JOURNAL
OF THE
ARNOLD ARBORETUM

HARVARD UNIVERSITY

B. G. SCHUBERT
EDITOR

T. G. HARTLEY C. E. WOOD, JR.

D. A. POWELL
CIRCULATION

VOLUME 49

PUBLISHED BY
THE ARNOLD ARBORETUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS
1968

DATES OF ISSUE

No. 1 (pp. 1–166) issued January 15, 1968.

No. 2 (pp. 167–290) issued April 22, 1968.

No. 3 (pp. 291–380) issued July 16, 1968.

No. 4 (pp. 381–559) issued October 17, 1968.

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JANUARY, 1968

PUBLISHED BY
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THE JOURNAL OF THE ARNOLD ARBORETUM

Published quarterly by the Arnold Arboretum of Harvard University.

Subscription price $10.00 per year.

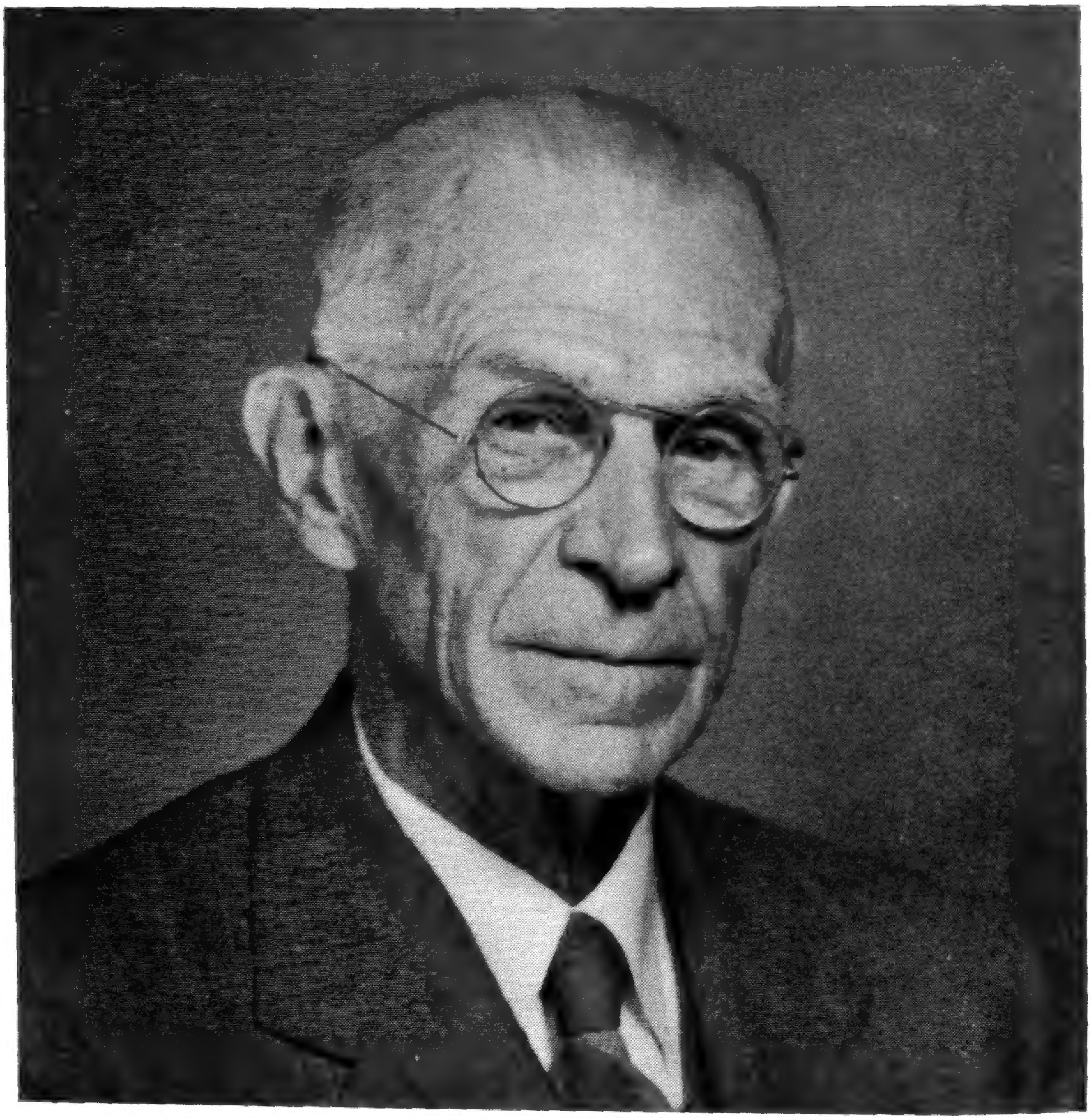
Volumes I–XX, reprinted, and back issues of volumes XXI–XLV are available from the KRAUS REPRINT CORPORATION, 16 EAST 46TH STREET, NEW YORK, N.Y. 10017.

Subscriptions and remittances should be addressed to MISS DULCIE A. POWELL, ARNOLD ARBORETUM, 22 DIVINITY AVENUE, CAMBRIDGE, MASSACHUSETTS 02138.

CONTENTS OF NO. 1

Volume 48, No. 4, including pages 363–588, was issued October 23, 1967.

Second-class postage paid at Boston, Massachusetts



Irving Widmer Bailey

JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. 49 JANUARY 1968 NUMBER 1

IRVING WIDMER BAILEY, 1884–1967

RICHARD A. HOWARD

With portrait *

THE SUDDEN DEATH OF Irving Widmer Bailey on May 16th ended the long and productive career of a brilliant scholar and a son of Harvard in every sense of the word. His place cannot be filled; his kind of contribution cannot be repeated; his leadership and inspiration are not to be duplicated. He was "Professor Bailey" to all but a very few, and the appellation was offered in respect and admiration.

Irving Widmer Bailey was born in Tilton, New Hampshire, August 15, 1884, the only child of Solon Irving Bailey and Ruth Elaine (Poulter) Bailey. His father, an assistant professor of astronomy at Harvard, was sent to Peru in 1889 to select a site for a high altitude observatory. He chose the summit of El Misti at 19,000 feet and, with his family in residence, supervised the operation of an observatory constructed there. Irving Bailey wrote later, "My reactions and activities in college and subsequent to graduation were profoundly influenced by the fact that eight of the first thirteen years of my boyhood were spent in remote parts of South America rather than in the environment of New England. Having no formal and stereotyped education until the age of thirteen, having no playmates of my own race and age, I was forced to rely upon my own resources for interests and activities. Much of my time was spent in hunting, in exploring the Andes at high altitudes, in learning at first hand the traditions and beliefs of Peruvian Indians, and in observing the spectacular activities of Catholic Spanish in peace and in revolution. I developed at an unusually early age, in association with my father and other astronomers, a keenly analytical interest in natural phenomena and in the activities and foibles of the human race under differing hereditary and environmental influences."

Irving Bailey entered Harvard College in 1903 and was graduated with the class of 1907. In his 50th anniversary report he related, "In college I browsed around in history, chemistry, geology and meteorology, but it was not until my senior year that speeches of Gifford Pinchot and President Eliot induced me to undertake a career in forestry, particularly owing

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* Photograph by John Brook, Boston, Massachusetts, 1955.

to the appeal of an out-of-door profession." Bailey entered the graduate school at Harvard in 1907, and his subsequent career was to parallel many changes in the administrative organization of botanical science at Harvard, in which he was to play a continuing and major role. The year 1907 marked the establishment of the School of Applied Science at Harvard with both Forestry and the Bussey Institution, the latter newly reorganized as a school for study of problems relating to agriculture and horticulture, transferred administratively to that School. The Harvard Forest was also acquired in 1907, and the following year a division of Forestry was initiated. In 1908 Bailey received his first Harvard appointment as Assistant in Botany. He was awarded the Master of Forestry degree in 1909 and almost simultaneously an appointment as Instructor of Forestry in the Graduate School of Applied Science. In 1912 a short-lived School of Forestry was formed, with Bailey on the staff as an Assistant Professor. In 1914 the Bussey Institution and the School of Forestry were combined as the Graduate School of Applied Biology, which was then known internationally and now historically as the Bussey Institution. Professor Bailey was promoted to Associate Professor of this Institution in 1920 and became Professor of Plant Anatomy in 1927. In 1931 further administrative changes abolished the Bussey Institution as a school and transferred its instruction and degree-granting privileges to the Division of Biology. At that time Professor Bailey was transferred to the staff of the Arnold Arboretum for budgetary purposes, although his office was to be in the Biological Laboratories in Cambridge until the year before his retirement. Then, with the completion of the Harvard University Herbaria building in 1954, Bailey moved his office and laboratory along with the wood collection into the new building. After his retirement in 1955, he continued to use work space in the quarters of the wood collection and followed a regular schedule in the laboratory until the heart attack that ended his life. This building represents the fulfillment of his own plan, presented to the Harvard Corporation at their request in 1945, for assembling most of the botanical institutions at Harvard under one roof.

Although he carried the title of Professor, Irving Bailey was not primarily a teacher. His students during the years at the Bussey Institution and later in the Department of Biology were those of graduate level and advanced instruction. Few students actually received their advanced degrees under his supervision. Because he was not directly responsible for student guidance, he was even more effective in giving help when it was requested and needed. The few courses he taught were organized throughout in the same meticulous fashion with which he wrote. His superb photographic techniques produced lantern slides that focused on the exact point to be made. His lectures were a pleasure to listen to and a student's delight to annotate, yet he worried incessantly before and after each scheduled presentation. His talent for teaching, however, was also evident in his association with younger people who served as his technicians. The junior authors of many, many papers, Mary Vestal, Anna Faull, Richard Howard, Charlotte Nast, B. G. L. Swamy, were assistants who shared the honor of being included in some of Bailey's writing and "graduated" to contributions of their own.

It is his research and his published contributions that are the expression of the true talents of Irving Bailey. His first paper was published in 1909, and one remained in manuscript at the time of his death. In the 58 years of his productive career Bailey published the 142 papers listed in the bibliography which follows. These cover a variety of fields and show a return, often years later, to an original subject for further elaboration or, when needed, a change in direction. Professor Bailey is credited with two books. In reality one is a small printed report on the status of forestry education and the other a collection of his papers reprinted in book form. He was often visited by representatives of book publishing firms pleading for him to write a book. He was most generous in giving his time to reading manuscripts of other writers and offering his criticisms or compliments. His own failure to write a book he once explained as his willingness to let others summarize for, while he could, he preferred to contribute his original ideas and investigations.

Bailey recalled in the Fiftieth Anniversary Report of the Harvard Class of 1907, "Upon obtaining my degree of Master of Forestry, I spent several years studying lumbering and wood-using industries, and became convinced that the existing economic, social and political status in North America was such as to inhibit for many years an extensive application of intensive European silvicultural methods. At the same time, I became increasingly impressed by the lack of accurate and reliable information regarding the anatomical structure, physical properties and chemical composition of wood and the vital processes by which it is formed in plants. Thus, since joining the staff of the reorganized Bussey Institution in 1914, I have devoted my attention largely to research in various aspects of this pioneering field. As data accumulated, they became increasingly significant in the discussion of theoretical botanical problems of plant identification, plant classification, plant physiology and evolution, as well as in the solution of practical problems of wood utilization. Therefore, at present I am generally regarded both in this country and abroad as a botanist rather than as a forester."

In reviewing his own publications for reprinting in book form in 1954, Bailey agreed to eight chapters grouping his contributions into the broad categories of cytology and ontogeny, biochemistry and biophysics, phylogeny, taxonomy, entomology, paleobotany, wood technology, and cooperation in scientific research. These areas truly reflect the scope of Professor Bailey's abilities, and each is used often in his writings or returned to in the course of his research.

Every scholar has in his background an individual influential in the development of his career. Regrettably, there is little acknowledgement of the role of Edward Charles Jeffrey in the development of the career of Irving Bailey. Jeffrey was Assistant Professor of Vegetable Histology and General Morphology at Harvard from 1902 to 1907, when Bailey was an undergraduate. He became Professor of Plant Anatomy in 1907 and retired in 1933. In many ways Irving Bailey can be regarded as his successor. Bailey's early publications, often recorded as "Contributions from the Phanerogamic Laboratories of Harvard University," acknowledged the valuable assistance of Jeffrey or the courtesies of his laboratory. Their subject matter certainly followed the same interests of Jeffrey and in the beginning followed his theories. In 1914 in the early numbers of a series of six papers titled "Investigations on the Phylogeny of the Angiosperms," Bailey and his co-author Edmund Sinnott dissented from Jeffrey's theories, the split largely starting with the subject of the "aggregate ray." Jeffrey's book, "The Anatomy of Woody Plants," published in 1917, contained many ideas and descriptions which Bailey did not accept, and a conflict between them continued in print. Following the appearance of two papers by Jeffrey and R. E. Torrey in the Botanical Gazette in 1921, Bailey and Sinnott wrote, "a vigourous attempt is made to discredit our work. The unfortunate tone of this attack we can afford to ignore but in view of the misrepresentation of our position which they have introduced into the discussion we feel that it is wise to restate our conclusions in the light of all the facts which have been brought forward, and to endeavor to clarify the real point at issue." The wounds created were never healed, yet the training Jeffrey had offered the young Irving Bailey came to an imaginative mind and an energetic body.

During World War I Bailey's talents as a wood technologist were used at Wright Field in Dayton, Ohio. His early interest in the preservation of wood he also associated with studies of the structure of the stem. At Wright Field he was Chief of the Wood Section of the Materials Engineering Department of the Bureau of Aircraft Production. The principal woods used in wing and frame construction of World War I aircraft were spruces and firs. The methods of cutting, curing, milling and splicing these occupied Bailey's interests and were his responsibilities. When the supply of spruce was threatened by insect attacks in the postwar years he took part in studies which led to nearly classical papers on the spruce budworm biocoenose. Bailey tendered his resignation as "Aeronautical Mechanical Engineer" effective December 23, 1918, and returned to the Bussey Institution in Jamaica Plain.

The two distinctive types of research which were to occupy Bailey's time on his return to academic life were to develop quickly. His war time studies of wood structure developed into a long series of papers on the cambium and its derivative tissues. At the Bussey he undertook a special study of the stem structure of some African myrmecophytes for the director, William M. Wheeler. This involved a study of the feeding habits of plant-inhabiting ants, and in 1920, Bailey spent the summer in British Guiana working at the tropical research station of William Beebe. He had received a grant of $500 from the AAAS for this field work and during a portion of the time he was in the company of Wheeler. The observations they made on species of *Cordia*, *Cecropia*, *Triplaris*, and other ant plants were not published until 1942, after Wheeler's death in 1937. The work in entomology with Wheeler and the expedition to British Guiana were apparently among the most enjoyable experiences of Bailey's life, for tales of these were often repeated in social gatherings.

In the course of the work in British Guiana, Bailey found a new species of *Cecropia* which he described in 1922. He was also able to make observations on other plants including species of *Marcgravia*. The flowers of the unusual inflorescences of *Marcgravia* plants were often considered to be pollinated by birds. Bailey's observations on these plants and their pollination formed a series of papers which also included two new species of *Marcgravia*. Bailey did not collect many plant specimens and his collections for that trip numbered 195 in the figures he cited.

Bailey's ventures into taxonomy were not many. In addition to the three species described from South America he is credited as the senior author of the family Degeneriaceae. This resulted from the cooperative study with A. C. Smith on plants of the Fiji Islands and was a phase of the study of the primitive Angiosperms which Bailey insisted on calling inaccurately the "woody Ranales."

Bailey is well remembered for his cooperation with taxonomists, and his work on the Icacinaceae is representative. Perhaps from his survey work with Sinnott on the nodal structure of plant families he had retained an interest in families of flowering plants which showed diverse habits or structure. His attention had been drawn to the anomalous structure in one genus of the Icacinaceae in the thesis of Benjamin Robinson, then director of the Gray Herbarium. Professor Bailey assigned to me the task of preparing the anatomical slides needed for an investigation of the remainder of the genera. These materials were then studied and discrepancies were soon obvious in the taxonomic classification of the specimens. In some cases the specimens were incorrectly named and in others the species were incorrectly placed. The value of anatomical characters in taxonomy soon became evident in this family. A series of papers by Bailey and Howard, by Howard, and by Dahl resulted from this work. One taxon of the Icacinaceae with distinctive anatomical characteristics could also be shown to be distinct on the basis of characters commonly used. The genus then distinguished was named in his honor, *Irvingbaileya*. In later years Swamy described a new species of vesselless angiosperms as *Sarcandra irvingbaileyi* to honor his early association with Professor Bailey and Bailey's long interest in such primitive plants.

Professor Bailey was frequently asked for his opinion on aberrant species or genera as plant materials came into the Arnold Arboretum for determination. The taxonomic research published in the Journal of the Arnold Arboretum often carries a few words of anatomical description or notes on relationships supplied by Bailey or an acknowledgement of his assistance in finding the right place for the material.

A report to the Dean of the Faculty of Arts and Sciences prepared by Professor Bailey and entitled "Botany and its application at Harvard" has been called the "Bailey Plan" or the "Bailey Report." It was the subject of an acrimonious controversy which lasted over two decades while Professor Bailey was active, and after his retirement. Although initially submitted as a confidential report in 1945, its recommendations were accepted by the Dean and an "unclassified" edition was prepared and published. The report and plan which Professor Bailey himself described at an annual meeting of the American Association for the Advancement of Science (1946) created discussion which was to involve the faculty, the Board of Overseers and its committee to Visit the Arnold Arboretum, the Corporation, many teams of lawyers, and two decisions of the Supreme Judicial Court of Massachusetts. In particular the wisdom of the recommendations regarding the Arnold Arboretum was challenged and after due consideration the Harvard Corporation as trustees of the Arnold Arboretum voted in 1953 that the "plan contained in the Bailey Report of June 1945 shall not apply to the Arnold Arboretum or to the principal or income of its endowment." The Harvard Corporation approved the construction of a new building in Cambridge, the implementation of the Bailey plan for other departments, and the removal of a portion of the collections of books and specimens of the Arnold Arboretum from Jamaica Plain to Cambridge. The transfer of these resources was approved with the understanding that a working herbarium and a library were to remain in Jamaica Plain. The division created an area of horticultural interest in Jamaica Plain with the library and herbarium there devoted to the study of plants under cultivation and associated with the living collections and the greenhouses. The second unit to be formed in Cambridge would contain the larger portion of the herbarium and library and would be specialized in its application to the native floras of the world, and to basic problems in plant anatomy and morphology.

Eventually, in 1967, the Supreme Court approved the division proposed but in the many hearings, published accounts, and reports the name of Professor Bailey was inevitably associated with the objectionable features. Professor Bailey was deeply disturbed, as he felt many of the attacks were directed at him personally and that he could not, or should not, reply. His loyalty to Harvard and his interest in increasing the rôle and the efficiency of use of botanical collections and botanical training at Harvard he put honestly before a personal concern for single departments or individuals.

Bailey's travels were not many. He did not attend international meetings and only infrequently attended those in the United States. His only trip to Europe was a survey of forestry schools and training made with Herman Spoehr. This resulted in the book, "The Role of Research in the Development of Forestry in North America," published in 1929. Dr. Spoehr was on the staff of the Carnegie Institution of Washington, and their cooperation resulted in Bailey's being appointed a research associate of the Carnegie Institution. For several summers Bailey regularly traveled to Arizona to work at the desert laboratory. His published papers during this period listed his association as either the Arnold Arboretum or Harvard University and as a research associate of the Carnegie Institution of Washington. Typical of Bailey is the fact that his association with a desert laboratory and studies on members of the Cactaceae in the decade

1930–40 would be revealed again in his studies of the leaf-bearing Cactaceae in the 1960's. Bailey made a trip to Cuba to visit the Atkins Laboratory at Soledad and to Honduras for a study of forestry problems associated with the United Fruit Company program in Central America.

In later years his summers were spent at his home in Norwell, where a physical battle with the brush with scythe and axe and clippers gave him a healthy skin color and a muscle tone envied by his colleagues. These were happy moments in his life which he shared with his family. A by-product of these summers usually was revealed around Christmas when special friends were presented jars of beach plum jelly which Professor Bailey made during the carefree summers, when fruits could be picked with his adored grandchildren.

Professor Bailey married Helen Diman Harwood on June 15, 1911. He is survived by his wife and their two sons, Harwood and Solon Irving II, and five grandchildren.

Bailey was a member of the National Academy of Sciences, being an Emeritus Member at the time of his death; the American Academy of Arts and Sciences, having served as vice-president from 1947 through 1949; the American Association for the Advancement of Sciences, of which he was a Fellow; the American Philosophical Society; the Botanical Society of America, of which he was treasurer 1921–24, vice-president 1928, and president in 1945; the Society of American Foresters; the American Society of Naturalists; the American Society of Plant Physiologists; the Torrey Botanical Club; the Society for the Study of Evolution; the Royal Swedish Academy of Sciences; the International Association of Wood Anatomists; the Linnean Society of London; the Ecological Society of America; the New England Botanical Club; the International Society of Plant Morphologists, of which he was president from 1960 to 1964, and an honorary member of the Indian Botanical Society. Professor Bailey served on the editorial boards of the American Journal of Botany 1915–18, the Proceedings of the Society of American Foresters 1914–16, the Journal of the Arnold Arboretum 1941–1957. He has been listed in Who's Who in America and its various subdivisions, the International Who's Who and American Men of Science. In the third edition of American Men of Science, Irving Bailey was listed for the first time along with his father, Solon Bailey. In 1931 Professor Bailey received an honorary degree of Doctor of Science from the University of Wisconsin. In 1954 he was honored with the Mary Soper Pope award from the Cranbrook Institute of Science which stated, "The wide influence of his fundamental work on the biological processes involved in the formation, growth and differentiation of cells in woody tissues has deeply affected the growth of other fields, histological chemistry, taxonomy and evolution among them. . . . As a teacher and administrator his inspiration and guidance have contributed to the growth of many leaders in modern botany."

