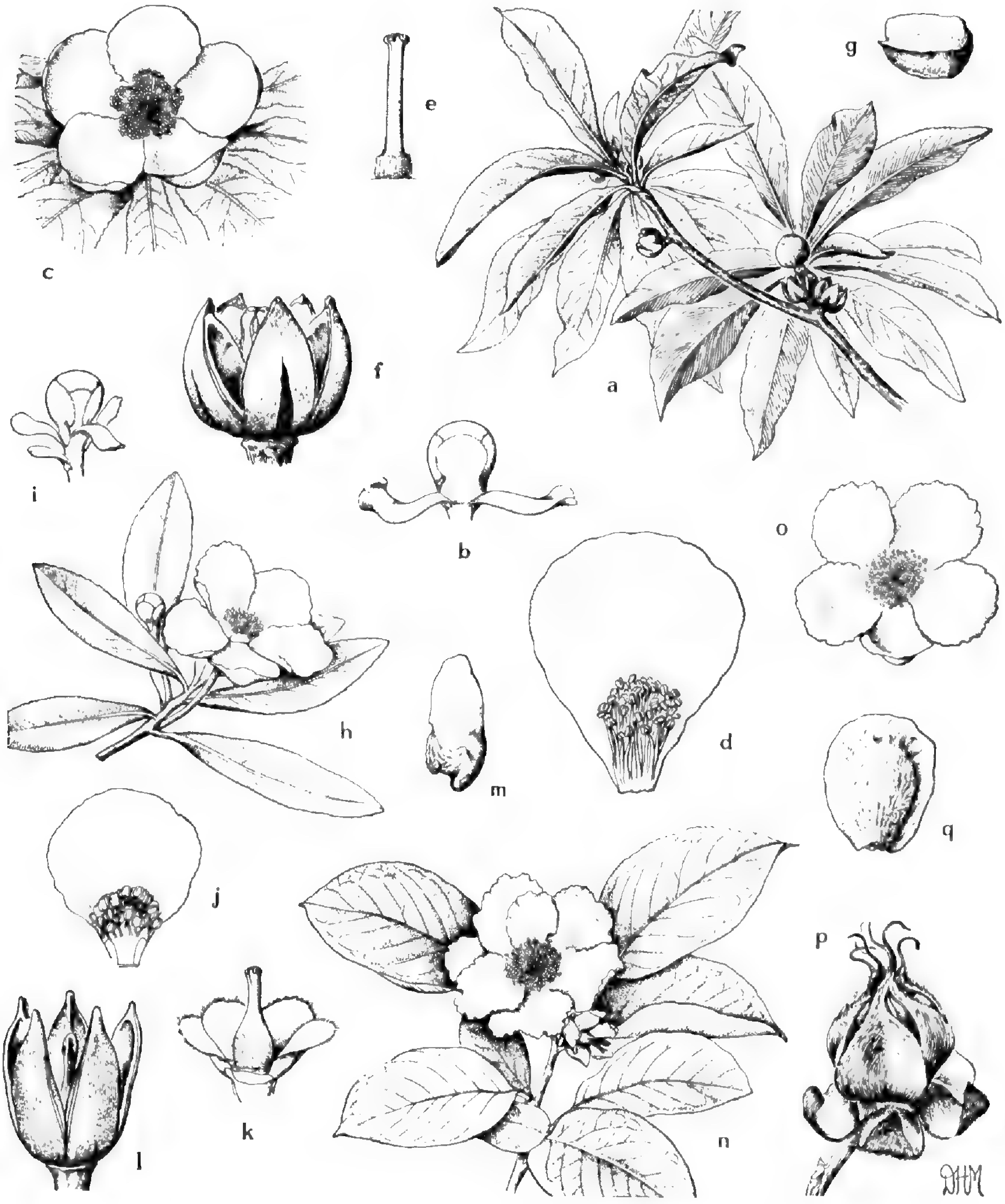

FIG. 1. THEACEAE. a–g. **Franklinia.** *F. Alatamaha*: a, fruiting branch prior to flowering, bearing fruit of two preceding years — note sympodial growth, × ⅙; b, bud showing outermost sepal and two bracteoles, × ⅔; c, flower, × ⅓; d, petal with group of stamens attached, × ⅔; e, pistil, × 1; f, old fruit from which seeds have been shed, × 1; g, seed, × 2. h–m. **Gordonia.** *G. Lasianthus*: h, tip of flowering branch, × ⅓; i, bud with four bracteoles, × ⅔; j, petal with stamens attached — note fleshy pad composed of united bases of stamens, × ⅔; k, calyx and pistil, the outermost sepal removed, × 1; l, fruit from which seeds have been shed, × 1; m, seed, × 2. n–q. **Stewartia.** *S. ovata*: n, flowering branchlet of f. *grandiflora*, × ⅓; o, flower of f. *ovata*, × ⅓; p, loculicidal capsule, partly opened, with persistent calyx, × 1; q, seed, × 2. (Drawn by Dorothy H. Marsh.)

oblong-lanceolate to oblanceolate leaves, tapering to the base. Flowers in the axils of crowded upper leaves, the buds with 2 quickly deciduous bracteoles below the calyx. Sepals 5, suborbicular, imbricate, coriaceous, deciduous at or soon after anthesis. Petals 5, up to 6 cm. long. Stamens in 5 distinct groups, the filaments free, adnate to the base of the corolla. Ovary rounded, truncate at the apex, densely pubescent, the sides conspicuously ridged by the pressure of stamen filaments, 5-loculed; style elongate, deciduous, the stigma 5-lobed. Capsule subglobose, woody, with a persistent central axis, dehiscing loculicidally from above to the middle, septicidally from below to the middle. Seeds 6–10 in each locule, closely packed in two rows, angular, the shape varying with the position within the locule, wingless. (*Lacathea* Salisb.) TYPE SPECIES: *F. Alatamaha* Marshall. (Named for Benjamin Franklin, American philosopher and statesman, 1706–1790.) — FRANKLINIA, FRANKLIN-TREE, LOST CAMELLIA.

A single species, *F. Alatamaha*, now known only in cultivation and formerly known only from an area of two or three acres of "sand-hill bog" or "branch-swamp" at the edge of sand hills about two miles from Fort Barrington, on the Altamaha (Alatamaha) River, in McIntosh County, Georgia, where it was first seen by John Bartram and his son, William, on October 1, 1765. The species was last seen at this spot by Moses Marshall, a nephew of Humphry Marshall, in 1790. It has not been found again in the wild in spite of repeated searches dating from about 1881. *Franklinia* has been cultivated in England since about 1774, however, and it is known that in 1777 William Bartram collected at Fort Barrington ripe seeds from which were grown plants which flowered in four years at Philadelphia. Most of the plants now in cultivation in the United States are thought to be descendants of a plant rescued by the Meehans of Philadelphia from Bartram's then-neglected garden some years before it was taken over by the city of Philadelphia. Attempts on the part of Humphry and Moses Marshall to fill large orders for *Franklinia* plants placed by a London firm in 1787 and 1789 may well have played a fatal part in the extinction of the colony at Fort Barrington.