In 1956 at the Fiftieth Anniversary meeting of the Botanical Society of America Professor Bailey was among those honored with certificates of merit, his stating "plant anatomist and inspiring teacher, for his outstanding contributions on the structure of the cell wall and the histology of the cambium and for his application of anatomy and morphology to problems of evolution of angiosperms."

The University of Syracuse also awarded him an honorary S.D. in 1961 with the citation: "Your name is synonymous with the role of research in the development of forestry. Your dedication to truth, zeal in research, and capacity to see the unexpected are gifts you have used to enhance and ennoble all the lives you have touched. Your solid and creative scholarship still guides and challenges forestry research. We honor you as forestry's pre-eminent wood anatomist and botanist and a truly inspired teacher."

The degree he valued most highly, however, was received from his Alma Mater at the 319th Commencement of Harvard, in 1955, on the occasion of his retirement. "Irving Widmer Bailey, Doctor of Science, today your university salutes you for your direction of botanical study and for your accomplishment in searching, in the anatomy of plants, for clues to the miracle of growth."

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INFLORESCENCE IN NANNORRHOPS RITCHIANA (PALMAE)

P. B. Tomlinson and H. E. Moore, Jr.[1]

Palm inflorescences in herbaria are largely represented by small fragments. Hence it is not surprising that botanical literature gives little aid to an overall appreciation of flowering processes in palms. Also the multiplicity of terms used in describing the parts of reproductive branches of palms — spathe, spadix, spathelet, rachilla, involucel, etc. does little to reveal the basic pattern of construction. These terms may have some use in description but lack of consistency in their application diminishes their value. As strict morphological terms they have no significance. There is no published account which clearly outlines the principles involved in the construction of palm inflorescences.

The present article aims at a clarification of some inflorescence features in palms by describing the unspecialized type found in *Nannorrhops ritchiana* (Griffith) Aitchison,[2] as it is cultivated in South Florida. A wide familiarity with inflorescence construction in palms both in cultivation and in the field shows that *Nannorrhops* can be used as a model for a general understanding of other palm inflorescences.

It is necessary first to appreciate that the flowering phase is a physiological state and it was as such that the term "inflorescence" was applied by earlier botanists, as Rickett (1944) points out, although the term subsequently has been adopted largely as a morphological one. A general discussion of shoot construction in palms and other arborescent monocotyledons (Tomlinson, 1964) has emphasized that each axis passes through three physiological states during its development, these phases being recognized by combinations of morphological features. There is a gradual transition from one phase to another and they may overlap. An initial juvenile phase, during which establishment growth (Tomlinson & Zimmermann, 1966) takes place, is followed by an adult vegetative phase, in turn followed by a reproductive phase, the physiological state of inflorescence. Each axis may grow from a seed, or from a lateral sucker.

In palms inflorescence is expressed in three distinct ways. Most commonly the reproductive parts are borne on lateral branches maturing in

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[1] Research on the taxonomy, morphology, and anatomy of palms is supported by individual research grants from the National Science Foundation, grant GB 2991 and its continuation GB 5762–X (P.B.T.) and GB 3528 (H.E.M.).

[2] The specific epithet is derived from *Chamaerops ritchiana* W. Griffith but is often spelled *ritchieana*. Though Griffith named the species in honor of Dr. Ritchie, he used the shortened epithet in the original publication (Calcutta Jour. Nat. Hist. **5**: 342, 343. 1844) and in the posthumously published *Palms of British East India* 135. 1850. Since it seems apparent that the omission of the terminal letter of Ritchie's name was intentional rather than a typographical error, the original spelling is retained.

acropetal order and the flowering process does not inhibit growth of the axis. Corner (1966, p. 124) applies the term pleonanthic to this method of flowering. Morphologists describe such palms as having "lateral inflorescences." In a second group the flowering process is hapaxanthic, vegetative growth is completely substituted by an axis with an acropetally-developed series of reproductive branches. The axis may elongate to produce a conspicuous "terminal inflorescence" as is most familiar in *Corypha, Nannorrhops* and species of *Metroxylon*. Here the hapaxanthic condition is obvious. Otherwise, as in *Raphia* and some other Lepidocaryoid palms, growth of the axis ceases with the production of lateral reproductive branches in the axils of relatively unmodified leaves in such a way that a conspicuous terminal "inflorescence" is not evident.

Another hapaxanthic type is so distinctive as to merit a third category. This is represented by and characteristic of the small but very natural subfamily Caryotoideae (Moore, 1963). Here the reproductive phase inhibits vegetative growth but in such a way that development of lateral flowering axes is almost invariably in a basipetal direction from successively older dormant axillary buds. In effect the whole vegetative axis becomes converted into a gigantic "inflorescence" with basipetal maturation. At least one exception to this rule is found in the recently described *Arenga retroflorescens* (Moore & Meijer, 1965).

Only in single-stemmed palms does hapaxanthic flowering terminate the existence of the individual, as in *Corypha*. These individuals may be described as monocarpic. Otherwise continued substitution of old axes by new ones arising as basal suckers continues the life of the individual, as in many Lepidocaryoid and Caryotoid palms. Substitution of axes in *Nannorrhops* is distinctive as described below. In these hapaxanthic palms the individuals are polycarpic.

The present article describes the morphological features found in the reproductive phase in *Nannorrhops*. This develops a gigantic terminal "panicle," using this term in the loose way recommended by Rickett (1944) to describe a much-branched inflorescence. This article complements the detailed accounts of floral anatomy by Gupta (1960) and Morrow (1965), neither of whom were concerned with overall inflorescence structure.

MATERIAL AND METHODS

Several clumps of *Nannorrhops ritchiana*, a member of the fan-leaved Coryphoideae, were available at Fairchild Tropical Garden and the Plant Introduction Station, Old Cutler Road, Miami, Florida. Observations have extended over a period of years and the expansion of several inflorescences has been watched. Two inflorescences (referred to as shoot 1 and shoot 2) have been cut down and examined in quantitative detail. Approximate measurements of essential parts on each of these shoots are presented graphically in FIGURES 1 and 2. In these figures, ordinates are arbitrary leaf numbers counted from the cut. Photographic (FIGS. 35–42) and other illustrations are largely from these two shoots. Fluid-fixed material of shoot 2 has been preserved for future anatomical study.

OBSERVATIONS

General habit. In its native habitat in northwest India and Afghanistan, *Nannorrhops* was described by Blatter (1926) as a low-growing gregarious shrub with a prostrate "rhizome," but exceptionally growing erect, as indicated by Gupta's photograph. This erect habit is the one largely adopted by specimens in cultivation in South Florida, no doubt as a result of the relatively luxuriant conditions for growth. In this facultative ability it recalls *Serenoa repens*.

The vegetative axis, whether erect or decumbent, is branched. Branching of the creeping axes and in the basal part of the erect axes is apparently axillary, suckers developing in a manner which again bears comparison with *Serenoa*. On the other hand distal branching of the aërial axes of specimens in South Florida involves an initial equal forking which suggests, at least superficially, a true dichotomy. This we have illustrated elsewhere (Tomlinson & Moore, 1966). This dichotomous-like branching, previously familiar only in *Hyphaene* (Schoute, 1909), seems more common in palms than hitherto suspected (Tomlinson & Moore, 1966; Tomlinson, 1967). Forking of the axis is initiated equally, but the two axes behave differently. One branch rapidly proceeds to inflorescence, producing the terminal panicle. The other branch repeats the forking, apparently in a plane at right angles to the first fork. Repeated forking with overtopping of a reproductive shoot by a vegetative shoot may continue for some time.

Reproductive phase. The onset of the reproductive phase involves direct transformation of one fork into an "inflorescence." Early stages are revealed by the asparagus-like aspect of the crown (FIG. 35). Subsequently, as the axis elongates the three main morphological features of the inflorescence become evident (FIGS. 36–38). These are (a) gradual modification of leaves (b) a narrowing and initial extension of internodes (c) development of axillary branches. The first two changes are quite gradual, the latter change is abrupt. At maturity the terminal panicle, 2–4 meters high, rises conspicuously above the vegetative clump (FIGS. 39, 40, 42).

Gradual modification of leaf shape along the main reproductive axis for both shoots is indicated in FIGURES 1 and 2. A continuous leaf series from shoot 1 is shown in FIGURE 41. No change in leaf insertion is involved, the 2/5 spiral phyllotaxis of the vegetative part of the shoot is continued into the inflorescence. Normal foliage leaves have a distinct blade, petiole, and sheath (FIGS. 1, 14, 15), but these undergo a progressive reduction along the reproductive axes; leaves are shortened, petiole first and then the blade are diminished and finally eliminated until distal leaves are represented by the sheath alone (FIGS. 5–13), the vestigial

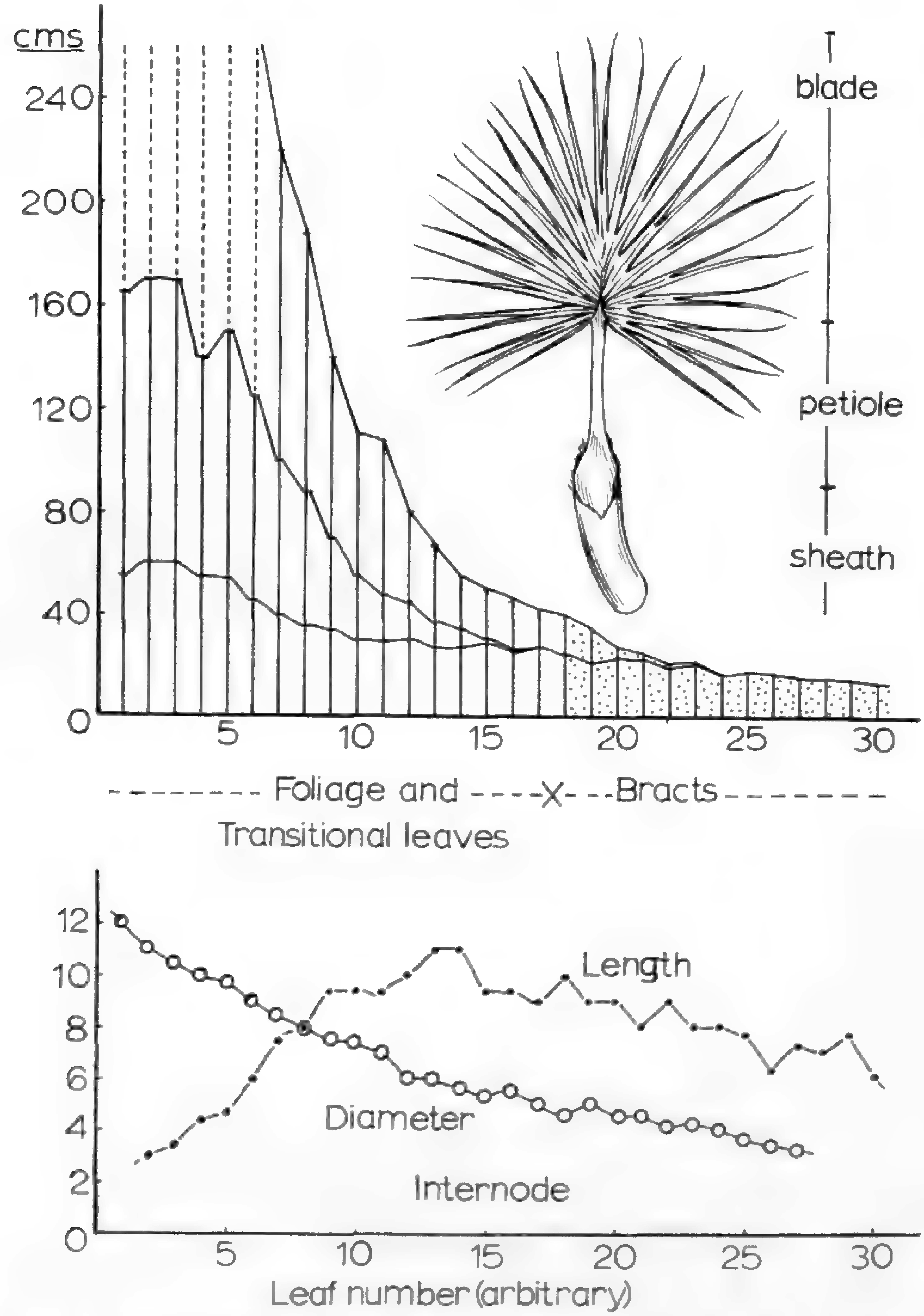


FIG. 1. *Nannorrhops.* Quantitative details of leaves and main axis in shoot 1. ABOVE: approximate length of sheath, petiole and blade of successive leaves along main axis, leaves numbered arbitrarily from level where the shoot was cut. Stippled area to right indicates branched portion of axis. BELOW: length and diameter of corresponding internodes.

petiole plus blade appearing only as a short distal appendage (FIGS. 11–13). This minute appendage, which establishes the plane of symmetry, is found even in the smallest bracts (e.g. FIGS. 28–30).

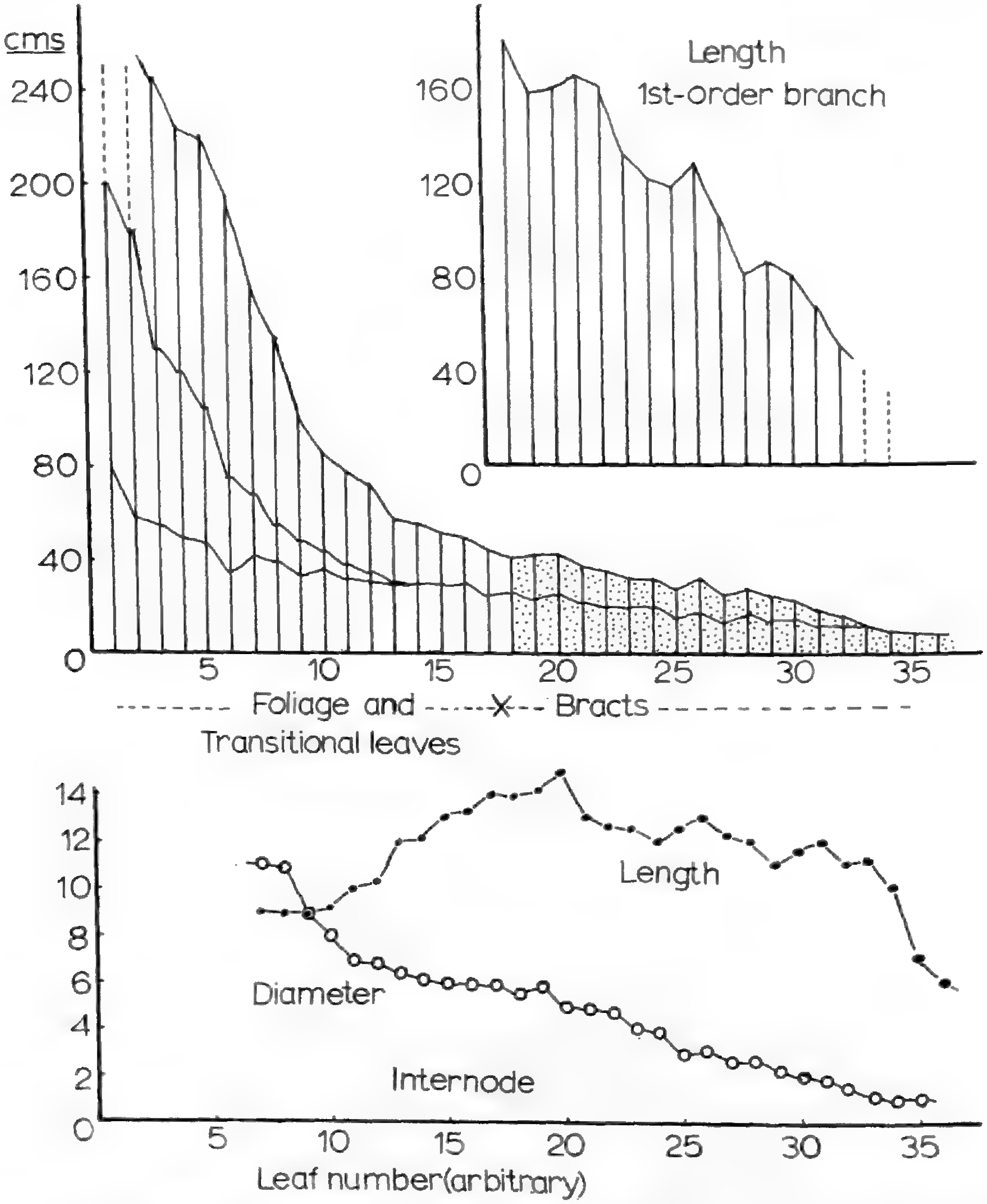


FIG. 2. *Nannorrhops*. Details of shoot 2, as for shoot 1. ABOVE RIGHT: approximate overall length of first-order branches subtended by leaves indicated below.

Associated with these changes in leaf shape and size is a gradual and uniform decrease in internode diameter; internode length, on the other hand initially increases, subsequently declining uniformly (FIGS. 1, below; 2, below). Maximum internode length is about the level of exsertion of the first branch but the agreement is not very precise and may be quite incidental.

The sheath of each reduced leaf remains a closed tube, as in the foliage leaves. *Nannorrhops* has the *Hyphaene*-type of foliage leaf base, in which a dorsal rhombohedral cleft (Fig. 5, detail to left) accommodates the mechanical stresses imposed by expansion of internal tissues and organs (Tomlinson, 1962). Progressive narrowing of the axis as the inflorescence develops gradually eliminates mechanical stresses on successive leaf sheaths. Consequently the dorsal cleft gradually disappears; in shoot 2, leaf number 10 is the last leaf to possess this cleft (Fig. 6, detail to right). Rarely a dorsal cleft is regained in some of the lower bracts, presumably to accommodate expansion induced by developing axillary branches.

In contrast to the above changes, initiation of lateral branches is abrupt. Normally there are no aborted buds below the level of first branching. The first branch is usually longest, subsequent branches being progressively reduced in proportion to the distal decline (Fig. 2, above right). Details of these branches may now be examined.

Branches and bracts. The main vegetative axis shows a gradual transformation as it becomes reproductive, most obviously in the long transitional series from foliage leaves to bracts. In contrast to the vegetative axis a series of elaborate branches is initiated on the reproductive axis. One of these branches is shown in Figure 3. Leaves on main and subsequent axes which subtend branches are defined as *bracts*. First-order bracts, *i.e.* bracts on the main axis which subtend first-order branches, are simply part of the transition series illustrated in Figures 1 and 2. From this series it is clear that bracts do not differ from foliage leaves in any fundamental morphological way. They are modified leaves distinguished only by position and definition.

Branching is straightforward and uniform and may be repeated up to five times. A simple one to one relationship between bract and branch is maintained. Each bract (br) subtends an axis (ax) of the next higher order. The main axis (ax_0) bears first-order bracts (br_1) which subtend branches of the first order (ax_1). These in turn bear second-order bracts (br_2) which subtend second-order branches (ax_2) and so on. On the proximal parts this may be repeated so that fifth-order bracts (br_5) subtend fifth-order branches (ax_5). The diameter and length of successive orders of branches are progressively reduced. Table I is a series of measurements from a lateral branch (cf. Fig. 3) which illustrates this reduction. This progressively reduced branch system ends in flower clusters which are themselves condensed branch systems as described below. Axes bearing flower clusters may be referred to as *rachillae* since this is a convenient and widely understood term. A rachilla is a visible axis which ends each branch, regardless of its order. This is shown most clearly in Fig. 17 which represents the end of a second-order branch. Even the main axis itself (ax_0) ends in a rachilla. However, rachillae

Table I. SIZE OF BRACTS AND BRANCHES OF SUCCESSIVE ORDERS (CMS.)

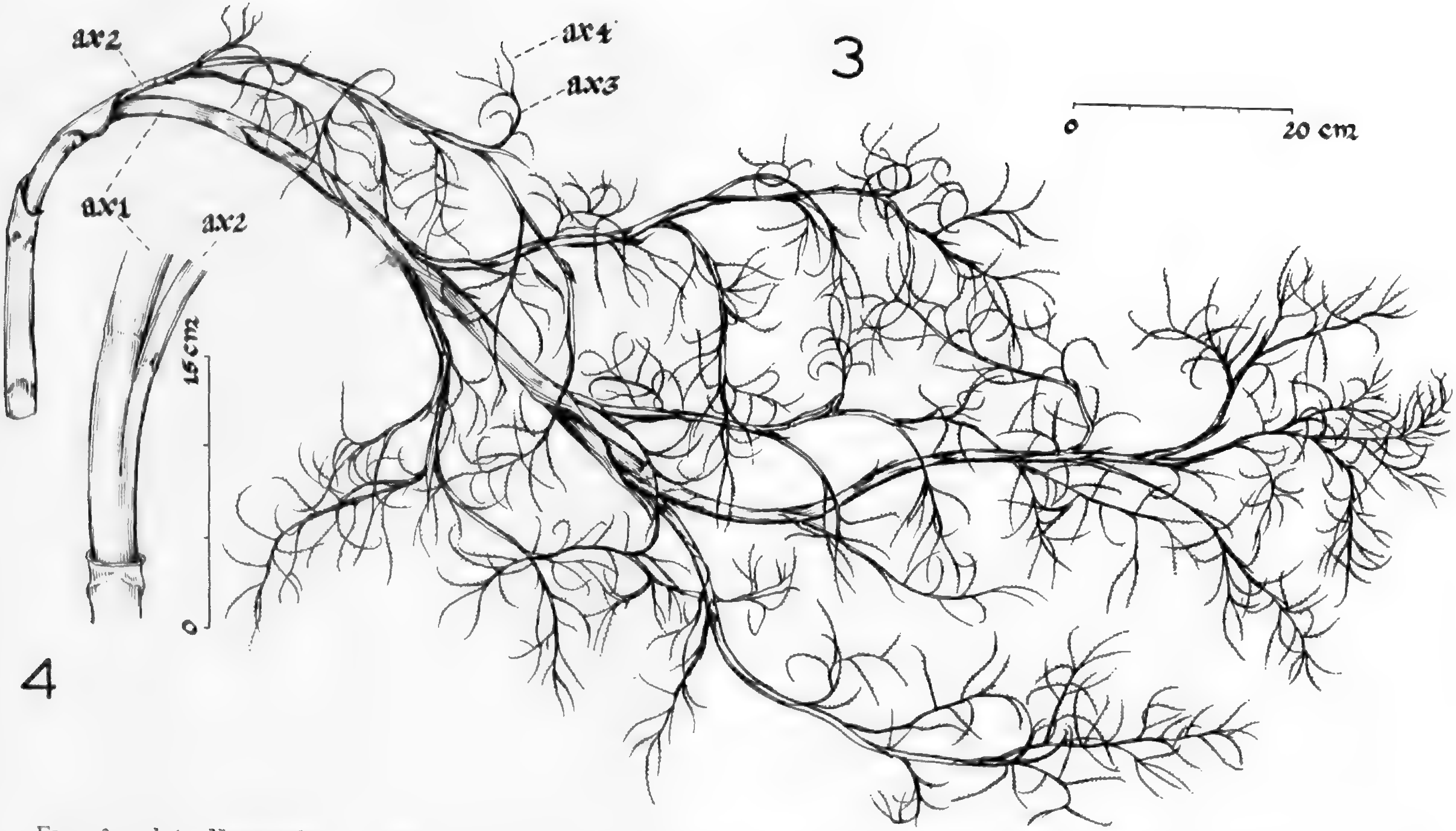
	OVERALL	TOTAL NO.		BRACT NUMBER; LENGTH AND DIAMETER					
AXIS	LENGTH	BRACTS	PROPHYLL	3	5	10	15	20	25
$3ax_1$ (on ax_0)	160	c. 32							
LENGTH			15			21	16	5	2
DIAMETER			3			1.5	1	0.4	0.1
$3ax_2$ (on $3ax_1$)	85	c. 22							
LENGTH			8			9.5	2		
DIAMETER			1.2			0.3	0.2		
$3ax_3$ (on $3ax_2$)	30	12							
LENGTH			2		2	0.3			
DIAMETER			0.4		0.2	0.1			
$3ax_4$ (on $3ax_3$)	10	2	0.5	0.2					
			0.1	<0.1					
RACHILLA $2ax_5$ (on $3ax_4$)	ca. 25 bracts, each subtending a flower cluster; distal clusters aborted; bracts each 2–3 mm. long, diameter of axis <1 mm. wide at base.								

Notes: Each axis referred to is third along the axis of previous highest order i.e. $3ax_n$ on $3ax_{n-1}$, except for the ultimate rachilla which is the second of the fifth-order branches ($2ax_5$) borne on $3ax_4$. Each axis ends in a rachilla, the approximate total number of bracts listed for each axis does not include the distal bracts subtending flower clusters on this rachilla. The third bract on $3ax_4$ is the first on the terminal rachilla and subtends the first flower cluster. Along any one axis bracts commonly show a slight increase in length before the distal decrease, e.g. $3ax_1$. The length of these bracts, however, includes a pronounced terminal appendage (e.g. FIGS. 20–22).

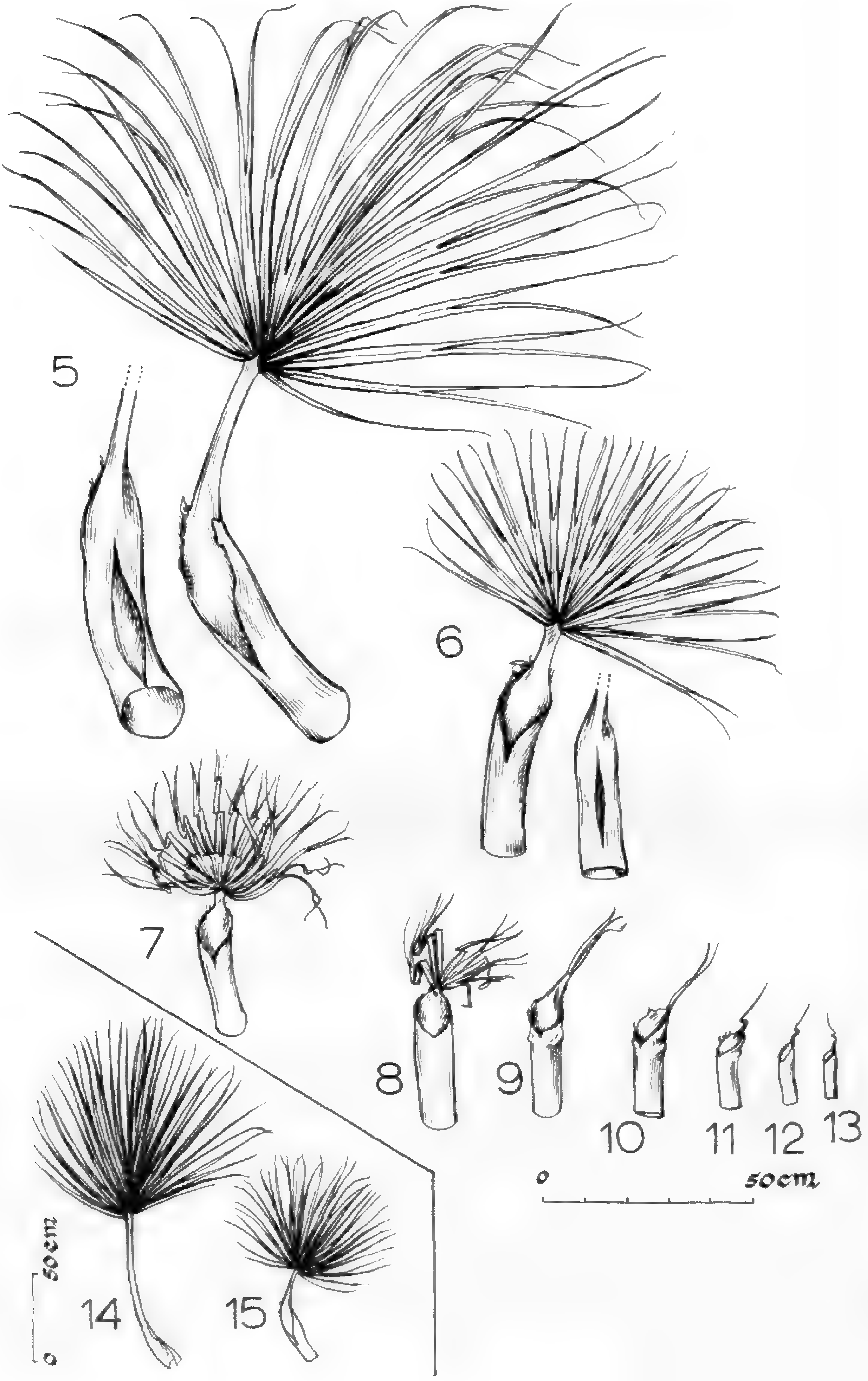
are not strictly the ultimate branch units because the flower clusters have to be interpreted as such, as is shown below.

Length of successive branches is progressively reduced, but not in the regular way recorded for the first order branches in FIG. 2, above right. Proximal branches of any one order tend to be short, presumably because they have limited space in which to develop. Therefore the largest branches tend to be in the middle of each axis (FIG. 3). Bracts, unlike branches, show more constant reduction along each axis and from the axis of one order to that of the next higher order. Some quantitative details which illustrate this reduction are indicated in TABLE I. Distally, bracts are narrow, tubular organs with asymmetric mouths and they bear little obvious relation to foliage fan-leaves, but their ultimate morphology is evident from the transitional series along main and subsequent axes (FIGS. 5–13 along ax_0; 18–22 along ax_1; 23 and 25 on ax_2).

Although they are progressively reduced in size, bracts overlap in all but the last stages of development and their value in protecting axillary units which develop within is quite obvious (e.g. FIG. 16). This protective function becomes less significant in successively narrower axes. The



FIGS. 3 and 4. *Nannorrhops*. First-order lateral branch (ax$_1$). FIG. 3. Lowest first-order lateral from shoot 2, the one subtended by leaf 18 in FIG. 2. FIG. 4. Detail of insertion of first-order branch (1ax$_2$) on the above axis, subtending bract cut off to show ax$_2$ adnate to ax$_1$.


5
6
7
8
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12
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50cm
14
15
50cm
0

initiation of branches is clearly in an acropetal sequence but their expansion seems to be basipetal, so that distal units of each branch order tend to expand as soon as they project beyond the mouth of the enveloping bracts (FIG. 37). Further developmental information has not been sought.

Arrangement of bract and branch on successive units follows a regular pattern. At the base of each branch, bracts (and consequently axillary branches) are distichously arranged, but distally there is a gradual change to a spiral arrangement. This change from distichy to polystichy is most evident on first order branches. Due to compression the distal spiral arrangement is often obscure. In fact the distribution of parts on distal branches tends to conform to the requirements of available space and any inherent phyllotactic arrangement is suppressed. The plane of distichy of distal branches (ax_3–ax_5) is always at right angles to the dorsiventral plane of their subtending bracts. This change in the plane of insertion allows greater space for expansion.

The first leaf on each branch is, by definition, a ***prophyll***. In the two lowest orders of branch (ax_1 and ax_2) this prophyll is empty, subtending no branch. Rarely on ax_1 the bract after the prophyll is also empty. Prophylls show some of the features normal for the leaf in this position in most monocotyledons. It is apparently inserted in the adaxial (***adossierte***) position even though the plane of insertion of subsequent leaves is at right angles to this. It is indistinctly 2-keeled. This is largely shown by two sub-lateral teeth at the mouth of the bract, rather than by a single dorsal tooth (FIGS. 18, 23). These prophyllar features are least evident on higher orders of branches. Here the branch subtended by a prophyll is also in a lateral position so that the change in plane of distichy starts with the prophyll.

Adnation of branch to main axis is a constant feature of the system (FIGS. 4 and 24). This probably reflects intercalary growth of the internode after a branch primordium has been initiated, together with compression of the developing system. Even beyond the level where a branch diverges from its parent axis the common interface is flattened. Adnation is more nearly complete and more pronounced on successively higher orders of branches. In the lower orders, a branch is adnate to the parent axis for a little over one-half the length of the internode above (FIG. 4), and the union is concealed within the enveloping spathe. Distally there is a progressive shortening of bract in relation to the internode above, the branch is adnate more or less completely throughout this internode so that the union is obvious (FIG. 24). Prophyll of branch and the next

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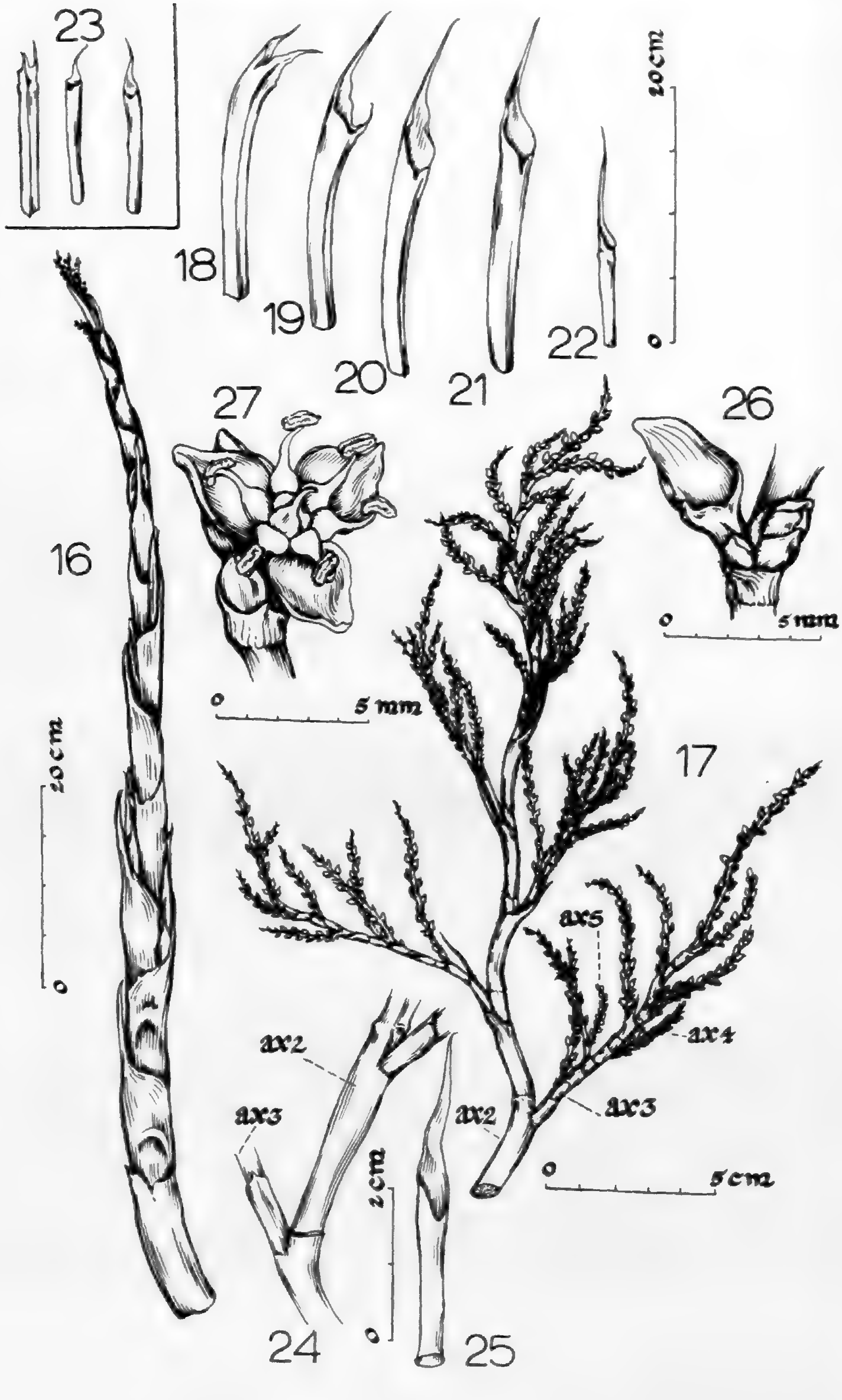
FIGS. 5–15. *Nannorrhops*. Transitional leaves and bracts from the main axis of shoot 2. This series includes every third leaf from shoot 2 starting with leaf number 7 (cf. FIG. 2). FIG. 5. Leaf number 7 (detail to the left, sheath from dorsal side showing cleft). FIG. 6. Leaf number 10 (detail to the right, sheath from dorsal side showing cleft). FIG. 7. Leaf number 13. FIGS. 8–13, leaves number 16, 19, 22, 25, 28, and 31, respectively. FIGS. 14, 15 (inset). FIG. 15 is leaf number 7 (FIG. 5) drawn on a smaller scale together with leaf number 1 (FIG. 14) to compare size of foliage leaves.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19
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27
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5 mm
26
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5 mm
16
20 cm
0
17
ax5
ax4
ax3
ax2
ax2
ax3
0
5 cm
2 cm
0
24
25

leaf above on the parent axis are at about the same level. In distal units, therefore, branches appear to diverge just below a leaf insertion.

Rachillae and Bracteoles. Flowers are usually in *clusters* of three on all terminating axes. The flower clusters (Fig. 28) are in an irregular spiral but so compressed to fit available space that any regular phyllotactic arrangement is lost. This regularity might be sought in the early stages of rachilla development. Each flower cluster is subtended by a scale-like bract 2–3 mm. high. The dorsal tooth is still distinct and establishes the plane of symmetry of the bract. This is still a tubular organ, enclosing the axis at its base but somewhat like an inverted funnel, the mouth being expanded by the developing flowers. Within the bract subtending each cluster is a series of bracteoles and flowers. We use the term *bracteole* simply to denote bracts associated with flowers. Each bracteole is identical with the bract subtending the whole cluster, but smaller. The arrangement of flower buds and bracteoles is indicated by the dissections of a flower cluster in Figures 29–32, all drawn from the same aspect, in which the bract and each bracteole and flower is removed in turn. These flowers and bracteoles are inserted more or less in one plane but compressed against the parent axis (Fig. 33). An inherent spiral arrangement of parts might be suspected, but if present it is obscured by compression. It can only be demonstrated by anatomical studies which we have yet to undertake.

The first bracteole, as indicated by its dorsal tooth, is inserted perpendicular to the dorsiventral plane of the subtending bract and encloses all organs within. It is also opposite the largest flower. Enclosing the base of the two innermost flowers is a second bracteole opposite the first. The second flower is opposite the first flower. The third bracteole, opposite the second, encloses the third flower. Between this third flower and its attendant bracteole is a minute bud (Figs. 31, 32) which represents the continuing axis of the system and a potential fourth flower bud. This flower does not seem to develop.

There can be several interpretations of this flower cluster. Lacking anatomical evidence we tentatively interpret it as a cincinnus. The

Figs. 16–27. Further details of branches and bracts of *Nannorrhops*. Fig. 16. Unexpanded first-order branch from another shoot. This corresponds to Fig. 3 at an earlier stage of development. Distal branches, although they are last to develop, are first to expand. Fig. 17. Distal part of a second-order branch (ax_2) shortly before anthesis of first flowers. This includes branches of next three higher orders (ax_3, ax_4, and ax_5). Figs. 18–22. Lowest bracts (br_2) from a first-order branch (ax_1) as in Fig. 3. Fig. 18. First bract (prophyll) (1 br_2). Fig. 19. Second bract (2 br_2). Fig. 20. Third bract (3 br_2). Fig. 21. Fourth bract (4 br_2). Fig. 22. Thirteenth bract (13 br_2) from this branch. Fig. 23. Three lowest bracts (1–3 br_3) from second-order branch (ax_2), the first (1 br_3) is a prophyll, slightly 2-keeled adaxially. Figs. 24 and 25. Details of distal branches. Fig. 24. Third-order branches (ax_3) adnate to second-order branch (ax_2). The bract (br_3) subtending the uppermost branch is cut off. It is shown in Fig. 25. Figs. 26 and 27. Flower clusters. Fig. 26. Left-handed flower cluster, flowers unopened. Fig. 27. Right-handed flower cluster with oldest flower expanded.