The probable associates of *Franklinia* at the type locality include *Pinckneya, Pinus serotina* Michx. f., *Magnolia virginiana* L., *Cliftonia, Persea, Liriodendron, Lyonia lucida* (Lam.) K. Koch, *Smilax laurifolia* L., and *Sphagnum*, with *Rhododendron* (*Azalea*), *Leucothoë, Serenoa, Kalmia hirsuta* Walt., and *Styrax americana* L. var. *pulverulenta* (Michx.) Rehd. between bog and sand hill. (See Harper and Leeds.) The plant should be looked for carefully in similar areas both up and down river from Fort Barrington and in the neighboring Altamaha Grit region. It is not a plant of river-swamps but of acid, nonalluvial bogs at the heads of sand-hill branches (about 20 feet above sea level at the Fort Barrington locality).

As a cultivated plant the handsome flowers are usually produced from July (or, in the North, from late August or September) until frost. According to Bartram, however, at Fort Barrington the plant flowered from "April untill the autumn when it ceases flowering, whilst the seed of the flowers of the preceding year are ripening," and at Thomasville, Georgia, it is reported to flower in April and May. Wherry suggests that the plant is nearly self-sterile and that seeds from self-pollinated plants do not germinate. Seedlings have been grown from plants in cultivation, however, and this matter needs to be checked. In spite of its extreme endemism on the coastal plain of Georgia, the plant is hardy as far north as Boston, flourishing in acid soils which are a prerequisite to its cultivation.

Although known for many years as *Gordonia pubescens*, and later as *Gordonia "altamaha," Franklinia* is distinct from all members of *Gordonia* in fruit shape and unique dehiscence, wingless seeds, and membranous and deciduous leaves. It differs further from *G. Lasianthus* in the deciduous calyx with two (instead of four) bracteoles, the sessile flowers, the free filaments, and the full year necessary for the maturation of the fruit.

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3. **Stewartia** L. Sp. Pl. 2: 698. 1753; Gen. Pl. ed. 5. 311. 1754.

Shrubs or small trees with membranaceous, serrulate leaves. Flowers with 1 or 2 bracteoles below the calyx. Sepals 5(6), somewhat unequal, persistent. Petals 5(6–8), obovate to rounded, crenulate, silky pubescent on the outer surface. Stamens numerous, the filaments united at their bases to form a shallow ring adnate to the base of the corolla. Styles 5, distinct, or united and stigmas 5. Capsule globose to ovoid, loculicidally dehiscent, lacking a central columella, woody, pubescent. Seeds compressed, 1–4, attached near the base of each locule, obovate-lenticular, the testa thick and crustaceous, with or without a thinner margin. (*Stuartia* L'Hér.; including *Malachodendron* Cav.) TYPE SPECIES: *S. Malacodendron* L. (The name in honor of John Stuart, 1713–1791, third Earl of Bute, who was distinguished in his day as a botanist.) — STEWARTIA.

A genus of about six species of eastern Asia and the southeastern United States, represented with us by two very distinct species. *Stewartia ovata* (Cav.) Weatherby (*S. pentagyna* L'Hér.), with five styles and dull, reddish-brown seeds with a narrow, thin margin, is primarily a plant of the southern Appalachians in southeastern Kentucky, eastern Tennessee, western North Carolina, northern Georgia, and to central Alabama. *Stewartia Malacodendron* L., with united styles and lustrous, angled seeds lacking an evident margin, ranges more widely, primarily on the Coastal Plain and in the Piedmont (with but a few mountain stations) from Virginia to Louisiana, and with a station in Ouachita County, Arkansas. Both species, although very distinct, are obviously closely related to each other and to the Asiatic species, so much so that the genus *Malachodendron* (*S. ovata*) can be regarded only as a purely artificial segregate. Like *S. Malacodendron*, all of the Asiatic species have united styles.

Both are showy plants, worthy of more widespread cultivation. *Stewartia Malacodendron* flowered in Catesby's garden in England in 1742, and *S. ovata* has been cultivated since about 1785. The latter is the hardier plant, withstanding the winters of eastern Massachusetts. An acid soil is necessary. Propagation is by seeds or softwood cuttings. *Stewartia ovata* f. *grandiflora* (Bean) Kobuski[2] is a handsome plant, often with more than five petals and with purple, instead of white, stamen-filaments. It occurs with the white-filamented form, f. *ovata*, in some localities. The filaments of *S. Malacodendron* are purple.

Anatomically, the genus is interesting in that those species thus far examined lack sclereids (except in the pedicels), in contrast to other members of the family.

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WEATHERBY, C. A. Two new combinations in *Stewartia.* Rhodora **41:** 198. 1939. [*S. ovata* and *S. ovata* var. *grandiflora.*]

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[2] **Stewartia ovata** (Cav.) Weatherby, forma **grandiflora** (Bean) Kobuski, comb. nov. *S. pentagyna* L'Hér. var. *grandiflora* Bean, Trees & Shrubs Brit. Isles **2:** 555. 1914. *S. ovata* var. *grandiflora* (Bean) Weatherby, Rhodora **41:** 198. 1939. *Malachodendron pentagynum grandiflorum* E. J. Alexander, Addisonia **19:** 1. *pl. 609.* 1935. Since the form of *Stewartia ovata* with purple filaments is well known in horticulture, it seems worth while to have a nomenclatural combination more nearly indicative of its taxonomic status which, it now appears, is not that of a geographical varietas. Both this and the typical form may occur together, and there appears to be no geographical segregation. In addition, one plant in the living collections of the Arnold Arboretum (No. 18244-B, from T. G. Harbison, Highlands, N. C., in 1925) behaves in much the same way as some of the mutable forms of *Camellia japonica*, producing 5-petaled flowers with either purple or nearly white filaments, or occasionally chimeric flowers with both. Another, more vigorous plant (18244-A) of the same collection produces only flowers with purple filaments and with 5–7 petals. (See *Fig. 1, n,* drawn from the latter plant.) — C. E. KOBUSKI.

THE DIRECTOR'S REPORT

THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1959

THE PAST YEAR has been a particularly satisfying one for the director and the staff of the Arnold Arboretum. Four years have been devoted to combining the non-horticultural herbarium collections of the Arnold Arboretum with those of the Gray Herbarium in the Harvard University Herbarium Building in Cambridge. The task was finished in May of 1959. Work continues on a reorganization of the horticultural herbarium in the Administration Building in Jamaica Plain. Both collections now are in excellent condition, well housed physically and arranged in the most convenient way for the horticultural, monographic and floristic work of the staff. The staff has justifiable pride in a job well done.