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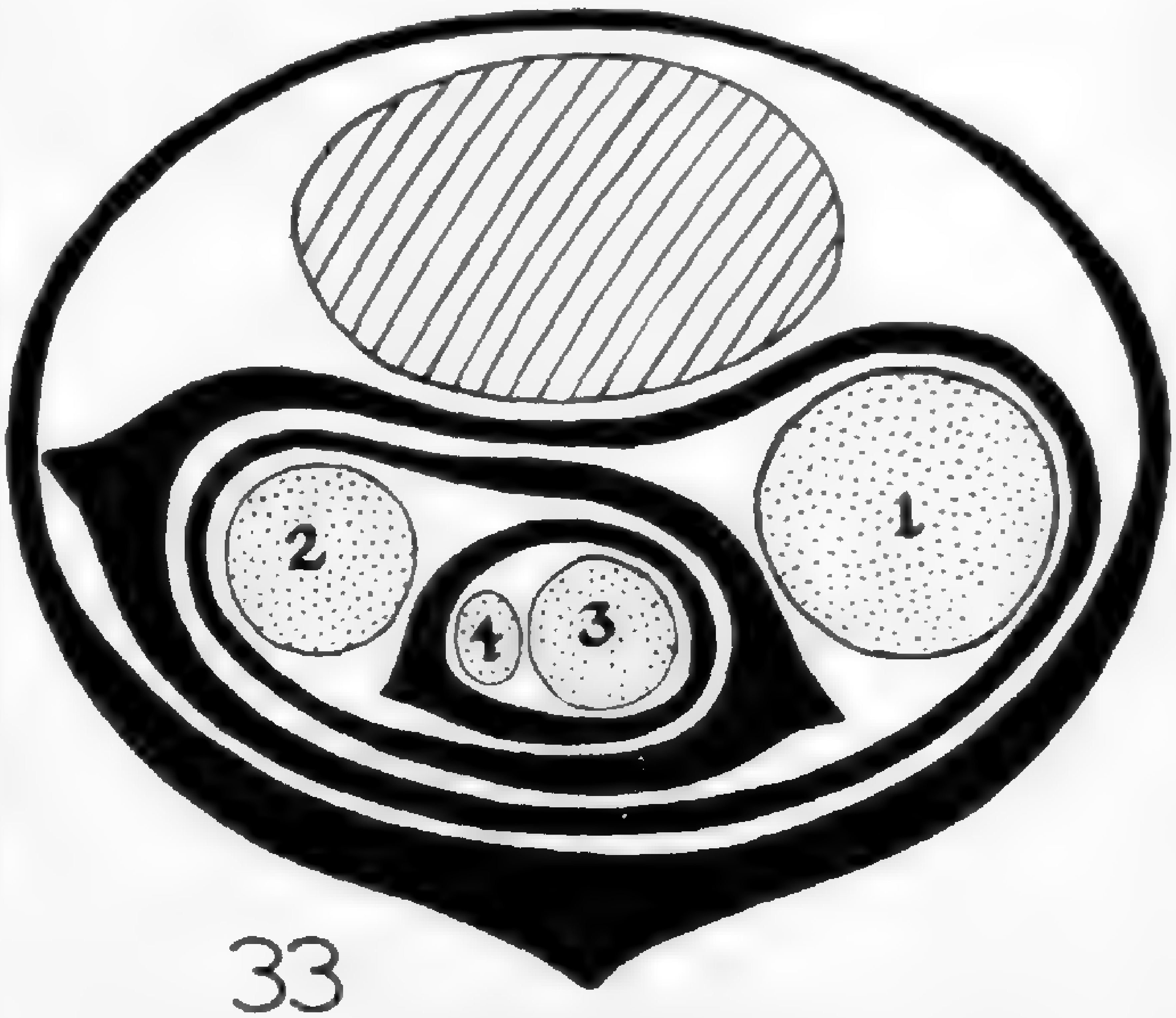

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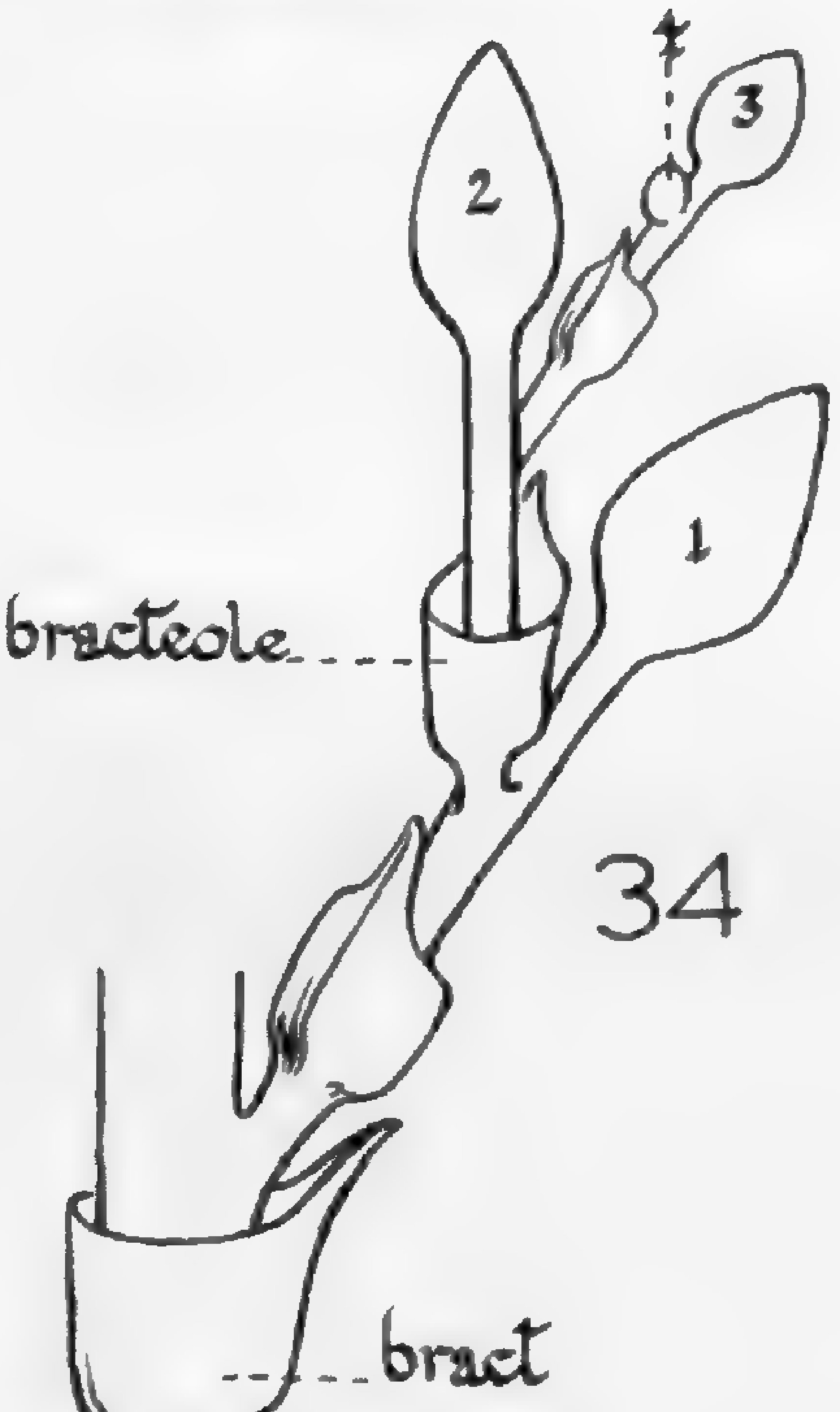

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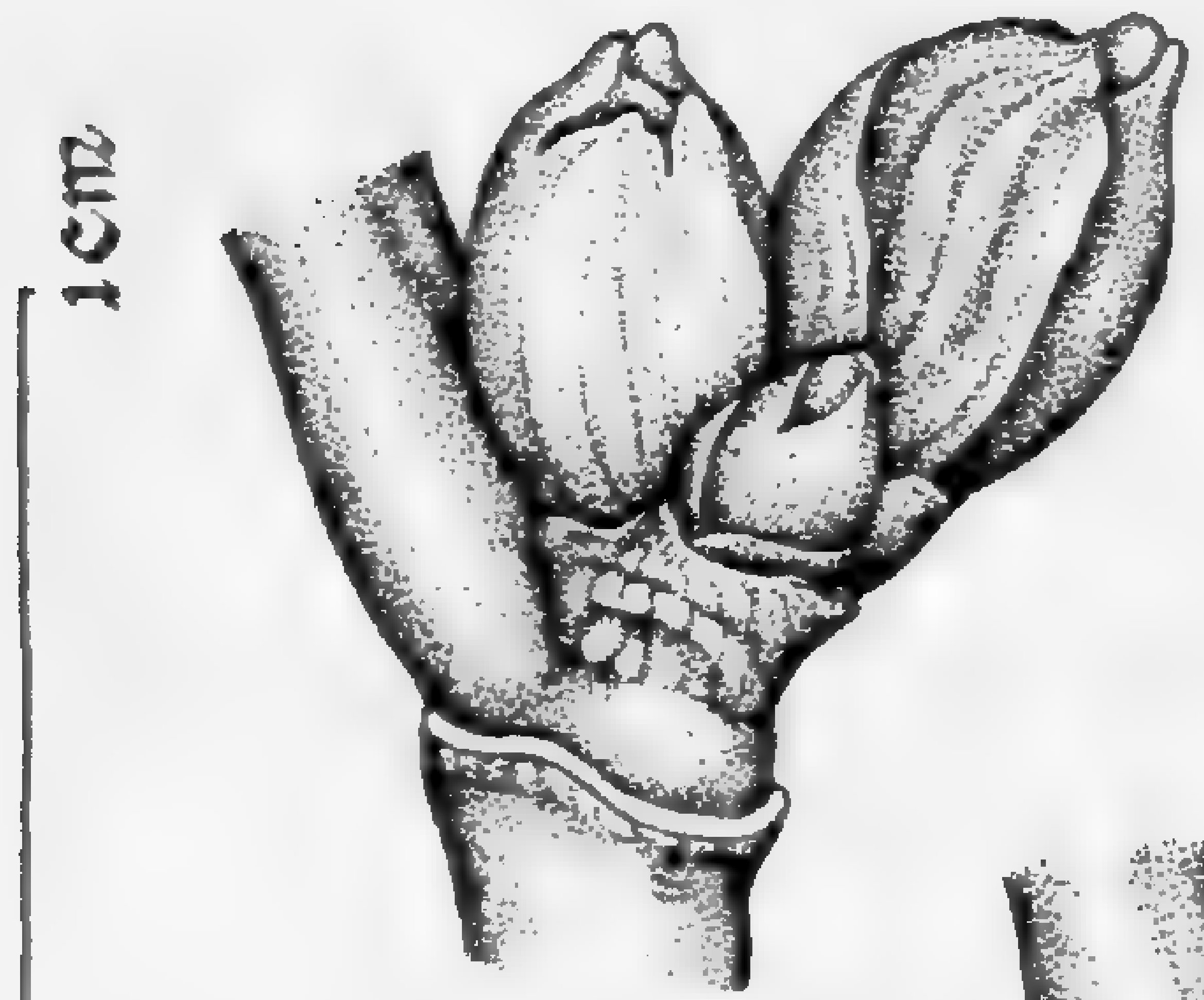

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processes involved in ramification of proximal parts of the branch system are continued into its ultimate axes which are, however, much condensed. Sympodial is now substituted for monopodial branching. The flower cluster (FIGS. 33, 34), therefore, represents a series of condensed branches of successively higher order, each branch bearing one bract (bracteole) and terminating in a flower (FIG. 34). Each successive branch unit originates in the axil of the bracteole of the previous order. As in the lower orders of branches, adnation and the requirements of close-packing modify the arrangement of parts. The position of the first unit at right angles to the plane of insertion of the subtending bract corresponds to that found proximally in branches of third and higher orders. Close-packing maintains the second and third units in this plane, but alternately on opposite sides. From its position each bracteole is a prophyll and more or less maintains the normal relation between prophyll and parent axis (FIG. 33). Regarding the flower cluster as a sympodium is the simplest interpretation which fits the available facts. We appreciate that additional information from development and anatomy may cause us to modify this opinion.

Flower clusters may be right- or left-handed, depending on whether the largest (lowest) flower is exserted to left or right of the dorsiventral plane of the subtending bract. The flower cluster in FIGURES 29–32 is a right-handed one, a left-handed one like that in FIG. 26 is the mirror image of this. Right- or left-handed clusters, appear at random along the rachilla (FIG. 28) and they may owe their distribution entirely to chance. It is quite possible, on the other hand, that the position of the first flower in each cluster is determined by a direct requirement of available space in close packing of the developing rachilla.

Flowers. Flowers (FIG. 27) are perfect and expand in order of their age. The structure and vascular anatomy of the flower of *Nannorrhops* has been dealt with in great detail by Gupta (1960) and Morrow (1965), and is not within the scope of this article.

DISCUSSION

The terminal inflorescence of *Nannorrhops,* of seeming complexity, is shown to be built up by repeated and uniform ramifications of a simple

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FIGS. 28–34. Rachilla and flower clusters of *Nannorrhops*. FIG. 28. Details of rachilla with several flower clusters. FIGS. 29–32. Single (right-handed) flower cluster and its dissection. FIG. 29. Entire flower cluster, the subtending bract removed. FIG. 30. Bract, lowest flower and its attendant bracteole removed. FIG. 31. Bract, 2 lowest flowers and their attendant bracteoles removed. FIG. 32. The same, but with uppermost bracteole removed to show continuing axis (or aborted flower bud). FIGS. 33 and 34. Diagrammatic representation of the flower cluster illustrated in FIGS. 29–32. FIG. 33. In cross-section. FIG. 34. Theoretical 2-sided cincinnus in expanded state. This is regarded as the most probable morphological interpretation of a flower cluster. The parts are drawn on elongated axes to show their relative positions more clearly.

FIGS. 35–38. Inflorescence in *Nannorrhops*. FIGS. 35–37. Developmental features. FIG. 35. Young inflorescence, October 4th, 1966. FIG. 36. Same, December 5th, 1966. FIG. 37. Same, one week later; distal branches exposed indicating their tendency to expand in a basipetal sequence. In FIGS. 36 and 37 the vegetative shoot to the left is the twin of the axis which is flowering, derived by dichotomy of a single parent axis. FIG. 38. Details of transition of shoot 2, an enlarged view of the axis shown in FIG. 42.

kind. Progressive distal reduction in diameter of axes and size of bracts produces a system which may be recognized as fundamental for many flowering plants (Troll, 1964). In the simple descriptive terms of classical morphology it would be called a panicle (*Rispe* of German authors). In

FIGS. 39–42. Overall features of inflorescence in *Nannorrhops*. FIG. 39. Shoot 2. October 4, 1966; expansion of main axis completed. Detailed measurements in FIG. 2. FIG. 40. Shoot 2, one week later, many flowers at anthesis. FIG. 41. Leaves from main axis of shoot 1 arranged serially to show transition from foliage leaves to bracts. Tubular base of each leaf has been split vertically to release it from the axis. The dorsal cleft of lowest (foliage) leaves is evident to left. Detailed measurements in FIG. 1. FIG. 42. Shoot 1, an old specimen, before dissection. Detailed measurements in FIG. 1.

Troll's more modern typological terminology it is a "polytelic synflorescence" (Troll, 1964; Weberling, 1964). The elaborate terminology which this typological outlook has developed could, no doubt, be applied to the mammoth inflorescence of *Nannorrhops* but it would become unnecessarily cumbersome. Our concept of this inflorescence, in which simple constructional principles are recognized, does away with the need to apply names to individual branches. The complexity of an inflorescence depends on the number of branch orders in which constructional principles are repeated. It is of interest that the inflorescence in *Nannorrhops* is constructed like that in many woody liliflorous plants of which Troll (1962) illustrates numerous examples. In none of these, however, is the branch pattern repeated as often as in *Nannorrhops*.

Using this simplified concept it is possible to make proper comparison between different palm inflorescences. The lengthy and elaborate terminology developed by earlier students of the palms is not only unnecessary but may even be misleading if it suggests to the uninitiated that "spathe," "bracteole" or "involucel" are distinct kinds of organs. "Spathe" itself is a redundant term. In our description of *Nannorrhops* we have found that axis and bract are sufficient terms to describe the branch system, rachilla is useful to identify an axis bearing flower clusters, bracteole to identify bracts associated with (and possibly subtending) flowers, prophyll to distinguish the first bract on each branch. No other terms seem necessary.

In many other Coryphoid palms (e.g. *Copernicia, Sabal, Washingtonia*) the lateral inflorescence is equivalent to one first order branch unit of *Nannorrhops* as shown in FIG. 3. In all these palms it is evident that exactly the same principles are involved in the construction of reproductive branches. *Sabal*, for example, differs from *Nannorrhops* largely in that vegetative growth of the axis continues into the reproductive phase. The "lateral" inflorescence is strictly a partial inflorescence and was recognized as such by many older taxonomists (e.g. Blatter, 1926). This concept tends to make redundant the idea that one type of inflorescence, "terminal" or "lateral," is necessarily more primitive than the other, as discussed by Holttum (1955) and Corner (1966) for example. The difference between them is physiological and possibly one of degree only. Both types do exist together in one genus (*Metroxylon*) and might exist together even in one species. An adaptive advantage in the pleonanthic mode of flowering is suggested by its predominance.

From the elaborate *Nannorrhops* type the multifarious inflorescence types of palms can be traced, although this article is not the place to carry out the analysis which is required. Briefly, within the Palmae several distinct trends may be noted. Reduction in the amount of branching produces less elaborate forms, the ultimate expression being the unbranched axis, an apparently "simple" spike. Recognition of this spike ("spadix") as a highly specialized type makes redundant any discussion of affinities between the Palmae and Araceae. Reduction in the number of bracts and their restriction to the base of the inflorescence is evident. There may be few bracts, commonly two, or even only one. These basal bracts are usually empty. The protective function of this reduced number of bracts is facilitated by their enlargement and inflation so that one, or more, wholly encloses the inflorescence. The stage of development of the axis at which bracts cease to be protective varies widely in different palms. The morphological equivalence of these specialized, inflated bracts ("spathes") with the sheathing base of a foliage leaf is not as evident as in *Nannorrhops*. Nevertheless, some vestiges of the foliage leaf may persist even in the most specialized bracts, as in the woody terminal spine of many Cocoid bracts which, by analogy with *Nannorrhops*, occupies the position of the vestigial petiole and blade.

Adnation of branch to parent axis may be even more pronounced than in *Nannorrhops*. The rachilla may be wholly adnate to a parent axis and this, together with further condensation of ultimate flower clusters, may produce highly specialized types whose fundamental morphology is difficult to decipher. Anatomical studies are beginning to reveal this complexity. *Aristeyera* is a recently described geonomoid type which exemplifies the degree of reduction and the approach needed in assessing it (Moore, 1966; Uhl, 1966). Further specialization in palm inflorescences involves changes to monoecism and dioecism.

Many morphological features of the palm inflorescence still await careful observation and recording. Developmental and anatomical aspects have scarcely been investigated. The subject is scope for a whole volume. It is hoped that this preliminary study of *Nannorrhops* will be of value in wider interpretations.

SUMMARY

Hapaxanthic flowering of the palm *Nannorrhops ritchiana* is described from specimens in cultivation in South Florida. Erect vegetative axes branch by an apparent dichotomy, one axis proceeding to inflorescence with a gradual reduction of leaf size and elimination of petiole and blade. Bracts are equivalent to the sheathing base of a foliage leaf with a vestigial blade. Lateral branches from the axils of first-order bracts are subdivided with up to 5 orders of branches leading to an elaborate paniculate inflorescence. A simple one to one relationship between bract and branch is maintained throughout the system. Lateral branches are basally adnate to their parent axis. The distal decline in bract size can be traced progressively to terminating branchlets (rachillae) where funnel-shaped bracts only 2–3 mm. long subtend flower clusters. The arrangement of bracteoles in each flower cluster suggests a condensed cincinnus. *Nannorrhops* has a basically simple branching pattern, despite its elaborate ramification, and can be used in the interpretation of other palm inflorescences.

ACKNOWLEDGEMENTS

We much appreciate the assistance of Miss Priscilla Fawcett who prepared FIGURES 3 to 34, the help with photography given by Dr. M. V. Parthasarathy, and the preparation of typescript by Miss Anne Bellenger. We gratefully acknowledge the cooperation of staff at the U.S. Plant Introduction Station, 13601 Old Cutler Road, Miami, Florida, in providing material.

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HARPEROCALLIS, A NEW GENUS OF THE LILIACEAE FROM FLORIDA

SIDNEY McDANIEL

As a result primarily of the botanical explorations of A. W. Chapman, the area around the Apalachicola River in western Florida is known for its endemism and for its exceptional variety of plant species. Approximately fourteen well-defined species are restricted to this immediate area. Other species such as *Baptisia megacarpa* Chapm., *B. simplicifolia* Croom, *Gentiana pennelliana* Fern., *Hedeoma graveolens* Chapm., and *Hypericum chapmanii* P. Adams are endemic to a wider area of the northeastern Gulf Coastal Plain. Within the Apalachicola River area also occur a number of uncommon, though wide-ranging, species such as *Leitneria floridana* Chapm., *Croomia pauciflora* (Nutt.) Torr., and *Schisandra glabra* (Brickell) Rehd. The variety of habitat within the area is exceptional and ranges from alluvial river bottom to sandy longleaf pine forests or to *Sarracenia* bogs. The diversity within the Apalachicola River area both of species and habitat and the known endemism within the area help to explain a previously undescribed, apparently endemic genus of the Liliaceae which has been discovered in Franklin County, Florida.

The relationships of *Harperocallis*, the remarkable new genus described below, seem to be with the tribe Tofieldieae Kunth of the Liliaceae. This tribe as circumscribed by Krause (1930) consists of *Tofieldia* Hudson, *Pleea* Michx., *Narthecium* Hudson, and *Nietneria* Klotzsch & Schomb. Bentham and Hooker (1883) and Hutchinson (1959) delimited the Narthecieae Benth. & Hook. (synonymous with the Tofieldieae in the sense here used) to include the genera listed above and several others morphologically more divergent. *Harperocallis* is markedly distinct from all other genera of this tribe and may be distinguished readily by its solitary flower, tuberculate ovary, and calyculus of three (or four) separate bracts.