To parallel this accomplishment, the grounds and the plantings of the Arnold Arboretum in Jamaica Plain and Weston are in superb condition and the spring bloom of the spectacular trees and shrubs has rarely been equalled. The Boston Department of Parks and Recreation completed the cleaning of the cobblestone gutters and plans a rehabilitation of the roads and benches. Rarely has the Arnold Arboretum, in all its aspects, been in such excellent shape.

The Staff:

Mr. John Thomas Park retired on May 31 as superintendent of the Case Estates of the Arnold Arboretum in Weston, Mass. Mr. Park had spent nearly all of his life on the Case Estates. He worked for Miss Marion Roby Case as a boy and was superintendent of the property when the estate was bequeathed to Harvard University for the Arnold Arboretum in 1945. It is obvious that a lifetime devoted to gardening and horticulture in New England will not end with his retirement and "Tom" will be available for consulting with the staff.

During the spring semester of 1959 Dr. Karl Sax, cytogeneticist for the Arnold Arboretum, was granted a sabbatical leave of absence to accept an appointment as Visiting Professor of Forestry at the University of Florida. Dr. Sax reached the age of sixty-five on November 2, 1957, and will retire on August 30, 1959, just two months after the start of the next fiscal year. His appointment as Visiting Professor of Botany at Yale University for the next academic year has been announced. Dr. Sax has also been awarded a Guggenheim Fellowship for continuing his research in Oxford, England, following the completion of his year at Yale. The Guggenheim appointment was announced in May, 1959. It is with pride we note that Dr. Sax was elected president of the Genetics Society of America for 1959 at the annual meeting of the Society held in Montreal.

Dr. Donald Wyman served for the fifth year as chairman of the "Norman Jay Colman Jury of Award" of the American Association of Nurserymen. He continues to serve as secretary and as treasurer of the American Horticultural Council.

Dr. Burdette Lewis Wagenknecht was appointed horticultural taxonomist at the Arnold Arboretum July 1, 1958. Dr. Wagenknecht received his early botanical training at the University of Iowa and his Ph.D. degree at the University of Kansas. Dr. Wagenknecht will be responsible for the horticultural herbarium under the direction of the curator and will assist in horticultural identification and carry on studies of cultivated woody taxa at Jamaica Plain.

It is a pleasure to note the award of a "large gold medal" to Mrs. Susan B. McKelvey by the Massachusetts Horticultural Society in recognition of her outstanding horticultural writings.

Horticulture:

The past winter was unusually hard on broad-leaved evergreens throughout the entire northeastern United States. At the Arnold Arboretum in Jamaica Plain, and especially at the Case Estates in Weston, the extreme

An aerial view of the Arnold Arboretum (delimited by the white line) looking approximately northeast from a point over Roslindale. Peters Hill is the grassy area in the foreground. Jamaica Pond shows in the left center, with downtown Boston in the background. (Photograph made August 20, 1958.)

foliage burn and actual death of many plants seemed particularly severe. The mountain laurel (*Kalmia latifolia*) and the several varieties of *Ilex crenata* suffered severe branch damage. At Weston, young plants of evergreen *Rhododendron* varieties were killed in large numbers and even established plants twenty years old were killed to the ground. Surprisingly, the *Buxus* collection was largely untouched by the winter weather, and there was little killing of deciduous plants or their flower buds. The damage appears to have been caused, first by an early and sudden freeze which eventually reached a depth of nearly four feet, and then by the many sunny and windy days without a snow cover. The plants did not show bark cracks or the usual signs of stem- and leaf-freeze but appeared to be in good condition until the first warm weather of spring revealed complete desiccation of the branch-systems. The spring months have produced very irregular leafing-out, and, in many cases, severe pruning will be required to re-shape the surviving plants. Much information can be obtained from a study of the cold-desiccation damage of the past winter.

The spring flowering season was one of the most beautiful of the past decade. The cherries, crab apples, forsythias and azaleas were especially outstanding. The magnolias, lilacs and flowering quinces were below average in quality and quantity of bloom.

During the two planting periods, the fall of 1958 and the spring of 1959, 257 different taxa were added to the Arboretum collections. These included plants completely new to our collection, additional clones for trial and replacements of taxa which have been lost. Small rhododendrons were added to the expanding collection on the steep slopes of Hemlock Hill, and the majority of these survived the winter without damage. Only a few were actually lost. The entrance to the Peter's Hill tract was graded properly and planted to extend the crab apple collection so that it can be seen from Bussey Street. A special planting of tree peonies (*Paeonia suffruticosa*) was established on the grounds, and fifty of the cultivars most promising for both hardiness and beauty were planted. The large collection of azaleas on Bussey Hill was pruned for rejuvenation. A cleaning program was continued on the top of Hemlock Hill where recent hurricanes and summer droughts have affected many of the older hemlock trees.

Modern spray equipment has enabled the grounds staff to maintain the plantings in particularly healthy condition. During the past year, time was available to study controls of specific pests of such genera as *Viburnum*, *Robinia* and *Sorbus* which are vulnerable to borer attacks. Due to the constant attention the plants receive, no new outbreaks of disease were found.

The staff particularly appreciates the co-operation received from the Department of Parks and Recreation of the City of Boston in some major repairs completed during the year. The cobblestone gutters are a mark of distinction on the Arboretum grounds. During the past three years sections of these gutters have been cleaned and repaired, and the work has now been completed throughout the grounds. Routine cleaning and the application of weed killers to discourage weed growth will prevent a repetition of the overgrown and unsightly appearance that existed five years ago. In addition, the stream near the administration building was straightened and deepened to prevent flooding. Flooding and erosion were also threatening the collections of *Pseudolarix* and *Larix* and one section of the stream bank in this area was lined with heavy stones. Excellent co-operation has been received from the Boston Police Department in policing the grounds.

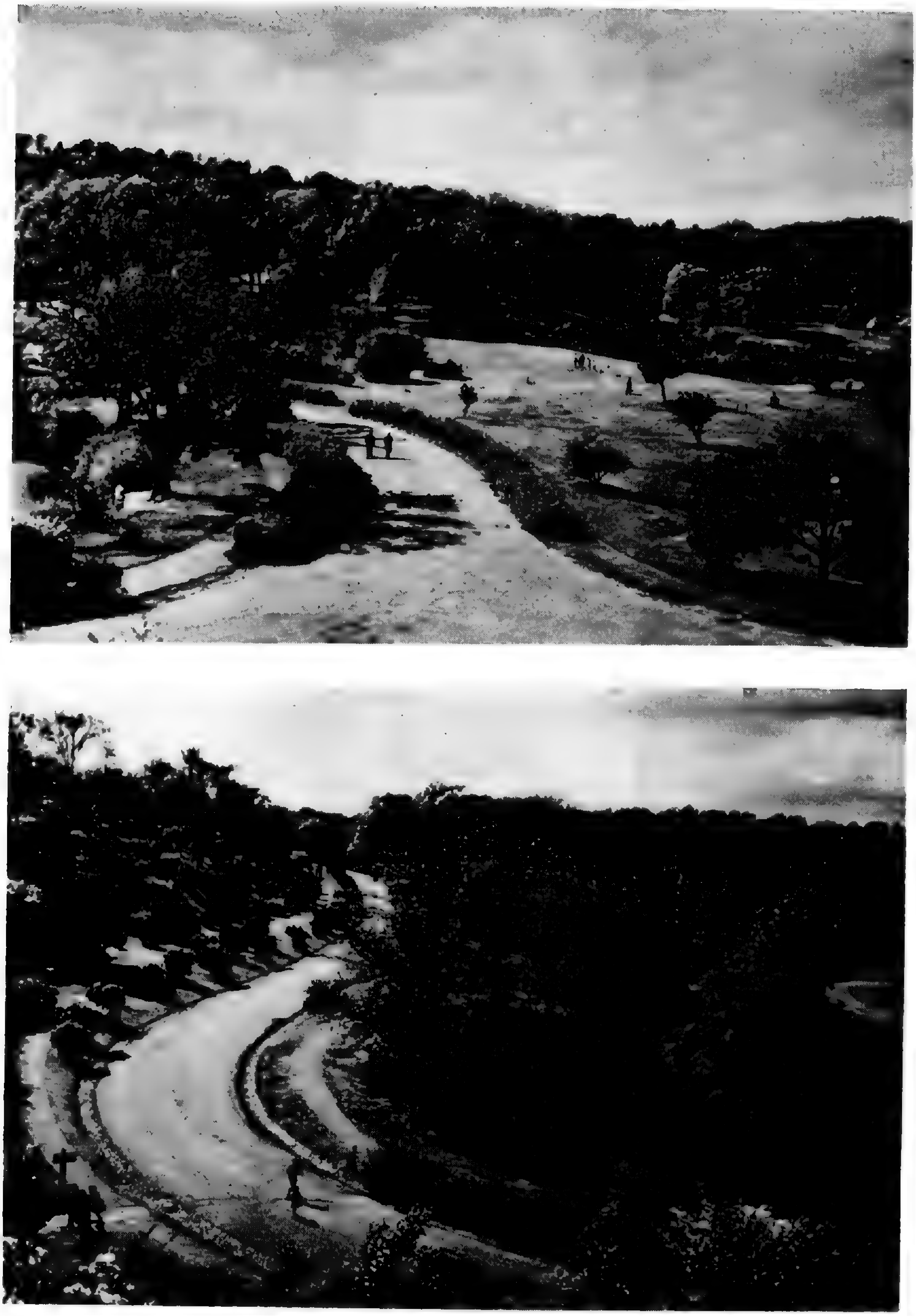
Dr. Donald Wyman continued to serve as co-ordinator for a committee representing the arboreta of the U.S. working in co-operation with the U.S. Department of Agriculture in introducing plants, the importation of which is prohibited at present. This spring 380 taxa were requested from foreign sources for eventual introduction into cultivation in America. Eleven taxa of cultivated plants were released from quarantine this spring and planted in the Arboretum. As part of our program to make little known plants available to commercial nurseries through a co-operating nursery program, eleven taxa of woody plants were offered. Plants were requested by 57 commercial nurseries which will propagate and advertise these unusual plants worthy of more extensive cultivation.

A series of special projects involving the horticultural herbarium and the living collections was inaugurated during the year. The Arnold Arboretum maintains one of the most extensive files of photographic negatives and prints of cultivated plants. Many of the introductions to our collections during the past five years have now reached the size where they flower heavily and can be considered typical in form. These plants are being photographed in color and in black and white for teaching purposes and for the illustration of staff papers. Herbarium specimens are being made of all plants introduced since 1949 when such work was stopped. These plants are being checked for correctness of name, and specimens are being filed for study in the horticultural herbarium. The Arnold Arboretum maintains the most completely and accurately identified living collection and the staff makes a continuous effort to keep it in this condition.

The propagation department under the direction of Mr. Alfred Fordham remains one of the busiest departments of the Arnold Arboretum. While visitors will continue to receive all aid possible for their individual problems it is obvious that some co-ordination of visitors to the greenhouse must be established. During the year nearly 100 classes and groups were taken on conducted tours through the propagation department. Numerous requests for aid in problems of plant propagation, insect control, and general horticultural practice are received by phone or personal visit and handled as possible.

During the year 223 shipments of seeds and plant materials comprising 611 taxa were received from the United States and 14 foreign countries. In response to requests 341 shipments of living plants, propagating materials, seeds, pollen or cytological material were made to other gardens or scientists in the United States and in foreign countries.

Experimental work in plant propagation continues in the greenhouses. Many of the plants in our living collections have never been adequately studied and complete records of propagation and of seed germination are



The Arnold Arboretum in late May, 1959. ABOVE: The Meadow Road near the shrub collection. BELOW: The road past the lilac collection to Bussey Hill.

being compiled from existing literature or from experiments. The routine work in propagation offers many opportunities for experimental variations in normal procedures. The use of different concentrations and types of root-inducing hormones in conjunction with different collecting techniques are examples of experimental projects of value. During the past year it has been determined that application of rooting hormones in the field as the propagating material is cut produces higher rooting percentages than if the application is delayed only a few hours until the worker returns to the greenhouse. *Rhododendron smirnowii* treated in the field at the time of collection rooted 100% while a control collection handled in the normal fashion and treated only hours later in the greenhouse rooted 66% with root systems inferior to the field-treated material.

Experimental work with cuttings of a larger diameter than usual have produced promising results, particularly in *Cedrus libani*, a plant normally difficult to root. Cuttings over one-fourth inch in diameter rooted well in a controlled experiment. This project is being continued.

The International Code of Nomenclature for Cultivated Plants published in 1958 proposes the registration of cultivar names for new horticultural plants. This principle has been accepted by horticulturists at the international as well as national level. Societies in some countries have accepted the responsibility for many specific groups of cultivated plants, such as *Tulipa, Iris, Rosa, Hemerocallis, Narcissus, Rhododendron, Populus* and others. The vast majority of woody plants which are the interest of the Arnold Arboretum, however, is not represented by societies willing to serve as registration authorities. The Arnold Arboretum has volunteered to accept the registration responsibility for woody groups not represented by societies. At a preliminary meeting of representatives of the American Association of Nurserymen, the American Association of Botanical Gardens and Arboretums and the American Horticultural Council it was voted that the responsibility for the over-all program of registering woody plants should be undertaken by the AABGA at the request of the American Horticultural Council. If approved by the membership of the respective organizations, the American Association of Botanic Gardens and Arboretums would then designate the Arnold Arboretum as the National Registration Center for Woody Plants. It was understood that an attempt would be made to find other organizations willing to assist in this large task as their location or staff interest permitted. Registration activity would be in accordance with the directives of the International Code of Nomenclature for Cultivated Plants. However, the Arnold Arboretum reserved the right to require and hold as part of its activity an adequate description, illustration, type herbarium specimen and a living specimen. A small charge would be made to individuals or companies wishing to register a cultivar name. The Arboretum agreed to compile and publish as soon as possible lists of cultivars in groups of registration interest. While the initial agreement when ratified will be for a two year trial period, it is fully expected that the registration, classification, publication and study of cultivated plants will be a major project continuing at the Arnold Arboretum where living collections, herbarium specimens, library, nursery catalogues and the Rehder Index combine to make this work practicable.