The members of the Tofieldieae, including *Harperocallis*, are all rhizomatous perennials, with linear, mostly basal equitant leaves and terminal inflorescences on simple stems. The leaves of *Harperocallis* are almost identical to those of *Narthecium* and certain species of *Tofieldia*. The simple stem has a few reduced bractlike leaves above and one or more sheathing leaves near the base. A calyculus of three or four bracts is immediately beneath the solitary terminal flower. Flowers of certain species of *Tofieldia* may have a calyculus, but the segments are united. In *Pleea* each individual flower is subtended by a large sheathing bract. *Narthecium* and *Nietneria* have single bracts subtending the individual flowers along the axis of the inflorescence. The stamens are six in all

Tofieldieae, except *Pleea* where they may be six to twelve but most commonly are nine. Except for the pilose filaments of *Narthecium* the filaments are glabrous. In the Tofieldieae the ovary is trilocular and often three lobed. The styles are distinct and suberect or slightly recurved in *Pleea, Tofieldia,* and *Harperocallis.* In *Narthecium* and *Nietneria* the styles are united and erect. The capsule in *Harperocallis* as in *Narthecium* and *Nietneria* is loculicidal. *Pleea* and *Tofieldia* have septicidal capsules.

The unique morphological characteristics of *Harperocallis* and the various morphological features held in common with different genera of the Tofieldieae suggest no particularly close relationship with any other genus. The presence of the calyculus and other morphological similarities suggest closest affinity to be with *Tofieldia.*

At the type locality *Harperocallis* is most frequent in the vicinity of isolated individuals of *Cliftonia monophylla* (Lam.) Britt. ex Sarg. and *Myrica inodora* Bartr. in areas slightly drier than the adjacent open bog. Within the bog *Harperocallis* is less frequent and is associated most prominently with *Sarracenia flava* L., *S. psittacina* Michx., and *Pleea tenuifolia* Michx. On the edge of the bog *Harperocallis* was noted growing in the detritus of an old pine log beneath *Cliftonia.* The open bog abruptly changes to the west to a dense thicket largely consisting of *Cliftonia* and an occasional individual of *Pinus serotina.* The whole area is surrounded by sandy, occasionally burned longleaf pine woods. Initially a few individuals of *Harperocallis flava* were observed in a roadside ditch slightly to the south of the type locality.

Although as earlier mentioned the Apalachicola River region is noted for its endemic species of plants, there are no previously described endemic genera. I have examined numerous areas from the vicinity of Tallahassee to extreme western Florida seemingly quite similar to the type locality without finding any sign of *Harperocallis.* Probably, however, the genus occurs elsewhere, for other endemics of the Apalachicola River area, such as *Rhexia parviflora* Chapm. and *Scutellaria floridana* Chapm., occur sporadically within the region. *Harperocallis* may eventually prove to have a similar type of distribution.

It is appropriate to associate with this genus of the Lower South the name of Roland MacMillan Harper (1878–1966) who greatly contributed to an understanding of the vegetation of this area. The latter portion of the generic name emphasizes the attractiveness of the flower. The specific epithet refers to the color of the perianth segments.

Harperocallis McDaniel, gen. nov.

LILIACEAE-MELANTHOIDEAE-TOFIELDIEAE

Herba perennis. Rhizoma gracile nodosum, saepe terminante in planta emergenti. Folia equitantia, lineares, rigidula, striata, quam flos multo breviora. Inflorescentia constans ex flore solitario et erecto. Bracteae subflore 3 vel 4, persistentes, plus minusve aequales, contiguae, deltoideae, apice acutae. Perianthium persistens, flavum interne et patentia per

FIG. 1. *Harperocallis flava*, × 2/3.

anthesin; segmenta 6, distincta, oblanceolata, acuta, hae subtentae a bracteae intimis segmentis longiora. Stamina 6, hypogyna, quam perianthium breviora; antherae lineari-lanceolatae, basifixae, loculis introrse dehiscentibus, filamentae glabrae, sensim latae basin versus. Ovarium sessile, trilobum, triloculare, ellipsoideum, valde tuberculatum, ovula in loculis numerosa; styli 3, suberecti, breves; stigmata capitata. Capsula vix maior quam ovarium per anthesin, triloba, ellipsoidea, loculicide dehiscens. Semina parva, anguste fusiformia, recta vel curvata. SPECIES TYPICUS: *Harperocallis flava.*

Harperocallis flava McDaniel, sp. nov.

Herba glabra, prope basin fibrillosa. Caulis simplex, 22–55 cm. longus. Folia 0.2–0.3 cm. lata × 5–21.5 cm. longa. Segmenta perianthii 10–12 nervata, hae subtentae a bracteis 12–15 mm. longa, segmenta interiora 9–12 mm. longa. Stamina 8–9 mm. longa. Ovarium 7–8.5 mm. longum. Capsula 8–9 mm. longa. Semina 2–3 mm. longa. HOLOTYPUS: *McDaniel 6205* (A)

Perennial herb, glabrous throughout, basally fibrillose. Rhizome slender, nodose with scarious scale leaves, often ending in an emergent plant. Leaves 0.2–0.3 cm. wide × 5–21.5 cm. long at maturity, equitant, linear, stiff, and striate, much exceeded by the scape; sheath scarious margined. Stem simple, 22–55 cm. long, with 3–5 much reduced leaves. Bracts 2–3 mm. long, persistent, usually 3 in number, contiguous, deltoid, forming a calyculus beneath the flower. Perianth persistent, yellow above and greenish beneath at anthesis, spreading, after anthesis becoming erect, revolute, externally green and internally purple margined; perianth segments 6, 10–12 nerved, oblanceolate, acute, those subtended by the bracts 12–15 mm. long, the inner series 9–12 mm. long. Stamens 6, 8–9 mm. long, hypogynous; anthers ca. 4 mm. long, linear-lanceolate, basifixed, introrsely longitudinally dehiscent, filaments glabrous, somewhat broadened toward the base. Ovary 7–8.5 mm. long, sessile, 3-lobed, 3-locular, ellipsoid, strongly tuberculate, ovules numerous; styles 3, suberect, ca. 1 mm. long, stigmas capitate. Capsule 8–9 mm. long, ellipsoid, loculicidal, tuberculate, almost hidden by the perianth. Seeds 2–3 mm. long, pale yellow, narrowly fusiform, straight or curved, often twisted.

SPECIMENS EXAMINED: **Florida.** FRANKLIN CO.: 2.2 mi. south of Sumatra, open bog surrounded by *Cliftonia-Pinus serotina*, May 11, 1965, *McDaniel 6205* (holotype, A; isotypes, BM, DUKE, FLAS, FSU, GA, MO, NCU, NY, PH, SMU, US), July 21, 1965, *McDaniel 6542* (A, FSU); 2.5 mi. south of Sumatra, roadside near pine woods, May 4, 1965, *McDaniel 6127* (FSU).

Many persons have aided in the preparation of this paper. I am especially grateful to Robert K. Godfrey for initial advice and for reading the manuscript, to Carroll E. Wood, Jr., for confirming the uniqueness of *Harperocallis* and for suggestions as to its affinity, and to Barbara N. Culbertson for her careful preparation of the illustrations.

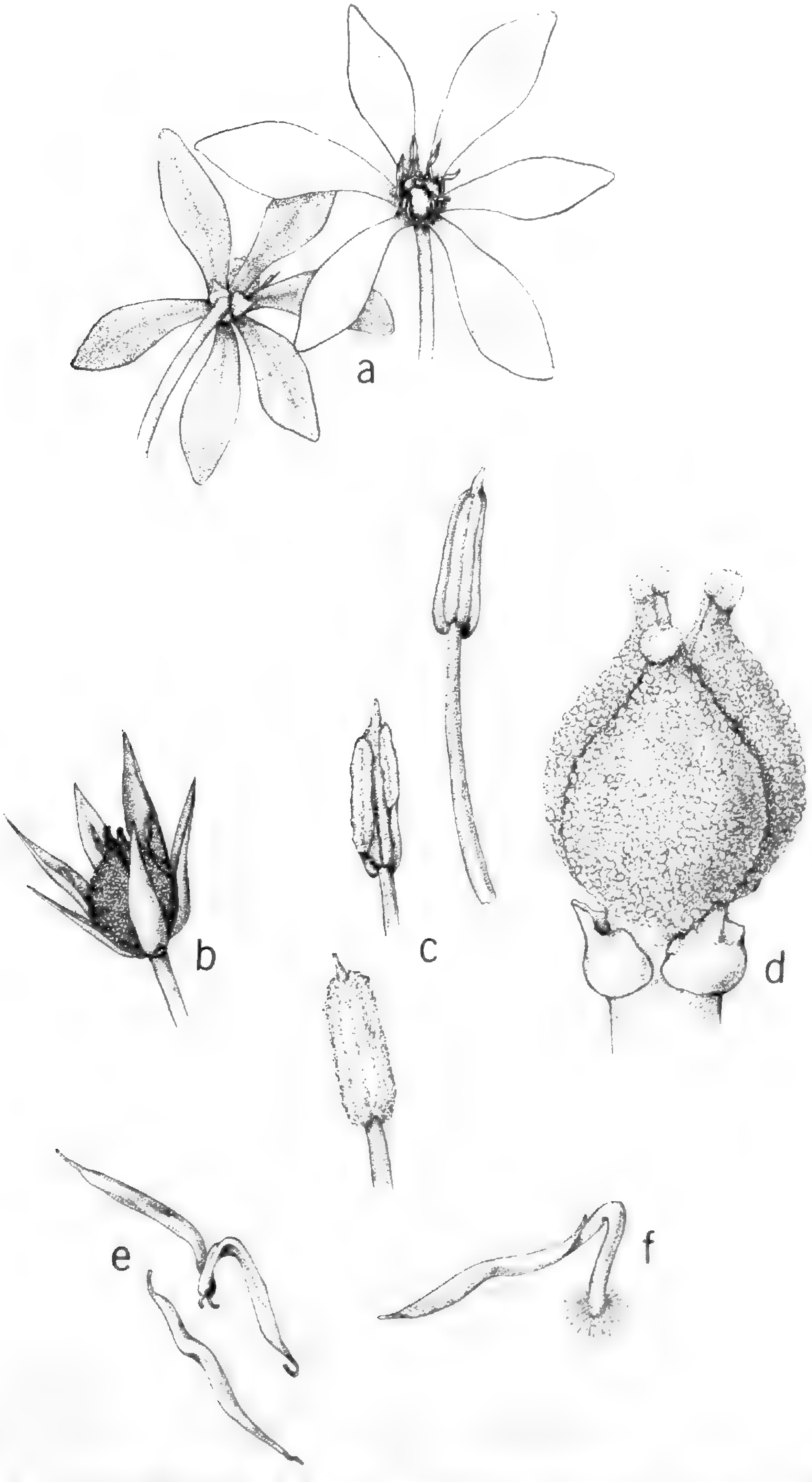

FIG. 2. *Harperocallis flava*: a, flower from below and above. × 2½; b, fruit. × 2½; c, anthers, showing dehiscence. × 6; d, ovary and calyculus. × 6; e, seeds. × 6; f, germinating seed with corona of root hairs at base of hypocotyl. × 12.

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CYTOTAXONOMY OF ILLICIUM FLORIDANUM AND I. PARVIFLORUM (ILLICIACEAE)

Donald E. Stone and Judith L. Freeman [1]

Recent chromosome counts of the Ranales by Raven and Kyhos (1965) provide new insight into evolutionary patterns of the most primitive members of extant angiosperms. They concluded that the basic chromosome number for the primitive angiosperms is probably $x=7$. It is argued that numbers such as $n=6$, 8 (Aristolochiaceae), $n=8$, 9 (Annonaceae), $n=10$ (Eupomatiaceae), $n=11$ (Calycanthaceae, Saururaceae), $n=12$ (Lauraceae), $n=13$ (Canellaceae, *Drimys* sect. Tasmannia), etc. are aneuploid derivatives of the base number 7 and its multiple, $n=14$. Stebbins (1958, 1966) has recently reiterated an alternative hypothesis which seeks to explain the higher numbers such as $n=12$ and $n=13$ as the result of "direct polyploidy," rather than a doubling of 7 followed by aneuploid reduction. He pictures aneuploid changes in chromosome number from a basic $x=6$ or $x=7$ to have gone both upward ($x=9$) and downward ($x=5$) at an early stage of angiosperm evolution. This period was followed by the build up of higher basic numbers in woody members through polyploidy. Once the polyploid levels were reached Stebbins implied that further evolutionary diversification was relegated to processes of speciation and generic differentiation at the homoploid level. While such a hypothesis is highly plausible and, in fact, is generally accepted in the derivation of $n=19$ in the Magnoliaceae from unknown $n=7$ and $n = 12$ (found in the related Degeneriaceae and Himantandraceae) ancestors (Stebbins, 1950; Darlington, 1956; Raven and Kyhos, 1965); evidence does exist in the Ranales for aneuploid changes at the polyploid level. The Piperaceae, for example, have $n=11$, 12, 14, and 16, numbers which are surely indicative of aneuploid derivation. Stebbins (1966, *Table 2*) overlooked another example cited by Raven and Kyhos (1965; Stone, 1965) in which *Illicium floridanum* Ellis with $n=13$ is a probable derivative of the basic $n=14$ common to other members of the Illiciaceae and the related Schisandraceae. It is the purpose of this paper to examine the karyotypes of two of the four New World species of *Illicium* and to document the aneuploid reduction from $n=14$ to $n=13$.

MATERIALS AND METHODS

The collections and chromosome numbers of *Illicium floridanum* Ellis and *I. parviflorum* Michx. ex Vent. are presented in Table 1. The populations that were sampled do not span the range of each species but presumably are representative. *I. floridanum* ranges from northwestern

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[1] Work done in conjunction with research supported by NSF grants GB-2313, GB-5233X, GY-2484, and the Duke University Council on Research. We wish to thank Dr. Carroll E. Wood, Jr. for his helpful comments on the manuscript.

TABLE 1. **Collections and chromosome numbers of Illicium floridanum and I. parviflorum**

SPECIES AND COLLECTION NUMBER	CHROMOSOME NUMBER		COLLECTION DATA
	n	*2n*	
Illicium floridanum Ellis (sect. ILLICIUM)			
Stone 1357	13		Washington Parish, near Warnerton, La. (NO)
Stone 1522		26	Hancock Co., near Logtown, Miss. (DUKE)
Stone 1819		26	Alachua Co., cultivated near Gainesville, Fla., by A. M. Laessle. (DUKE)
Illicium parviflorum Michx. ex Vent. (sect. CYMBOSTEMON)			
Stone 1422	14	28	Alachua Co., cultivated near Gainesville, Fla., by A. M. Laessle. Cuttings originally obtained from Norwalk, ne. corner of Ocala National Forest. (DUKE)
Stone 1820	14	28	Orange Co., Chapel Hill, N.C., cultivated on Univ. of North Carolina campus. (DUKE)
Stone 1821		28	Orange Co., Chapel Hill, N.C., cultivated on Univ. of North Carolina campus. (DUKE)

Florida to eastern Louisiana and northward to central Alabama. *I. parviflorum* is restricted to a few localities at the headwaters of the St. Johns River in northeastern Florida and is quite often marketed by Florida nurserymen as *I. anisatum* (pers. comm., A. M. Laessle).

Flower buds suitable for studies of meiosis were fixed in 3 (absolute ethanol): 1 (glacial acetic acid) and stored in 70% ethanol until prepared for examination by the standard acetocarmine squash technique. Karyotype analyses of mitotic chromosomes were conducted on the root tips of young seedlings or cuttings stimulated to produce callus and adventitious roots with hormone treatment. Most satisfactory preparations were obtained by treating root tips in a 0.1% colchicine solution for 3 to 4 hours before fixation.

Chromosome squashes deemed satisfactory for analysis were photographed with a Leitz Ortholux microscope (× 90 objective, N.A. 1.32) and Kodak Contrast Process Ortho sheet film. Prints of the negatives were standardized at × 3000 for measurement with a millimeter rule. Measurements were made of the total chromosome length and length of each arm. The measurements of homologous chromosomes were averaged and expressed in percent as a function of the total chromosome length of the genome (i.e. mean percent length, Martin and Hayman, 1965). This procedure was an attempt to reduce variation in chromosome length introduced by variable cell-sizes and squash preparations, while at the same time expressing the results from different cells on a standard scale.

RESULTS

Karyotype analyses. The data from untreated and colchicine treated cells were processed separately. The differences due to treatment were negligible, however, and the samples were subsequently pooled. While the basic proportions of the karyotype were unaffected by treatment, the highly contracted colchicine-treated chromosomes were less suitable than untreated chromosomes for analyses of secondary constrictions. The results presented in TABLE 2 are based on ten cells each from seedlings and cuttings of *Illicium parviflorum* (*Stone 1422, 1820*) and a combined total of eight cells from seedlings and cuttings of *I. floridanum* (*Stone 1522, 1819*).

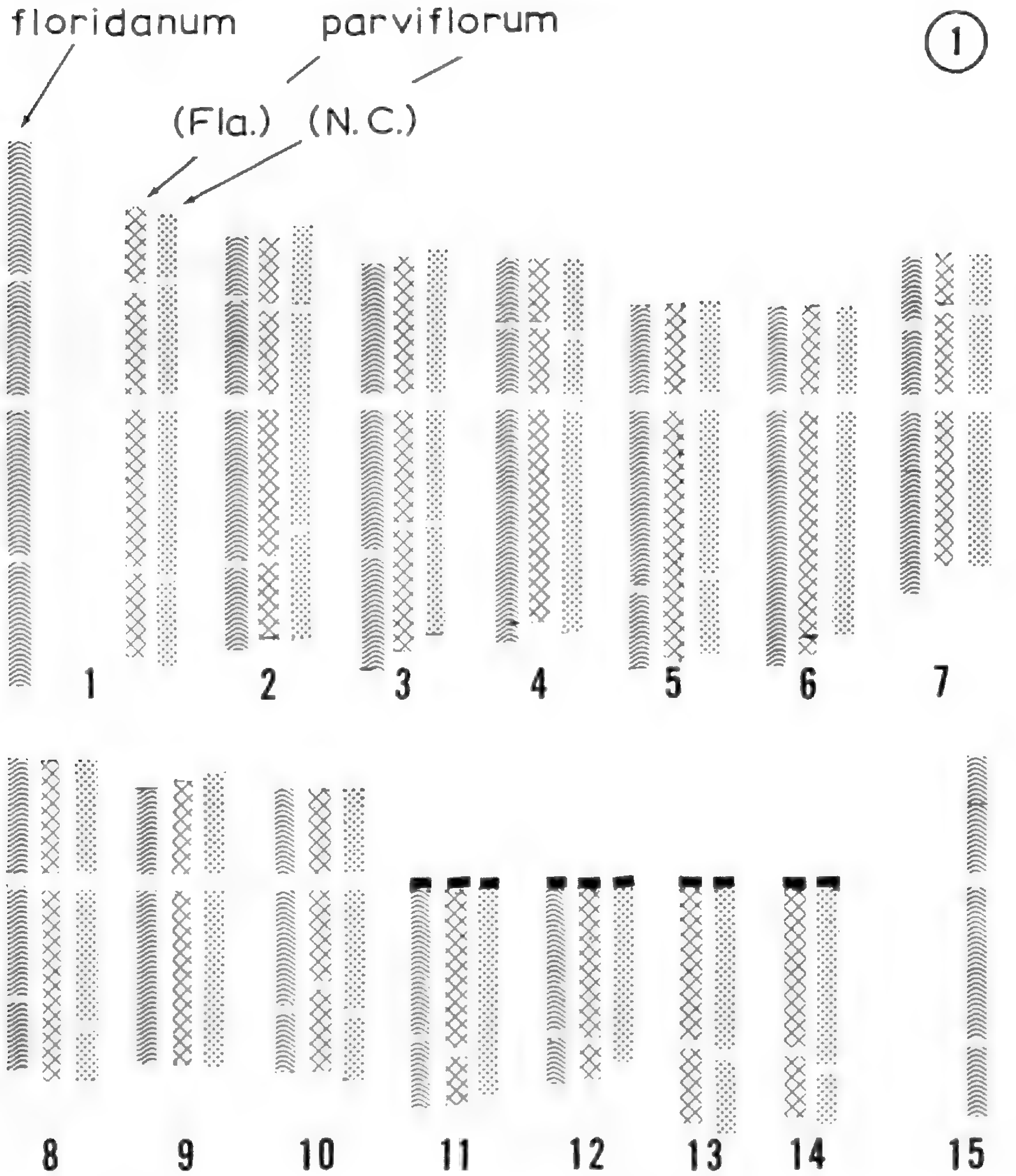
The data from the native Florida (*Stone 1422*) and cultivated North Carolina (*Stone 1820*) plants of *Illicium parviflorum* are presented separately to show the remarkable similarity in karyotypes (FIG. 1). Since these samples were independently analyzed, we consider the good agreement in results to be ample vindication of the techniques employed.