Case Estates:

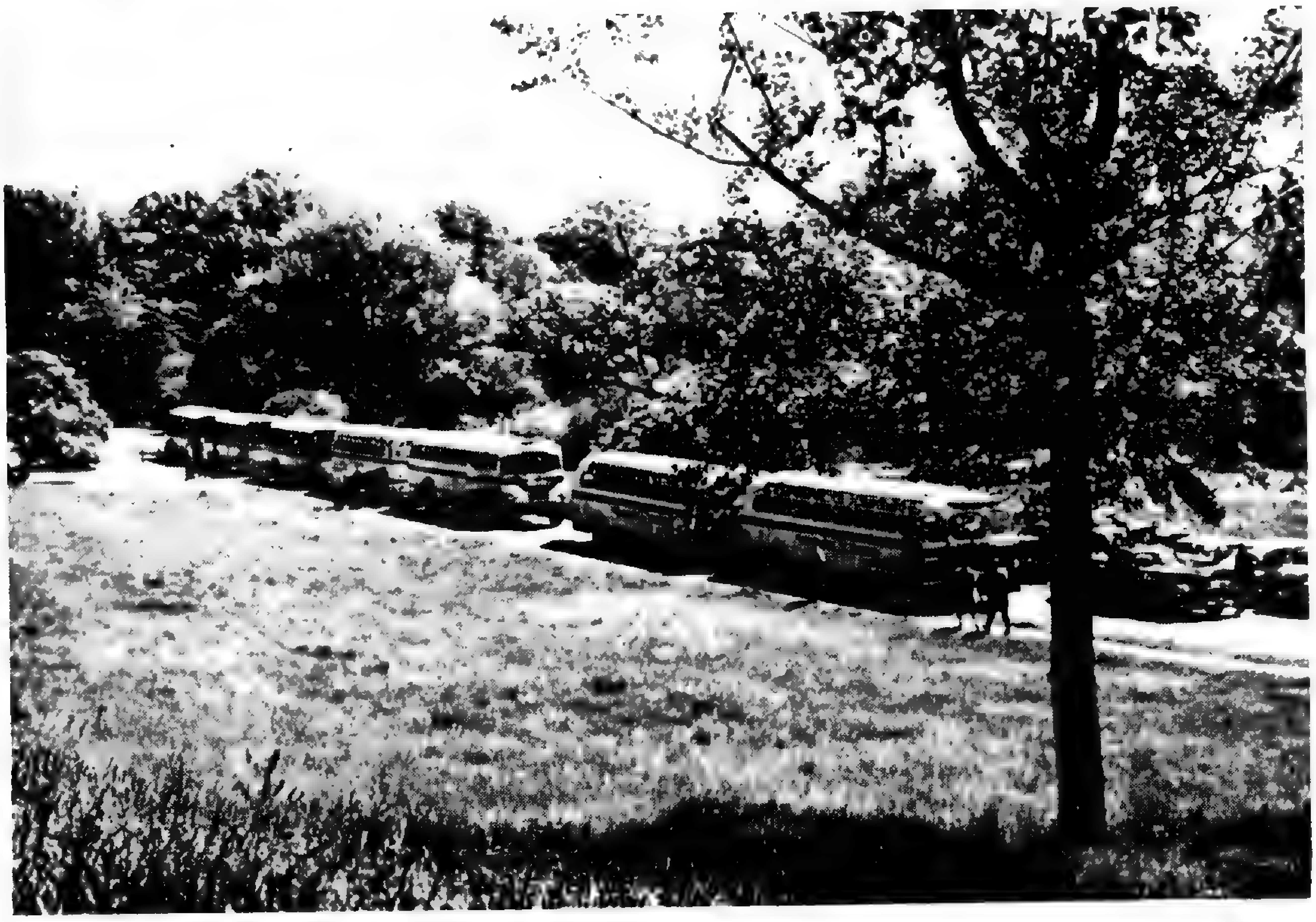
The more rigorous climate of the Case Estates as a nursery and testing area for the Arnold Arboretum was clearly demonstrated during the past winter. Young plants from the greenhouse in Jamaica Plain are normally transferred to Weston where more adequate space is available for young plants to develop. The Weston environment is more open than that of Jamaica Plain and temperatures may average 12 degrees colder. The severe winter produced a much higher proportion of kill in comparable nursery plants in Weston than in Jamaica Plain. Dead or severely damaged plants were evident in all but the most protected areas on the Case Estates. Considerable replanting of the ground-cover collection was necessary and the time and labor required to renovate the collections prevented the scheduling of an Open House in the first weeks of May as has been our custom.

An area of the Case Estates was taken by the town of Weston for new schools, as was mentioned in last year's report. Construction of the new school began in the fall, and during the winter it was found necessary to clear new fire lanes to protect the rear boundaries of our wooded areas. We expect to construct several new access roads for fire protection during the next year. Since these back areas will also be visible to the public from a new direction, considerable labor has been devoted to clearing and cleaning out brush from the wooded areas.

The Department of Buildings and Grounds was offered surplus trees and shrubs for planting on the Harvard campus and in conjunction with the building program for Harvard College. This is in accordance with the terms of the Arboretum trust. About 350 plants of 130 species and varieties were selected for planting in the Cambridge area.

Education:

The popular classes in horticulture and botany offered by staff members continued during the year with over 230 people registered. The largest classes again proved to be those conducted by Dr. Wyman in Jamaica Plain and Dr. Howard at the Case Estates. New classes offered included advanced plant propagation, classification of the lower plants, and preparation of botanical specimens. The demand for advanced work in the field of plant propagation was met in part by an advanced class offered by Mr. Alfred Fordham. The class met in 12 sessions at irregular intervals during the year when appropriate propagating techniques could be effectively used. Mr. G. Safford Torrey, professor emeritus of the University of Connecticut, was invited to offer a class in the classification of the mosses, fungi, lichens and algae. This class met on the Case Estates in Weston and proved to be extremely rewarding. Each student made a collection of these often-neglected lower plants, and an extra set of specimens was prepared to be presented to the biology class of Weston High School. Sufficient rain during



ABOVE: Professor G. S. Torrey points out lichens on a rotted stump to a group of students at the Case Estates.

BELOW: Seven busses await participants in the annual Field Day of the Massachusetts Horticultural Society held at Jamaica Plain and conducted by staff members of the Arnold Arboretum.

the month of May kept this flora in excellent condition for the course. Dr. Wagenknecht offered an evening class at Jamaica Plain for students interested in classification of flowering plants and the preparation of specimens for class-room or personal collections. Students brought sufficient material for the preparation of duplicate specimens of cultivated plants to be added to the horticultural herbarium.

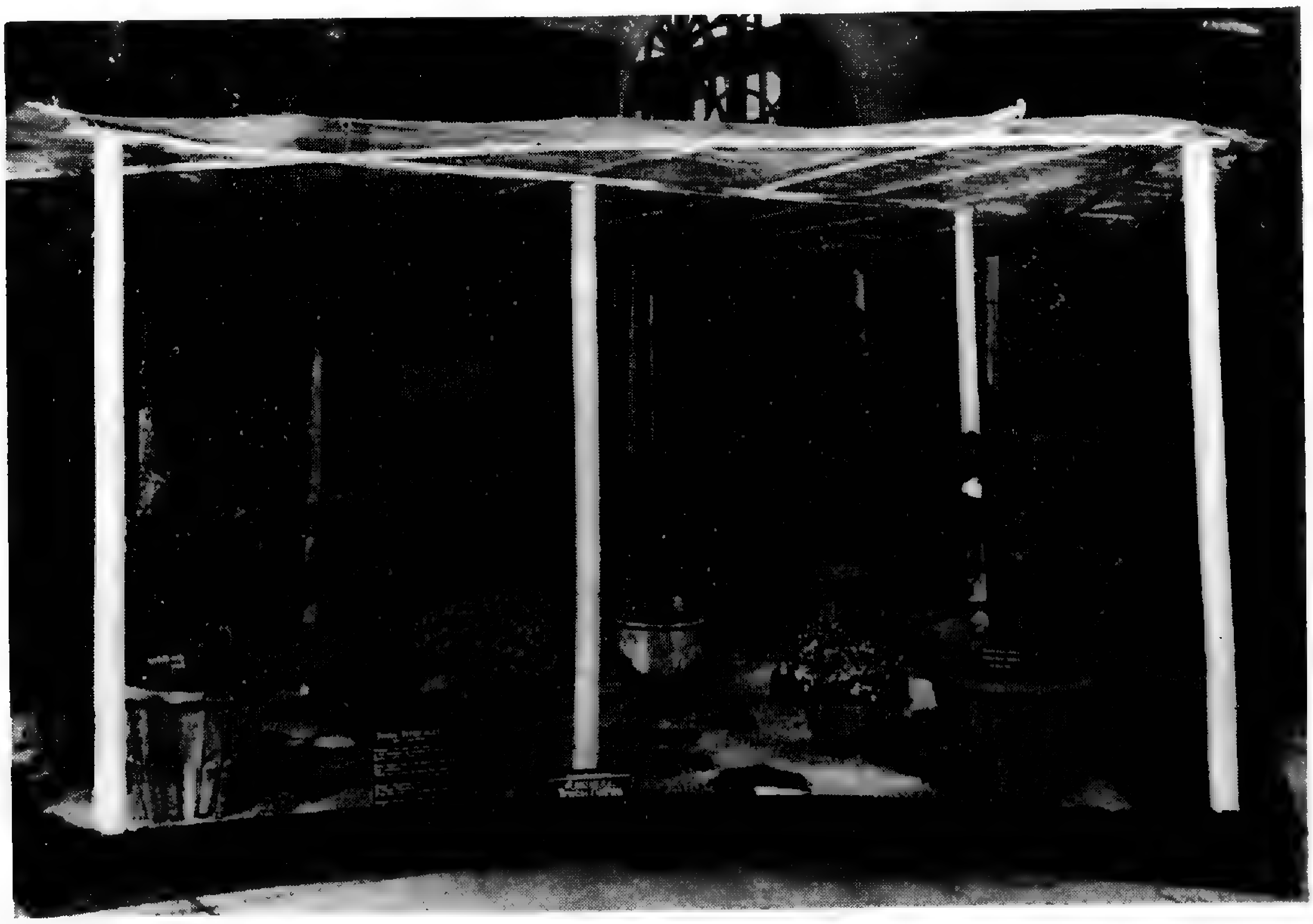
Approximately fifty special tours were conducted on the Arboretum grounds for groups requesting such trips. The largest tour again this year was the Massachusetts Horticultural Society Field Day, held on May 23, the peak of lilac bloom. Approximately 500 people were conducted around the grounds in chartered busses.

Staff members represented the Arboretum at scientific meetings or presented lectures for various groups interested in horticulture. Dr. Sax and Dr. Howard were again appointed lecturers for the visiting lecturer program sponsored by the American Institute of Biological Sciences. Under these auspices Dr. Sax lectured on the Fort Valley College campus, in Fort Valley, Georgia, and Dr. Howard visited the Franklin and Marshall campus, in Lancaster, Pa. Dr. Sax presented the Sigma Xi lecture at the University of Florida and, in returning to Jamaica Plain, lectured at the University of North Carolina, the Blandy Experimental Farm and Florida State University. He also presented by invitation a talk at the meeting of the Association of Southeastern Biologists in Knoxville, Tenn. Dr. Howard was a speaker at the 13th Annual Garden Symposium held at Williamsburg, Va. He attended the annual meeting of the American Institute of Biological Sciences where his paper on the anatomy of the petiole as a taxonomic character was awarded the George R. Cooley prize for the best paper presented to the section on plant taxonomy. Dr. Howard presented a paper on the same subject at the meeting of the northeastern section of the American Society of Horticultural Sciences. Dr. Wagenknecht spoke on the rules of horticultural nomenclature at the same meeting. Mr. Fordham attended the annual meetings of the Plant Propagators Society held in Cleveland, Ohio, and spoke on soft-wood cuttings to the horticultural chairmen of the Garden Club Federation of Massachusetts. Dr. Wyman was the principal speaker at the dedication exercises of the Minnesota Landscape Arboretum at St. Paul, Minnesota, and, with Mrs. Wyman, presented a program on Christmas decorations, plants and plant materials for the Garden Club Federation of Massachusetts. Mrs. Weber participated in the field trip of the American Society of Plant Taxonomists through eastern Kentucky in late August and then attended the meeting of the American Institute of Biological Sciences at Indiana University. Dr. Kobuski attended the Symposium on the Taxonomic Consequences of Man's Activities held by the Missouri Botanical Garden on October 24–25. Dr. Wood and Dr. Wilson attended the meeting of the Association of Southeastern Biologists, in Knoxville, Tennessee, in the course of their spring collecting trip.