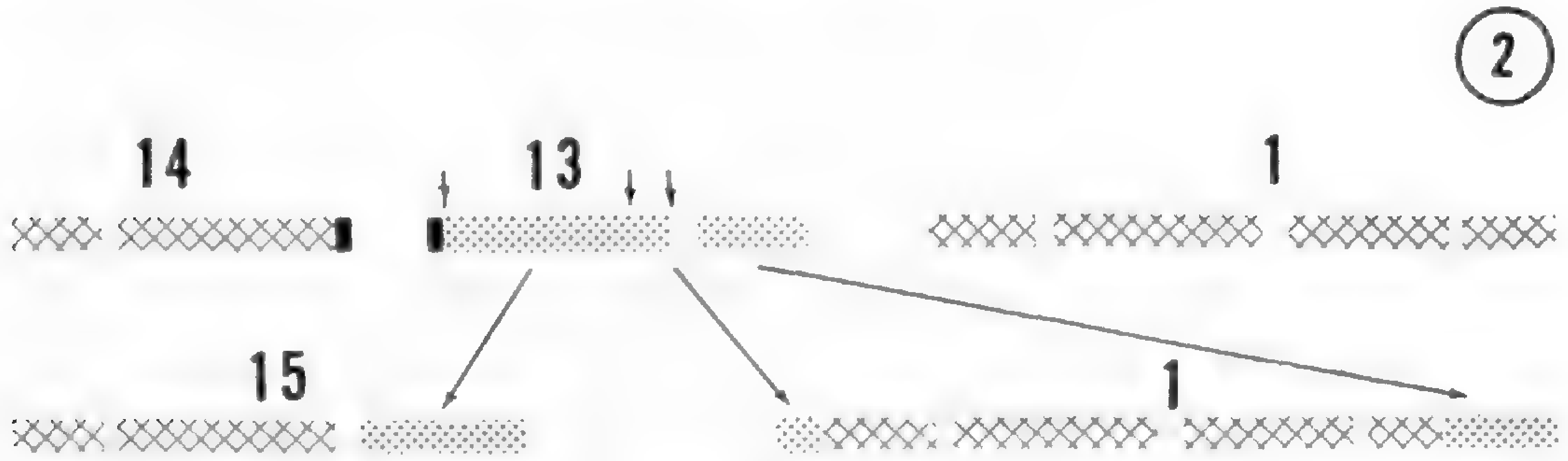
Illicium floridanum has $2n = 26$ (FIG. 3) and a karyotype consisting of 1 V-shaped, 10 J-shaped, and 2 rod chromosomes. *I. parviflorum* has $2n = 28$ (FIGS. 7, 8) and a karyotype which includes 10 J-shaped and 4 rod chromosomes. On the basis of total size, relative arm lengths, and secondary constrictions, it has been possible to match 9 J (#2–10) and 2 rod chromosomes (#11, 12) of the *I. floridanum* and *I. parviflorum* complements (FIG. 1). Chromosomes 1 and 15 of *I. floridanum* and chromosomes 1, 13, and 14 of *I. parviflorum* do not have identical equivalents. Since *I. floridanum* (sect. ILLICIUM) and *I. parviflorum* (sect. CYMBOSTEMON) are representative of two clearly demarcated sections of the genus, direct derivation of one from the other is not possible. However, if we assume the 14-chromosome karyotype of *I. parviflorum* is probably not too dissimilar from other 14-chromosome species, including *I. anisatum* of sect. ILLICIUM, then the simplest explanation is that three *parviflorum*-like chromosomes have undergone reciprocal translocations of unequal chromosome segments to be repatterned into the two of *I. floridanum*. The basic scheme proposed by Darlington (1937) shows how the entire euchromatic arm of a rod-shaped chromosome could be transferred to the heterochromatic arm of a second rod chromosome. This process, sometimes referred to as centric fusion, followed by loss of one heterochromatic centromere region, would result in gametes with one less chromosome but without any loss of genetic material. Of course, proof for this type of rearrangement must necessarily come from meiotic studies of F_1 species hybrids, as Togby (1943) has demonstrated in *Crepis* ($n = 4$ to $n = 3$) and Kyhos (1965) in *Chaenactis* ($n = 6$ to $n = 5$).

TABLE 2. **Data on the karyotypes of Illicium floridanum and I. parviflorum**
(Measurements expressed in percent as a function of total genome length)

SPECIES	CHROMOSOME LENGTHS	CHROMOSOME NUMBER 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
floridanum	Short Arm	5.99	3.73	3.11	5.22	2.19	4.42	5.16	4.30	4.30	4.78	0.00	0.00	—	—	2.73
	Long Arm	6.31	5.41	5.79	3.22	5.89	3.15	2.25	2.66	2.12	1.85	4.78	5.15	—	—	5.29
	Total Length	12.30	9.14	8.90	8.44	8.08	7.57	7.41	6.96	6.42	6.63	4.78	5.15	—	—	8.02
	Long/Short	1.05	1.45	1.86	1.62	2.68	1.40	2.30	1.62	2.03	2.45	—	—	—	—	1.94
	Absolute Length (μ) *	12.4	9.2	9.0	8.5	8.2	7.5	7.7	7.0	6.5	6.8	5.2	4.8	—	—	8.1
	Chromosome Shape	V	J	J	J	J	J	J	J	J	J	R	R			J
parviflorum (Fla.)	Short Arm	4.21	3.53	3.36	3.19	2.46	2.37	3.43	2.57	2.26	1.92	0.00	0.00	0.00	0.00	—
	Long Arm	5.47	5.20	5.12	4.85	5.61	5.45	3.87	4.89	4.47	4.45	5.11	4.54	5.50	5.36	—
	Total Length	9.68	8.73	8.48	8.04	8.07	7.82	7.32	7.46	6.73	6.37	5.11	4.54	5.50	5.36	—
	Long/Short	1.30	1.47	1.52	1.52	2.28	2.30	1.13	1.90	1.98	2.32	—	—	—	—	—
	Absolute Length (μ) **	10.4	9.4	9.1	8.6	8.7	8.4	7.8	8.0	7.3	6.8	5.5	4.9	5.9	5.8	—
	Chromosome Shape	J	J	J	J	J	J	J	J	J	J	R	R	R	R	—
parviflorum (N.C.)	Short Arm	4.09	3.95	3.43	3.12	2.43	2.30	3.37	2.52	2.35	1.85	0.00	0.00	0.00	0.00	—
	Long Arm	5.56	5.24	4.98	4.91	5.58	5.15	3.81	4.78	4.57	4.50	5.08	4.43	5.89	5.61	—
	Total Length	9.65	9.19	8.41	8.03	8.01	7.45	7.18	7.30	6.92	6.35	5.08	4.43	5.89	5.61	—
	Short/Long	1.36	1.33	1.46	1.57	2.25	2.24	1.13	1.90	1.95	2.43	—	—	—	—	—
	Absolute Length (μ) ***	10.4	9.4	9.1	8.5	8.6	7.7	8.0	7.9	7.4	6.9	5.5	4.8	6.3	6.0	—
	Chromosome Shape	J	J	J	J	J	J	J	J	J	J	R	R	R	R	—

* Average of 8 untreated cells ** Average of 5 untreated cells *** Average of 4 untreated cells





FIGS. 1 and 2. Morphology of **Illicium** chromosomes. 1. Idiogram of karyotype of *I. floridanum* (chromosomes #1–12, 15) and two populations of *I. parviflorum* [Fla. (*Stone 1422*), N.C. (*Stone 1820*); chromosomes # 1–14]. 2. Theoretical derivation of two chromosomes of *I. floridanum* from three *parviflorum*-like chromosomes by reciprocal translocations of unequal chromosomal segments.

FIG. 3. **Illicium floridanum.** Mitotic metaphase, $2n = 26$, *Stone 1522*, × 1780.

Neither hybrids between these shrubs nor studies of pairing configurations in meiosis have been attempted. However, the simplest explanation for the derivation of $n = 13$ from $n = 14$ would involve centric fusion. Fusion of rod chromosomes 13 and 14 (FIG. 2) might have produced chromosome 15 of *I. floridanum*. Chromosome 1 of *I. floridanum* (FIG. 1) is very similar to chromosome 1 of *I. parviflorum*. Both chromosomes are the longest of their respective genomes and both have secondary constrictions located in approximately the same region in each arm. The

J-shaped morphology of *I. parviflorum* could have been transformed into the v-shape of *I. floridanum* by adding segments to the ends of the arms (FIG. 2).

Meiotic analyses. Acetocarmine squashes of pollen mother cells were prepared. Meiosis was found to be normal in both species with a base number of $n=13$ in *Illicium floridanum* (FIGS. 4–6) and $n=14$ in *I. parviflorum* (FIGS. 9–10). An analysis of 19 cells of *I. floridanum* revealed an average chiasma-frequency of 1.31 per bivalent (TABLE 3).

TABLE 3. **Chiasma-frequency at diakinesis in Illicium floridanum** *

TYPES OF CHIASMATA	NO. OF CHROMOSOMES	NO. OF CHIASMATA	% CHIASMA-TYPES
Zero	16	0	6.5
One terminal	69	69	27.9
Two terminals	35	70	14.2
One interstitial	73	73	29.6
Two interstitials	25	50	10.1
One terminal — one interstitial	25	50	10.1
Two terminals — one interstitial	4	12	1.6
TOTALS	247	324	100.0

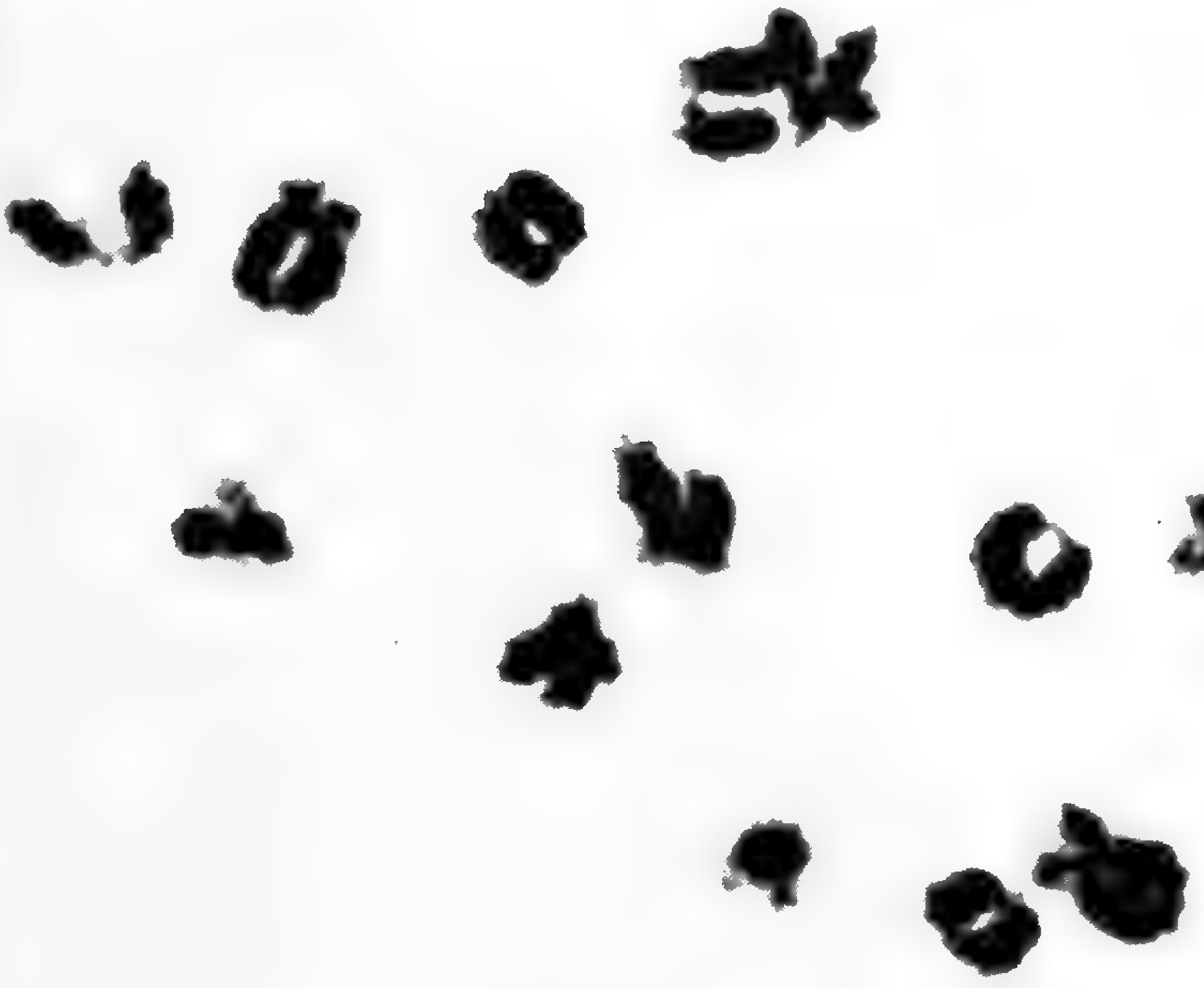
Chiasma-frequency/bivalent = 324/247 = 1.31

* Based on 19 cells

SUMMARY AND CONCLUSIONS

Chromosome counts on the related Schisandraceae (Whitaker, 1933; Stone, 1965) and two of the three members of the Illiciaceae (Whitaker, 1933), suggest that 14 is the base number for the alliance. Viewed in this light, $n=13$ in *Illicium floridanum* clearly seems to be the product of aneuploid reduction. Though we have made direct comparisons between the karyotypes of *I. floridanum* (sect. ILLICIUM) and *I. parviflorum* (sect. CYMBOSTEMON), it should be re-emphasized that these species are representatives of the two sections of the family. It would be most interesting to examine the 14-chromosome karyotype of *I. anisatum* (Whitaker, 1933), for this species is one of the twelve Smith placed in section ILLICIUM (formerly sect. BADIANA) with *I. floridanum*. The cytology of section CYMBOSTEMON is equally unknown. The $n=14$ count of *I. parviflorum* is the only report on the 29 species recognized by Smith (1947). While it is quite likely that the 14-chromosome species of both sections have similar karyotypes, it will be necessary to analyze close relatives of *I. floridanum* and meiotic pairing configurations formed in $n=13 \times n=14$ hybrids before the exact nature of aneuploid reduction is established.

Centric fusion (FIG. 2) of rod chromosomes 13 and 14 of *I. parviflorum*



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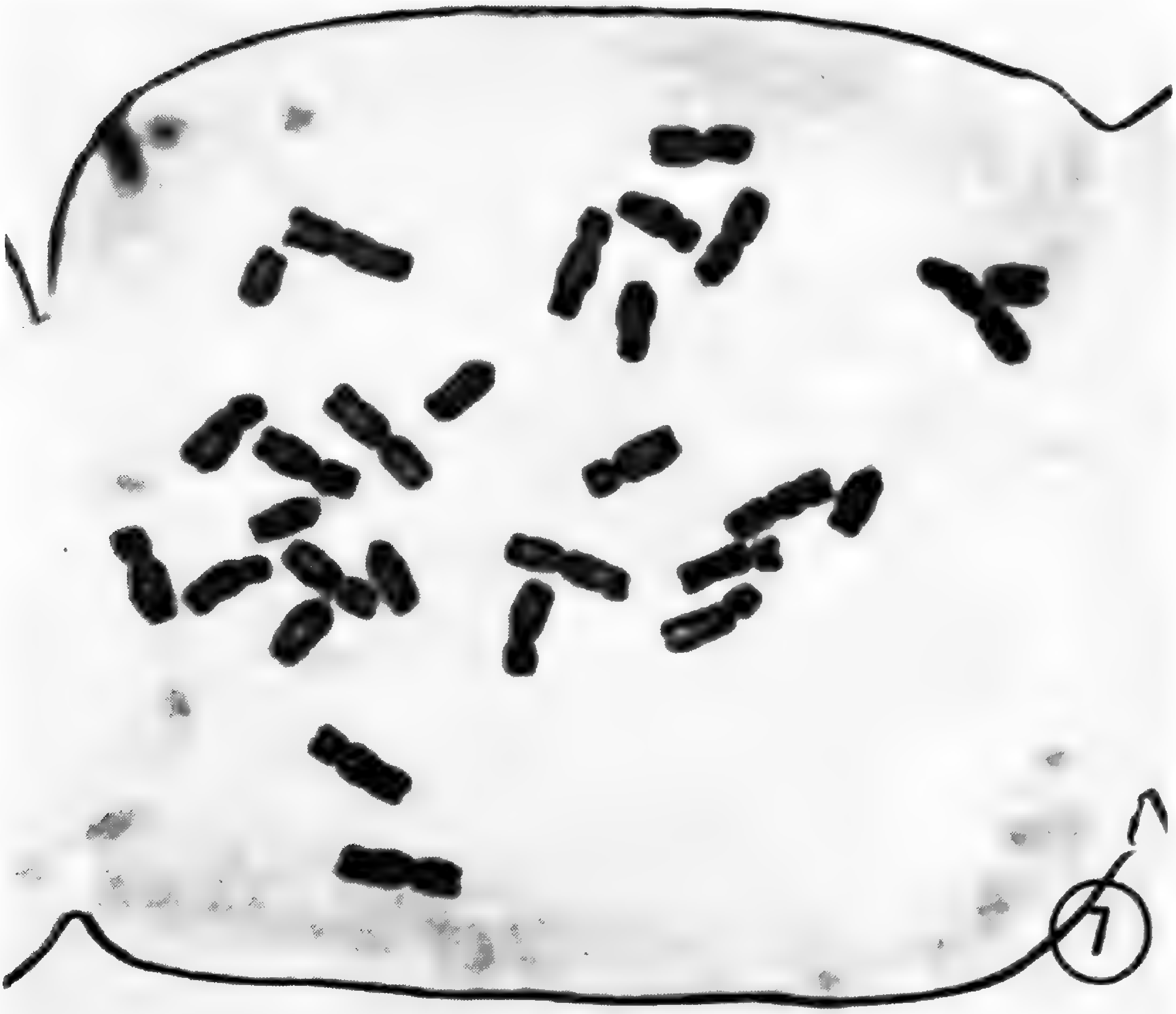
FIGS. 4–6. **Illicium floridanum.** Meiosis in pollen mother cells, $n = 13$. *Stone 1357*. × 1000. 4. Diakinesis. 5. Metaphase I. 6. Anaphase I.



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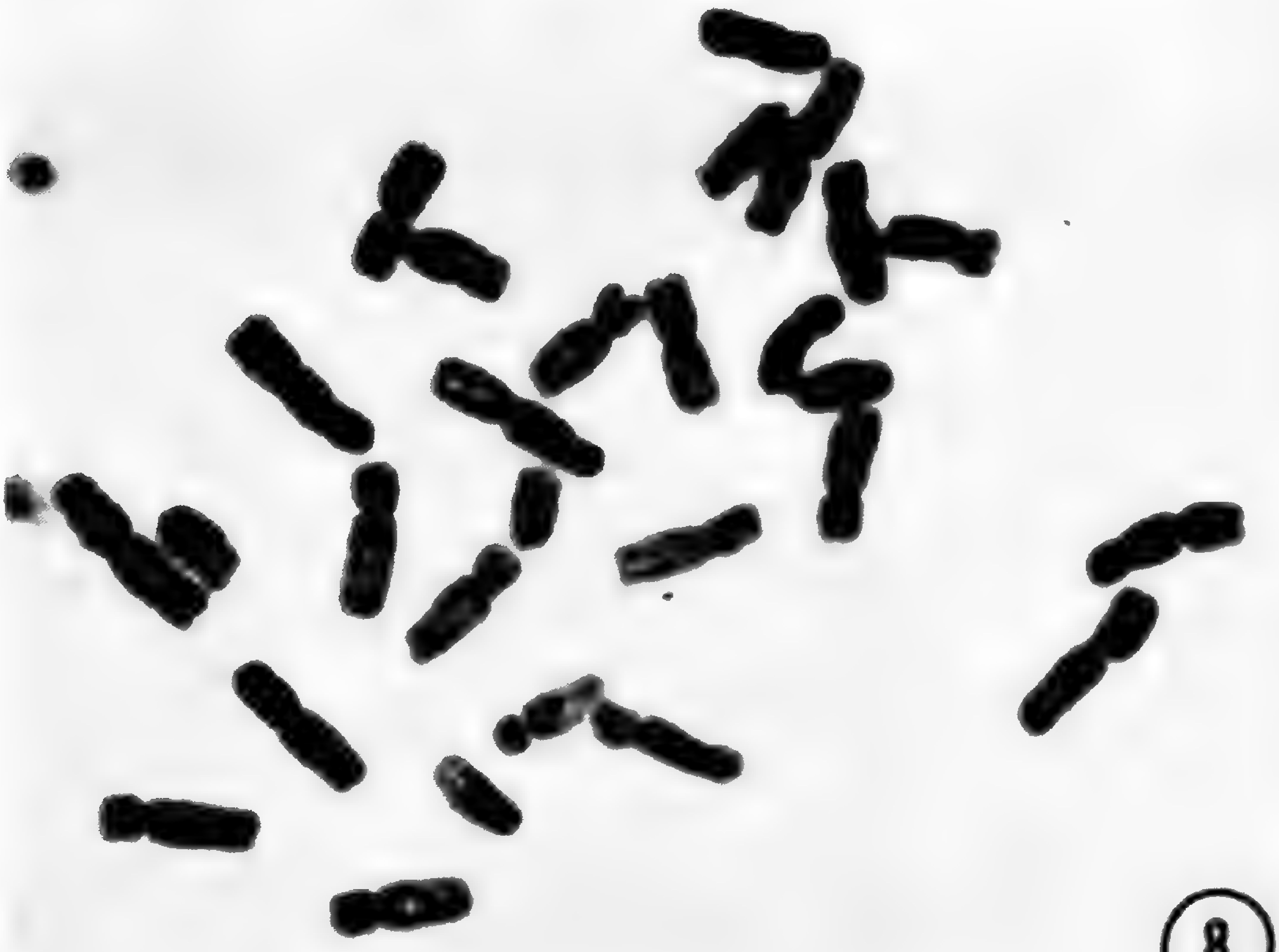

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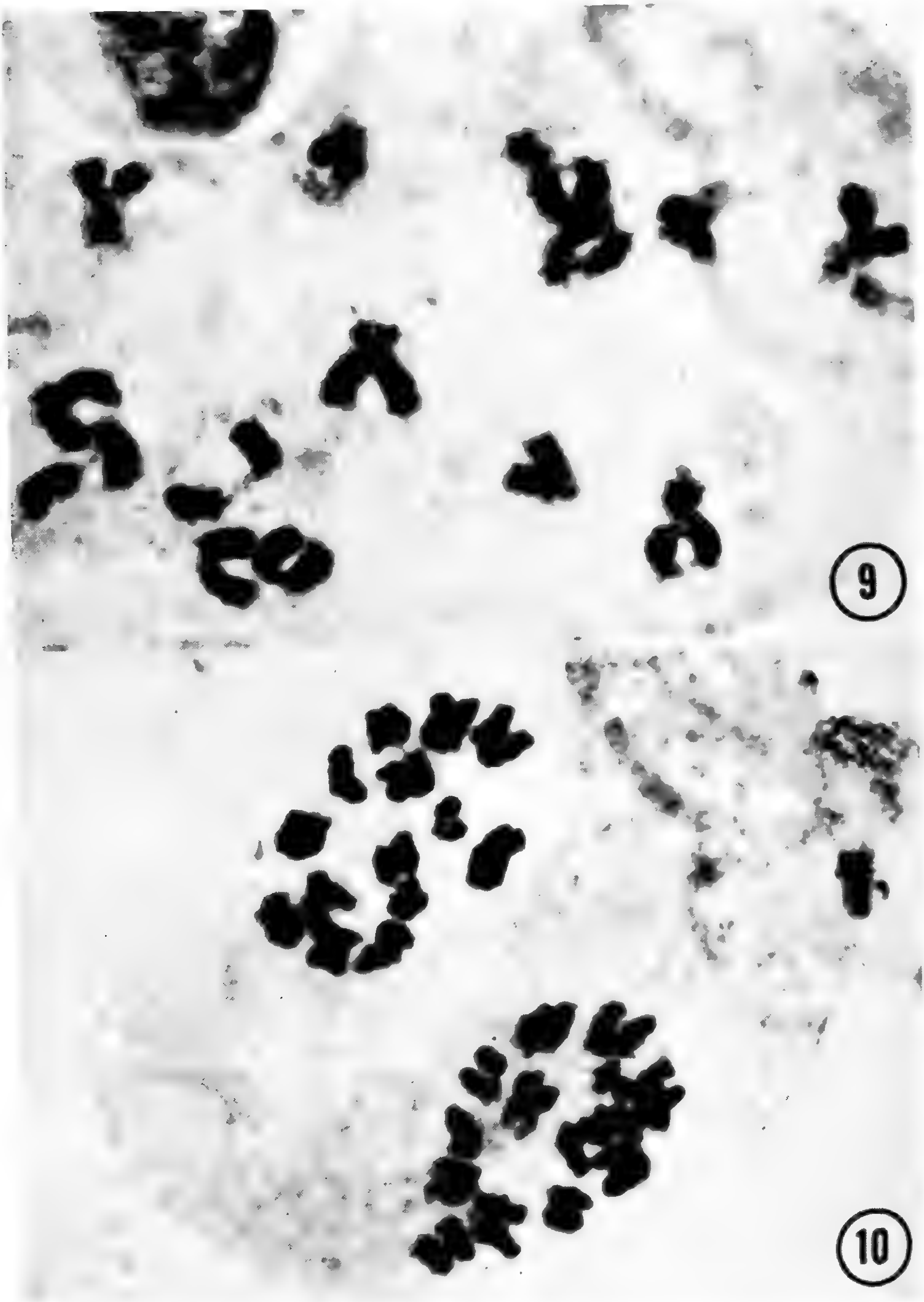
FIGS. 7 and 8. **Illicium parviflorum.** Mitotic metaphase, $2n = 28$. × 1780. 7. North Carolina population, *Stone 1820*. 8. Florida population, *Stone 1422*.



FIGS. 9 and 10. **Illicium parviflorum.** Meiosis in pollen mother cells, $n = 14$. *Stone 1820*. × 1500. 9. Diakinesis. 10. Anaphase I.

could account for number 15 of *I. floridanum* (FIG. 1). In addition, if the residuum of number 13 was transferred to the terminal ends of the arms of chromosome 1 (FIG. 2), a v-shaped chromosome similar to chromosome 1 of *I. floridanum* would result.

We have no information on the significance of the reduction from $n=14$ to $n=13$. Whitaker (1933) originally reported $n=14$ for *Illicium anisatum* L. (as *I. religiosum*) and *I. floridanum*. As we have shown, his report for *I. floridanum* is probably incorrect. Unfortunately, as Wood (1958) has noted, Whitaker's counts were not documented with voucher specimens and there is no way to tell if he miscounted or misidentified the material. It does open the question, however, of whether *I. anisatum* of the same section might not also have $n=13$. If not, then $n=13$ may be exclusive to the American species of section ILLICIUM. For as Smith (1947) commented, "The species [*I. floridanum*] is clearly separable from all Old World members of § *Badiana* [= § ILLICIUM] on the basis of its comparatively long pedicels, numerous stamens, and brightly colored perianth segments. Its only close relative is the following new species [*I. mexicanum*]."

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FURTHER MORPHOLOGICAL STUDIES ON ANASTOMOSES IN THE DICHOTOMOUS VENATION OF CIRCAEASTER

ADRIANCE S. FOSTER

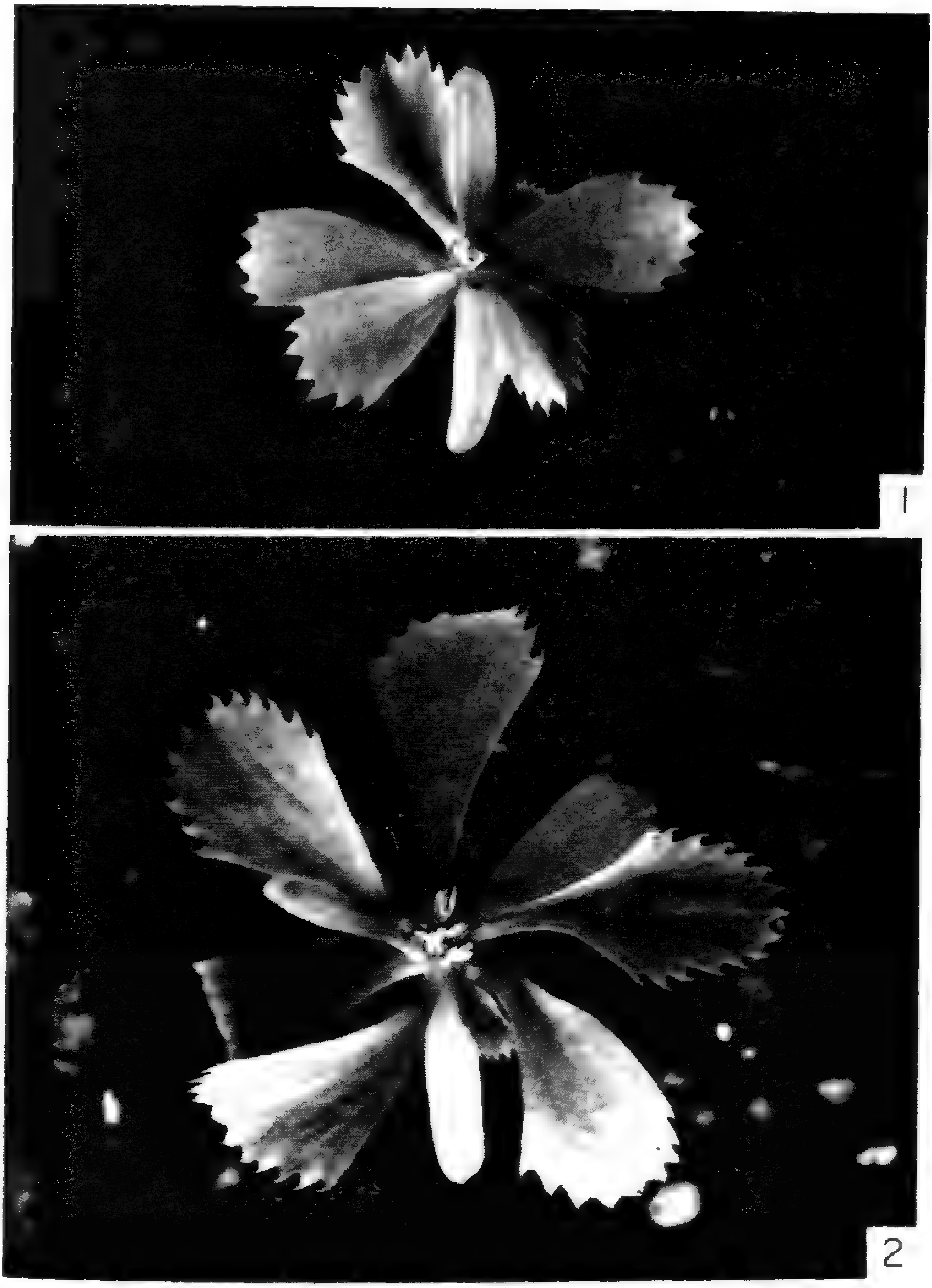
CONTINUED RESEARCH ON DICHOTOMOUS LEAF VENATION in specimens of *Circaeaster agrestis* Maxim. grown at the University of California Botanical Garden, Berkeley, during 1965 and 1966 revealed that the three kinds of anastomoses described in my last paper (Foster 1966) do not include the full range of variation in types of vein unions which are developed in this genus. The main purpose of the present article, therefore, is to describe the additional forms of anastomoses and their associated vein approximations which have been found, and to compare their morphology with the types previously considered.

A further objective of this paper is to present a brief account of the early phases of development of the seedling and the complex organography of mature flowering and fruiting specimens. This phase of my study is illustrated by photographs of living plants (FIGS. 1–3) which it is believed will convey a realistic idea of the general organization and development of the leaf-rosette and the condensed fascicles of flowers characteristic of this remarkable little dicotyledonous herb.

MATERIALS AND METHODS

The cultivated plants which provided the material for this study were grown during 1965 and 1966 from the collection of fruits given to me through the kindness of Dr. M. Anantaswamy Rau, Regional Botanist of the Botanical Survey of India. He had collected these fruits on October 22, 1963, from the colonies of *Circaeaster* originally discovered in 1962 by Bhattacharyya (1964) "growing gregariously on shady and flat mossy rocks under the shade of *Viburnum* bushes" near Gangharea, North Garhwal, India, "at an altitude of nearly 3300 meters."

Fruits were stored at a temperature of approximately 40°F until needed and under such conditions retained for more than three years an ability to germinate. The seedlings were raised in pots of soil in a growth chamber illuminated for 16 hours a day and maintained at a constant temperature of 42° F. Some variation in the time required for germination was noted over the successive years but in general a period of 3 to 4 weeks elapses before the conspicuously elongated hypocotyl elevates the cotyledons above the surface of the ground. Young plants were kept in the growth chamber for about a month during which time a series of leaves and, in some plants, the first fascicles of flowers were formed. The plants were then taken to the Botanical Garden, transplanted into small individual pots and placed



Figs. 1 and 2. General organography of young cultivated specimens of *Circaeaster* photographed from above to show the cotyledons and primary leaves. 1, seedling, with two linear cotyledons and six expanded primary leaves. 2, older stage. The small structures in the center of the rosette are young involute leaves. Both figs. × 3.

either in a lath house or a cool greenhouse. Mature fruits collected from potted plants during mid- or late summer of 1966 have proved viable and some of them this spring (1967) are producing a new crop of seedlings in the growth chamber. Seedlings are also now developing in the open from fruits which had fallen from a group of plants which were grown last year in an especially prepared bed in the rhododendron dell in the Botanical Garden. It is hoped that from these plants a "permanent" colony may become established, comparable to the colonies maintained for a number of years at the Botanical Gardens at Upsala and Edinburgh (Foster 1963, p. 302).

When fully mature, the leaf-rosettes of a large number of plants were either preserved directly in 70 percent alcohol or in some cases were first killed and fixed in formalin-acetic acid-alcohol before storage in alcohol. All of the foliar organs of each plant (including the innermost small bracts of the flower-fascicles) were subsequently removed by means of small scissors, carefully examined for vein approximations and anastomoses, and the data recorded in tabular form. The leaves selected for venation studies were cleared in 5 percent NaOH followed by concentrated chloral hydrate, dehydrated in the usual alcohol series, stained in a 1 percent solution of safranin in equal parts of absolute alcohol-xylene and mounted in "Piccolyte."

I am extremely grateful to Mrs. Irene Baker, who has undertaken each year the planting of the fruits and has kept careful records of the beginning and the extent of the period of germination and early development of the seedlings. The line drawings in this paper represent direct tracings of photomicrographs and were prepared by Mrs. Emily R. Reid. I wish also to thank my wife for her assistance in proof-reading the manuscript.

ORGANOGRAPHY OF SEEDLING AND ADULT PLANT

The present description of the germination and general organographic development of *Circaeaster* is intended to supplement my previous account which was based entirely upon the study of a very limited number of herbarium specimens (Foster 1963, pp. 304–306).

During the early phases of germination, the curved, elongating hypocotyl, bearing the pair of closely appressed cotyledons at its apex, emerges from the soil. As a result of differential elongation, the hypocotyl soon becomes erect and the two linear cotyledons reflex and assume a horizontal position. These appendages remain green and persist throughout the life of an individual plant.

Approximately a week after the cotyledons have reflexed, a series of small, cuneate primary leaves begins to expand (FIGS. 1 and 2). The form and relatively simple dichotomous venation patterns of these earliest foliage leaves has already been described (Foster 1963, pp. 308, 309). The vernation of the primary leaves, like that of the adult type of leaf, is involute.

As elongation of the hypocotyl continues, the terminal rosette becomes large and morphologically complex because of the development of additional crowded adult leaves followed by the rapid formation of bracts and their axillary fascicles of small flowers (FIG. 3). Since there is no clear

FIG. 3. A maturing cultivated specimen of *Circaeaster* showing the rosette of dichotomously veined leaves, the central fascicles of flowers and, at center left, a maturing fruit with characteristic uncinate hairs. × 3.

demarcation either in form or venation between foliage leaves and well developed bracts, the latter were included in the total number of leaves in each of the 80 plants which were dissected and analysed in the present study (TABLE 1). Using this admittedly imprecise method of tabulation, it is nevertheless apparent that the number of leaves varies widely from plant to plant, ranging from 11 in very small precociously flowering individuals to as high as 180 in a few very robust plants. The "average leaf number" for *all* plants studied is approximately 60.

In an earlier paper (Foster 1963, p. 304) the question was raised whether the compact rosette of leaves and tiny flowers of mature plants is borne in an upright or prostrate position in nature. Cultivated plants, growing under the best horticultural conditions which could be provided, throw some light on this question. During the maturing stages of these plants, many of them became "top heavy" and there was a marked tendency for the slender hypocotyl to be bent towards the ground. In fact it was necessary, in most cases, to use a miniature "Carnation-type" plant-supporter to hold each plant in a more or less erect position. In maturing plants in nature it seems possible that the rosette also may ultimately become prostrate but this conjecture needs to be tested by extensive field observations.

The full cycle of development in *Circaeaster* is relatively short and follows the general pattern of many dicotyledonous herbs. As accurately as could be determined, the life span of cultivated plants is about five months from seedling to complete maturity. This cycle is somewhat longer than that of the plants growing in their native habitat in Gangharea, North Garhwal, India, according to notes kindly given to me in a recent letter by Dr. M. A. Rau. He writes: "Regarding the growth cycle in nature, I do not have precise information about the time of appearance of seedlings. At these heights snow remains till the first week of June and it is, therefore, likely that germination takes place sometime during June. They are in full bloom by the middle of August and by the end of September the plants will have fruited. The plants are spent out by October and when I collected the ripe fruits on October 22 (1963), the fruits were all on the ground and the plants had collapsed. There may be some little variation in the dates given above from year to year depending on the environmental factors but in general you may take the above as the schedule in nature."

VEIN APPROXIMATIONS AND ANASTOMOSES

Résumé of Previous Studies. Before presenting the results of the present investigation, it seems highly desirable to review briefly (1) the classification i.e. "typology" of the anastomoses proposed in my recent paper (Foster 1966) and (2) to re-emphasize the morphological significance of vein approximations i.e. transitions between open dichotomous venation and true anastomoses. The latter represent the union between two xylem strands while in a typical vein approximation the tracheary elements of the adjacent branches of a pair of very closely spaced veins are separated by parenchyma (see Foster 1966, *Figs. 26, 27* for histological details).

The interrelationship between open dichotomous venation, vein approximations and Types I to III anastomoses are represented in FIG. 4. It should be emphasized that the very symmetrical vein approximation shown in this figure is not hypothetical but is based upon actual patterns observed in a number of leaves (Foster 1966, *Figs. 3, 4, 6, 8*). The distally "open" areole created by this kind of vein approximation is strikingly similar in form to the "closed" areoles formed by both Type I and Type II anastomoses. These two kinds of vein unions differ from each other in that xylem fusion in Type I is "transient," i.e. the extent of contact is relatively short while in Type II, the two veins completely merge to form a single, unbranched excurrent vein. Both of these forms of anastomoses are funda-

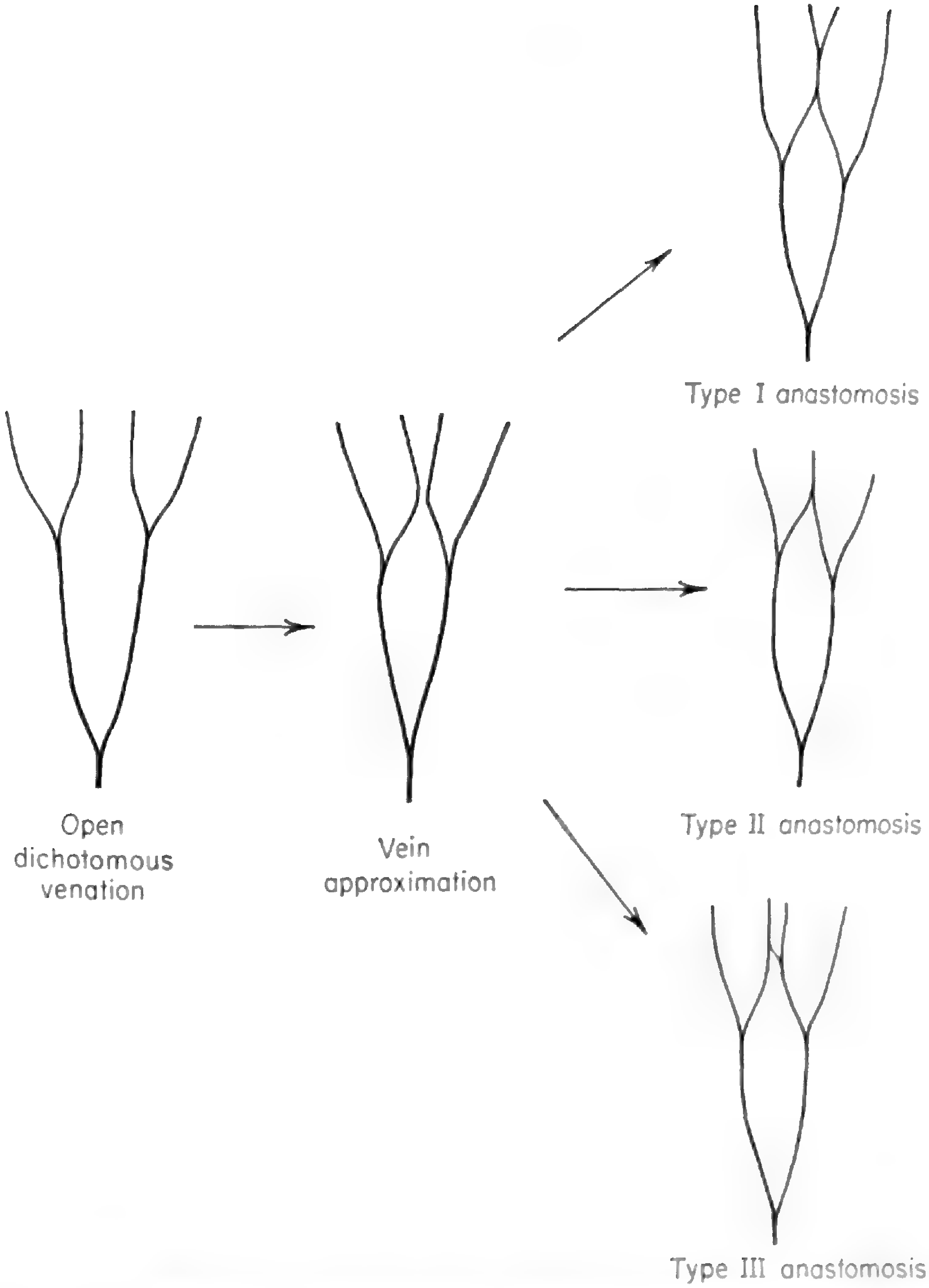


FIG. 4. Diagrams representing the morphological relationships between open dichotomous venation, symmetrical vein approximation and Types I to III anastomoses. Further explanation in text.

mentally similar however in that the union occurs between the adjacent branches of *two vein-dichotomies* (Foster 1966, *Figs. 1, 2*).