Nearly all staff members were called upon as speakers for horticultural programs of gardens clubs in the five New England States.

Exhibits and Displays:

The Arboretum exhibit at the Spring Flower Show of the Massachusetts Horticultural Society by request featured the Larz Anderson collection of Japanese dwarfed trees. These trees, normally housed near the Arboretum greenhouses, were forced into leaf and flower for the March show. Because of the razing of Mechanics Building, the Spring Flower Show was held in Horticultural Hall and Symphony Hall. Unfortunately, a much smaller space than usual was available for our exhibit and the plants could not be shown to their best advantage. Nevertheless, the exhibit set up under the direction of Dr. Wyman, Mr. Williams and Mr. Fordham was awarded a first prize, a cultural certificate and a ribbon from the Massachusetts Department of Agriculture.



The Arnold Arboretum exhibit of *Bonsai* at the Spring Flower Show of the Massachusetts Horticultural Society.

The Christmas show of broad-leaved evergreens, Christmas plants and decorations was held in the lecture hall of the Administration Building. The Christmas tree decorated with native fruits, the wreath-making display prepared by Mrs. Wyman and the information on Christmas trees around the world compiled by Dr. Wagenknecht proved to be of interest to the visitors.

A special exhibit of recommended trees and shrubs for permanent and unusual plantings was prepared for the New England zone meeting of the Garden Club of America held at Cohasset. The New England sources of exhibited plants supplied by the staff proved to be of real interest. Apparently, many people feel that the plants seen at the Arboretum are not readily available. Information on commercial sources of specific plants in the Arboretum collection is supplied by the staff at any time. Where possible, several commercial nurseries are suggested with selection being made only in consideration that a nearby nursery will encourage the prospective buyer more than the information that a mail order is necessary.

Library:

Following the completion of work on combining the library facilities mentioned in the last annual report, the activities of the library and its staff fell into more normal patterns of work. The library of the Arnold Arboretum is one of the outstanding botanical research libraries in the country. When considered in conjunction with the books comprising the library of the Gray Herbarium, the libraries are unsurpassed in quality for taxonomic and horticultural research. The library staff continued the work of reclassifying the extensive pamphlet collection, elaboration of the card index and a reconditioning of many of the books. The service offered to students, staff and visiting scholars was outstanding.

During the year 311 volumes were added to the library by purchase, exchange, transfer or binding, bringing the total volumes on hand to 50,515. Of the additions, 57 volumes were significant to horticultural research and were housed in Jamaica Plain. Several sets of periodicals considered more useful to horticultural work were transferred to the horticultural library. The pamphlet collection was improved and 462 items were added which, with some discarding of duplicates or unwanted materials, brought the pamphlet collection to a total of 16,984 items.

The Gray Herbarium Index to American Plants, maintained in Jamaica Plain, received 3000 new entry cards during the year. About 1200 new entry cards were added to the main index to aid in cross references. Services to other libraries and scientists included the dispatch of 198 books on inter-library loan.

Herbarium:

The work of combining the non-horticultural herbarium specimens of the Arnold Arboretum with the specimens of the Gray Herbarium was completed during the year. The progress and procedure of this major herbarium reorganization has been noted in the annual reports of the past five years. It is with gratitude that I acknowledge the energy and devotion of the Curator, Dr. C. E. Kobuski, who carried the responsibility for this task, and the contribution of the staff members who completed this major task in so short a time. The staff may now return to individual research programs with routine duties maintaining the excellent condition of the herbarium research facility.

During the year 5,918 specimens were mounted and added to the herbarium, bringing the total to 705,370 sheets. Considerable effort is made to repair damaged sheets as they are encountered, and 2,381 such sheets were reconditioned by the mounters.

Our records indicate that 16,581 specimens were received during the past year. Of the total, 15,260 were in exchange, 3,246 as gifts, 339 for identification and 264 by purchase. The largest single shipment, consisting of 5,020 specimens from many parts of Russia, was received from the Academy of Sciences of the USSR. One of the most valuable collections was received by special arrangement from the Museum of Science in the Philippines through Dr. Eduardo Quisumbing. This collection consisted of 2,528 specimens made by the Spanish botanist Vidal in the Philippines between 1872 and 1890. Vidal's collections remained unstudied at the Museum de Ultramarino, in Madrid. During the past year Dr. Quisumbing, while on a Guggenheim Foundation grant, received permission to divide the Vidal collection, in return for its identification. Dr. Quisumbing felt that the most important location for this significant collection was in the Herbarium of the Arnold Arboretum, to supplement what probably is now the most important study collection of Philippine flora. Dr. Quisumbing spent six months of his Guggenheim Fellowship studying our collections from the Philippine archipelago.

The staff filled requests for 90 loans, totaling 13,855 specimens, from the combined herbaria to 46 different institutions, 33 in the United States and 13 in other countries. Sixty-eight loans numbering 10,272 specimens were requested from 44 institutions, 33 American and 10 foreign, for the use of staff members and students. It is interesting to note that incoming loans averaged 151 specimens and loans sent out on request averaged 154 specimens.

With the completion of our major effort in Cambridge, attention was turned to the horticultural herbarium in Jamaica Plain. Portions of the herbarium were painted, new fluorescent lighting was installed, and the entire herbarium was shifted to allow room for expansion. The addition of specimens of cultivated plants is included in the figure given above.

The significant taxonomic work of Rehder, Sargent, Palmer and others in the field of horticultural plant taxonomy antedated the current international rules of botanical and horticultural nomenclature. In anticipation of developing taxonomic work it is necessary to reconsider the work of these earlier Arboretum staff members. In many cases type specimens were not selected or, if selected, were not indicated as such in the original publication of the taxon. Staff members are proceeding to examine the specimens studied by these workers, to separate the types and to indicate lectotypes when necessary. Much of the work of Rehder and Sargent was based on plants growing in the living collections of the Arnold Arboretum. Such plants often were grown from seed collected in the wild at the same time as the herbarium specimen which is the type of a horticultural taxon. In other instances, the type of a horticultural taxon came from a living plant on our grounds. It is desirable to indicate the living plants which are either filial-types (progeny of the type collection) or living holotypes. Age, hurricanes and landscaping changes have destroyed many of these types in the past two decades. Labeling the survivors properly will enable us to preserve such specimens in future emergency situations, to propagate them and make such important specimens available to other arboreta.

The Rehder Index of horticultural nomenclature has been brought up to date and is being maintained current with the literature.

Comparative Morphology:

Professor I. W. Bailey, Professor of Plant Anatomy, *Emeritus*, continued to serve as curator of the wood collection of the Arnold Arboretum. His care of the collection, including filling requests for wood samples, is greatly appreciated. Professor Bailey has initiated an investigation of the anatomy of the Cactaceae under a three-year grant from the National Science Foundation. He is concentrating first on a comprehensive study of *Pereskia* and *Pereskiopsis*. The trees, large shrubs and vines that comprise these genera not only have a more normal dicotyledonous habit of growth than most cacti, but also have leaves and well-developed cotyledons. They are generally considered to be the most primitive living representatives of the cactus family. Thus they afford clues regarding the significance of morphological and physiological changes that occur during salient phylogenetic trends of specialization within the highly succulent and xerophytic tribes, *Opuntieae* and *Cereeae*.

Professor Bailey is also studying the structure and chemical composition of the intine of gymnospermous and angiospermous pollen under an assisting grant from the American Philosophical Society.

Cytogenetics:

Dr. Karl Sax has reported the following information on his work in the field of cytogenetics during the past year:

Some of the hybrids of the *Pinus* species made several decades ago are now producing male flowers. Cytological studies of meiosis in F_1 hybrids between *Pinus griffithii* and *P. strobus*, between *P. parviflora* and *P. strobus*, and other hybrids between Old and New World white pine species show almost normal chromosome pairing and a high degree of fertility. The fact that these hybrids are relatively fertile even though the parental species have been separated geographically for very long periods of time indicates that the species of pine have undergone little cytological change in recent evolution.

An induced tetraploid of *Forsythia* called 'Arnold Giant' has been used in breeding work to produce triploids. One of several dozen progeny of this tetraploid *Forsythia* proved to be relatively fertile, although triploids are usually highly sterile. A study of the fertile segregate showed it to be a tetraploid. Since there was only the one tetraploid clone in the Arnold Arboretum at that time the tetraploid progeny must have resulted from self pollination, although diploid forsythias are heterostylic and self-sterile. Apparently tetraploidy induced some degree of self-fertility in the short-styled *Forsythia* 'Arnold Giant.'

The *Forsythia* 'Arnold Dwarf' is a good ground cover, but it is slow in flowering and the flowers are of poor quality. Segregates are being grown to produce types with the fine foliage and spreading habit but with good flowers.

Breeding experiments with two outstanding ornamental crab apple varieties, 'Dorothea' and 'Katherine,' have resulted in several very desirable segregates which have been propagated for further testing.

While at the University of Florida, Dr. Sax applied the methods used on dwarfing fruit trees to grafted pine trees for the establishment of "Seed Orchards." If the techniques induce pines to produce seed at an earlier age and, therefore, smaller size, it would facilitate both spraying and harvesting of the cones.

Instruction:

Staff members were scheduled to offer three classes in the Department of Biology during the past year. During the fall term Dr. Sax presented his class on cytotaxonomy and, in the spring semester, Dr. Howard taught the principles and practice of horticultural plant taxonomy. Dr. Wagenknecht assisted Dr. Howard. During his leave-of-absence as visiting professor at the University of Florida, Dr. Sax offered a course in horticultural and cytological problems for the Department of Botany at Gainesville. Dr. Johnston's class in advanced plant taxonomy was not given.

A series of luncheon seminars presented for staff and graduate students considered the problems of plant distribution and centers of origin. In addition to regular programs presented by the staff members, visiting colleagues, including Dr. Eduardo Quisumbing, of the Philippines, Dr. R. D. Hoogland, of New Guinea, and Dr. André Kostermans, of Indonesia, spoke on plant science in their respective areas of the world.

Travel and Exploration:

Dr. Carroll Wood and Dr. Kenneth Wilson completed a month-long, 4,000-mile collecting trip involving field studies for their work on the flora of the southeastern states. They visited areas in Tennessee, Alabama, Florida, Georgia and North and South Carolina. A number of living collections in the genera *Liriodendron*, *Calycanthus*, *Philadelphus*, *Malus*, *Amelanchier*, *Robinia*, *Lonicera* and *Diervilla*, mostly from northeastern Alabama, were sent to the Arboretum for trials. All of these were wild clones of recognized ornamental genera worthy of cultivation. It is apparent that the area is worthy of more detailed collection and selection, for, in the past, it has yielded such ornamental plants as *Oxydendrum, Halesia, Liriodendron*, *Cladrastis*, *Catalpa*, *Fothergilla* and several deciduous rhododendrons.

During the spring, Dr. Donald Wyman visited azalea collections in Virginia and adjacent states to continue his studies and selections of ornamental subjects in this important group. Dr. Ivan Johnston collected in Texas and Mexico during the year, and Dr. Richard Howard continued his studies of vegetation on bauxite soils in Hawaii. Dr. Frances Jarrett spent a month in England studying the Moraceae in the herbaria of the Royal Botanic Gardens, at Kew, the British Museum (Natural History), and the Botany School, Cambridge University.

Gifts and Grants:

Again this spring the "Friends of the Arnold Arboretum" were generous in their response to the annual appeal for gifts to support the horticultural work of the Arboretum. The financial support obtained is used to supply assistants in the work of plant propagation and for additional labor on the grounds during the summer months. A special gift was received from the Godfrey Cabot Charitable Trust to install an acoustic tile ceiling in the lecture hall of the Administration Building. It is expected that this work will be completed during the summer and will make the auditorium a more pleasant place for meetings.

Special gifts or grants from individuals and foundations were received to support the research work of various staff members. A gift from Mr. George R. Cooley will support the work of Dr. Carroll E. Wood and Dr. Kenneth Wilson on the flora of the southeastern United States. Dr. Karl Sax received a continuation of his grant from the Massachusetts Society for Promoting Agriculture for work on dwarf rootstocks and for methods of promoting the growth and fruiting of fruit trees for New England. The award of a Guggenheim Fellowship to Dr. Sax for work in Oxford, England, after his retirement, has already been announced. Professor I. W. Bailey has received a grant from the National Science Foundation to aid his investigation of the anatomy of the leafy cacti, *Pereskia* and *Pereskiopsis*. Dr. Richard Howard was also awarded a second National Science Foundation grant for work on the anatomy of the petiole as a taxonomic character in the flowering plants.

Publications:

The regular twelve issues of *Arnoldia*, under the editorship of Dr. Donald Wyman, and the four issues of the *Journal of the Arnold Arboretum*, edited by Dr. Carroll Wood, were published during the year. In addition, two special publications were sponsored by the Arboretum. The important pamphlet, "Abbreviations of Titles of Serials Cited by Botanists," compiled by Mrs. Lazella Schwarten and Dr. Harold Rickett and issued first in the *Bulletin of the Torrey Botanical Club*, proved invaluable to botanists. The original supply of reprints was quickly exhausted and the pamphlet was reprinted. A new edition of "The Arboretums and Botanical Gardens of North America" was compiled by Dr. Wyman and issued by the Arnold Arboretum as a special publication. This work was originally published as an issue of *Chronica Botanica* in 1947. More up-to-date information was obtained by questionnaire and the new edition was issued in May, 1959.

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RICHARD A. HOWARD, *Director*

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