Type III anastomoses, as shown in FIG. 4, are less easily interpreted because the approximated branches of two vein-dichotomies remain discrete and are only interconnected by a very short obliquely oriented "commissural vein." The xylem of the latter may consist of one or at most of only a few tracheary elements (see Foster 1966, *Figs. 28, 33a, b*). Whether the "commissural vein" should be regarded (1) as a much "reduced" branch of a vein-dichotomy or (2) as a "new formation" is problematical, although my previous study indicates a reasonable probability in favor of the first alternative. As I have pointed out, comparable difficulties arise in the interpretation of the short "commissural veins" in the leaves of certain ferns (Goebel 1922, pp. 19, 20) and in the petals of *Ranunculus* (Arnott & Tucker 1963, *Fig. 16*, type C").

Although multiple anastomoses (i.e. two or more vein unions in one leaf) were not observed in any phase of my investigations on *Circaeaster*, several leaves were encountered each of which had formed two vein-approximations. A striking illustration is represented in FIG. 5 which shows a small bract (13 mm. long × 3 mm. wide) with two symmetrical vein approximations, each forming a very elongate distally open areole. A venation pattern of this type suggests the strong possibility of the occasional formation of multiple anastomoses in *Circaeaster* but thus far no examples have been discovered either in leaves from a wide range of herbarium specimens or in those of the numerous cultivated plants which I have studied.

New Observations. TABLE 1 provides further evidence for the conclusion previously reached that anastomoses are very uncommon in the leaves of *Circaeaster* (Foster 1966, p. 592). In more than 5000 leaves critically examined in the present survey, only 54 or about 1 percent of them had formed an anastomosis. Vein approximations were slightly more frequent and occurred in 2 percent of all the leaves studied.

Despite the sporadic distribution of anastomoses in the leaf sample *as a whole*, the percentage of anastomoses in the leaves of certain *individual plants* was comparatively high and ranged from 1.8 to 6.6 percent. As shown in TABLE 2, the 12 plants in which this higher frequency of anastomoses was observed, were distinct from all the other plants because of the presence of solitary vein-unions in two or more leaves of the same individual. It seems reasonable to postulate that the number of anastomoses per plant may be under some type of genetic "control" but this is an idea which requires confirmation by appropriate breeding and experimental techniques.

From a morphological viewpoint, the majority of the vein unions analysed could readily be classified under either Type I or II anastomoses (FIG. 4). But 22 percent of the anastomoses found in the present survey are sufficiently distinctive to justify their segregation into new categories which for convenience are designated as Types IV and V. (FIG. 6).

In both of the new types of anastomoses, the areole is formed by the union between an *unbranched arcuate vein* and one of the branches of its sister vein lying above it (FIG. 14). This pattern is clearly different from that represented by Types I to III anastomoses in which union occurs between two of the branches of a *pair* of adjacent vein dichotomies (cf. FIGS. 4 and 6). As shown diagrammatically in FIG. 6, Types IV and V

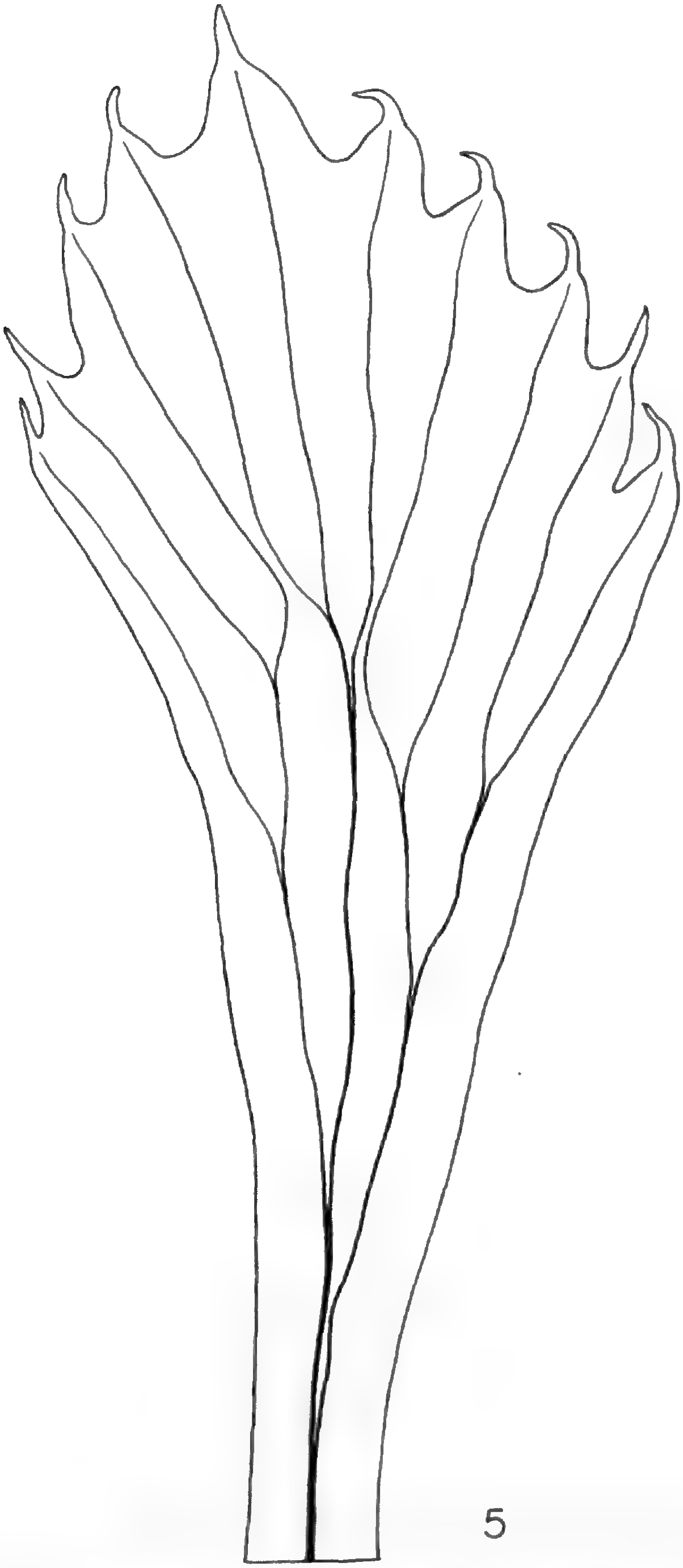


FIG. 5. Floral bract showing the rare occurrence in *Circaeaster* of two vein approximations, each forming a greatly elongated areole "open" at its distal end, × 24.

TABLE 1. **Summary of anastomoses and vein approximations in leaves of cultivated plants of Circaeaster agrestis**

	PLANTS GROWN IN 1965	PLANTS GROWN IN 1966	TOTALS
TOTAL NUMBER OF PLANTS	40	40	80
TOTAL NUMBER OF LEAVES	2248	2772	5020
NUMBER OF LEAVES WITH ANASTOMOSES	29	25	54
NUMBER OF PLANTS WITH ANASTOMOSES IN 2 OF MORE LEAVES	8	4	12
NUMBER OF LEAVES WITH VEIN APPROXIMATIONS	45	75	120
NUMBER OF PLANTS WITH VEIN APPROXIMATIONS IN 2 OR MORE LEAVES	11	18	29
% OF LEAVES WITH ANASTOMOSES	1.2	0.9	

TABLE 2. **Percent of anastomoses in plants with vein unions in two or more leaves**

PLANT NUMBER	TOTAL NUMBER LEAVES	NUMBER OF LEAVES WITH ANASTOMOSES	% OF LEAVES WITH ANASTOMOSES
5a	30	2	6.6
15a	109	2	1.8
16a	93	2	2.1
27a	109	3	2.7
29a	145	3	2.0
33a	80	2	2.5
34a	45	2	4.4
35a	45	2	4.4
4b	95	2	2.1
19b	80	2	2.5
21b	84	4	4.7
26b	60	4	6.6
TOTALS	975	30	

anastomoses are morphologically connected, by corresponding vein approximations, with an asymmetrical form of open dichotomy which commonly occurs in the leaves of *Circaeaster*. This pattern is termed "asymmetrical" because one of the derivatives of a vein-dichotomy remains unbranched throughout its course while its sister derivative bifurcates one or more times before reaching the distal margin of the lamina (FIGS. 9, 11, 18, 21, 23).

With the preceding analysis as a general basis, it is now appropriate to describe in detail the new forms of anastomoses and their interrelationships with vein approximations.

Type IV Anastomoses. The distinguishing character of this type of anastomosis is the very short extent of xylem-contact between the arcuate vein and the branch of a contiguous vein-dichotomy (FIG. 6). After separation of the two strands, the upper portion of the arcuate vein either terminates in a marginal tooth or ends blindly in the lateral margin of the lamina (FIGS. 11, 13).

The resemblances between vein approximations and Type IV anastomoses are indeed striking and support the idea that the two patterns differ from one another only in degree (compare FIGS. 7, 10, 11). In some cases, a relatively wide strip of parenchyma separates the region of approximation between the arcuate vein and its contiguous strand (FIG. 8). But very commonly, the interval is so narrow that it is impossible to draw a distinction between an anastomosis and a vein approximation until a leaf has been thoroughly cleared in NaOH and chloral hydrate. FIG. 7 is a good example of this because it shows the extremely close approximation between the two veins at the upper left margin of the leaf. Additional illustrations of closely approximated veins are evident in FIGS. 9, 10, and 12.

Type V Anastomoses. In this type of vein union, the tip of an arcuate unbranched vein converges toward and becomes confluent with the branch of a vein-dichotomy situated above it. Two "variations" of this kind of anastomosis have been discovered and, as is shown in FIG. 6, each of them is morphologically related to a corresponding type of vein approximation.

In the simpler of the two "variations," the arcuate vein joins the outer branch of a *first order* vein-dichotomy, creating a conspicuous and relatively symmetrical areole (FIGS. 14, 16–19). The exact point of anatomical union between the xylem strands fluctuates. Commonly the two xylem strands merge well above the level of the adjacent vein dichotomy (FIGS. 14, 16–18) but the union may take place very near the point of bifurcation of the vein (FIG. 19). An interesting example of the arrested development of a Type V anastomosis is shown in FIG. 15. Examination of this leaf under high magnification reveals that the terminal tracheary elements of the marginal arcuate vein at the left are not in direct contact with the xylem of the neighboring vein, and hence that the areole is of the "open" type.

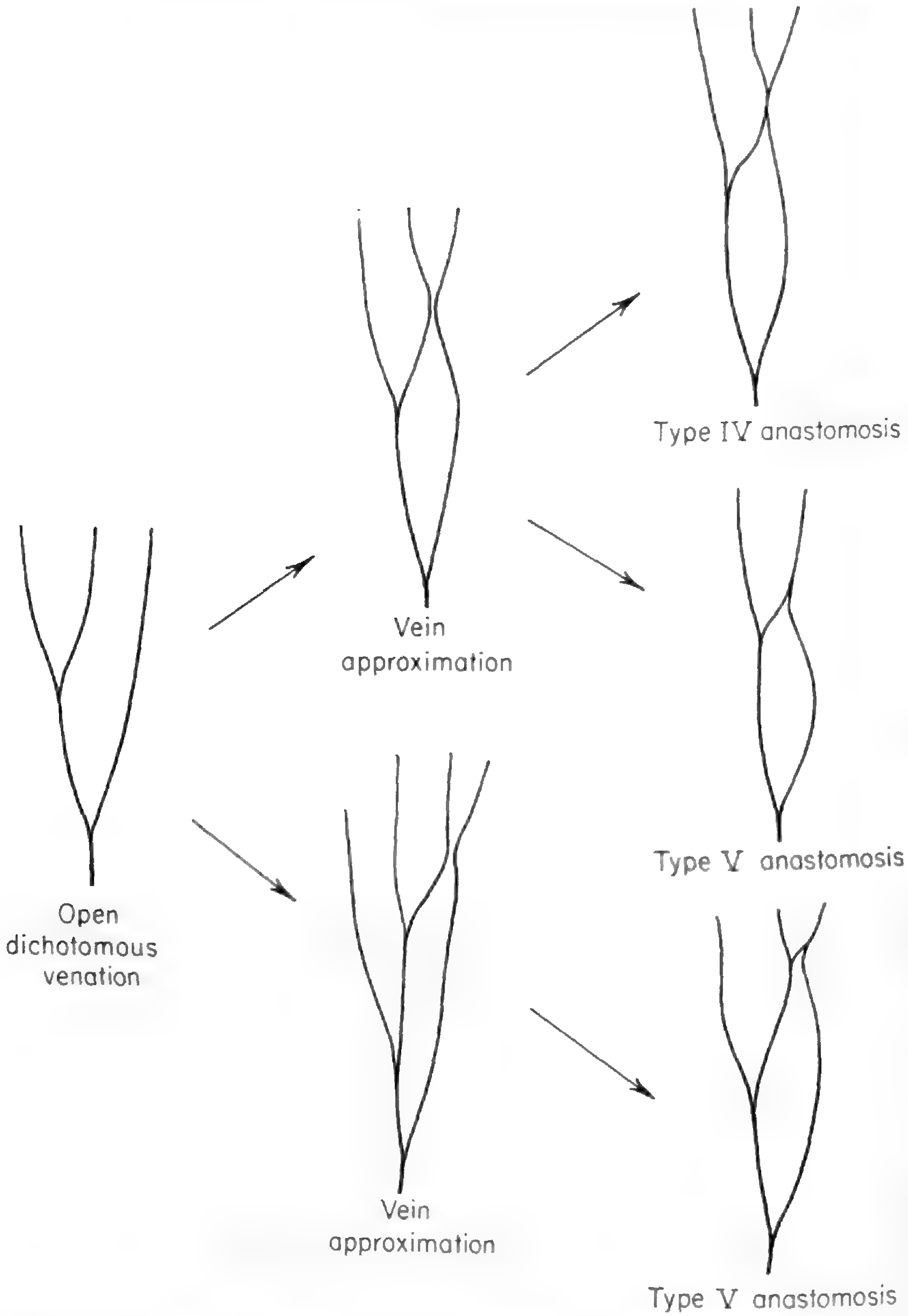


FIG. 6. Diagrams representing the morphological relationships between open dichotomous venation, vein approximations, and Types IV and V anastomoses. Further explanation in text.

In the other Type V "variation," an areole is created by the union of the arcuate vein with the outer branch of a *second order* vein-dichotomy lying above it (FIGS. 6, 21–23). Vein approximations which morphologically connect such anastomoses with open venation are not common but the leaf shown in FIG. 20 apparently developed such a transitional form.

When examples of Types IV and V anastomoses were first encountered in this survey it seemed possible that they might be restricted to that part of the vein system adjacent to the lateral margins of the lamina. (FIGS. 13, 16, 21, 22). Further study however clearly indicated that both of the new types of anastomoses may also occur in a more central position in the venation (FIGS. 11, 18, 19, 23).

DISCUSSION

The various forms of vein approximations which occur in the leaves of *Circaeaster* are regarded as morphological "transitions" which connect the different types of anastomoses with open dichotomous venation (FIGS. 4–7). This conclusion seems fully justified by the present comprehensive survey and it is important in this connection to note that "near fusions" of veins were also observed by Arnott (1959, p. 408) in the foliage leaf of *Ginkgo* and by Arnott and Tucker (1963, p. 822) in the petals of *Ranunculus repens* var. *pleniflorus*. In both of these examples, anastomoses are considerably more frequent than in *Circaeaster* but the fundamental pattern of venation is dichotomous. It is of further comparative interest that anastomoses and vein approximations remarkably similar to those in *Circaeaster*, also occur in the dichotomous venation of certain living ferns. In a brief unpublished study on the venation of *Anemia herzogii* Rosenstock, I observed that the most common types of anastomoses correspond to Types I and II (see FIG. 4). In proportion to the relatively high number of dichotomously branched veins in each pinna however, anastomoses and their coordinated types of vein approximations in this fern seem just as sporadic and "unpredictable" in position as in the leaves of *Circaeaster*.[1]

These brief comparisons between *Circaeaster* and other living taxa with dichotomously veined foliar appendages clearly support my concept that a parallel evolution of similar types of anastomoses has very probably occurred in morphologically divergent and taxonomically unrelated plants (see also Foster 1961, p. 974 and 1966, pp. 596, 599). But even with this idea in mind, the question nevertheless arises as to the original or most ancient type or types of vein anastomoses in vascular plants as a whole.

Although there appear to be very few published descriptions of the details of venation patterns in extinct groups of the Pteropsida, Types I and II anastomoses, as defined in the present paper, seem to represent extremely ancient trends in the evolution of areolate venation. Both of these types

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[1] According to Mickel's (1962) study on *Anemia*, the pinnae of species classified in the subgenus *Coptophyllum* are open dichotomously veined and devoid of anastomoses while in the subgenus *Anemia*, weakly anastomosed (e.g. *A. herzogii*) or conspicuously areolate venation (e.g. *A. phyllitidis*) is typical. It is of considerable interest that in *A.* × *ulbrichtii*, a hybrid between *A.* (subg. *Coptophyllum*) *raddiana* and *A.* (subg. *Anemia*) *phyllitidis*, the venation is "intermediate" in character, i.e., rather weakly anastomosed. An intensive study of venation patterns throughout the genus *Anemia* is obviously highly desirable.

of vein unions were observed in *Neuropteris* and other fern-like plants of the Paleozoic by Potonié (1912, pp. 111–117) and Type II anastomoses evidently created the lax areolate venation characteristic of various species of *Ctenis* (Florin 1933, pp. 53–80) and *Gangamopteris* (Zimmermann 1959, p. 284 and *Fig. 148b*). Very recently, my attention has been kindly directed, by Mr. William Glen of the Department of Paleontology at Berkeley, to the illustrations of typical Type II anastomoses in *Psygmophyllum flabellatum* (= *Ginkgophyton flabellatum*) given by Seward (1919, p. 83, *Fig. 666*). In this Paleozoic plant of uncertain affinities, Seward observed that "the veins spread from the base of the lamina and are repeatedly forked; they may be very numerous and in some forms occasionally anastomose, as in *P. flabellatum*" etc.

On the other hand, how should one interpret phylogenetically the apparently extremely simple type of anastomosis in which an areole is created by the union of the two branches of a single vein-dichotomy? Is this form of anastomosis, which is the most common type in *Ginkgo* (Arnott 1959, *Fig. 3*), "primitive" or "advanced" in vascular plants as a whole? As far as I am aware, this kind of anastomosis, designated as "Type A" by Arnott, has not been recorded in paleobotanical literature. In living plants aside from *Ginkgo*, however, "Type A" anastomoses occur in the dichotomous venation of certain cycads (e.g. *Stangeria*, *Dioon*, *Encephalartos*, and *Zamia*), in a few ferns which I have personally examined such as *Stenochlaena palustris* (Burm.) Bedd. and *Anemia herzogii* Rosenstock, and in the petals of *Ranunculus* where, however, they are very infrequent (Arnott & Tucker 1963, p. 827). A single example of a "Type A" anastomosis was found in my survey of *Circaeaster* but the leaf in which it occurred was so damaged in processing that it had to be discarded. In a few leaves, as illustrated by FIG. 24, a very rare type of vein approximation was noted which might be regarded as "transitional" between a "Type A" anastomosis and a normally bifurcated vein. It should be clear from this brief discussion, however, that the "phylogenetic status" of "Type A" anastomoses in the living ferns and seed plants must for the present remain an entirely open question.

There remains for final consideration the morphology and possible phylogenetic significance of Types IV and V anastomoses (FIGS. 6, 14). I know of no record of these forms of anastomoses in extinct tracheophytes but I have seen excellent examples of Type V unions in the marginal veins of certain pinnae in the leaves of *Anemia herzogii*. Among angiosperms, Type V anastomoses are abundantly formed during the ontogeny of the venation in the cotyledons of *Pulsatilla vulgaris*. In this case, the anastomoses are interpreted by Höster and Zimmermann (1961, pp. 85, 86, p. 93 and *Figs. 12–14*) as morphologically comparable with the "Goniopteridis" type of vein union previously recognized by Zimmermann (1959, p. 277, *Fig. 142*) as primitive in his phylogenetic series of reticulate venation patterns in "Pteridophylls." Type V anastomoses are also common in the dichotomous venation of the petals of *Ranunculus*. Arnott and Tucker (1963, 1964) regard these anastomoses as a "variation" of their "Type C" vein union

(= Type II anastomosis in *Circaeaster*). On the basis of these few, scattered examples it is clearly impossible, however, to reach a phylogenetic conclusion, although I suspect that both Types IV and V anastomoses ultimately may prove to be relatively "primitive" in an evolutionary sense.

In conclusion, I wish to emphasize the need for more detailed attention by paleobotanists to the diversified trends of specialization of areolate venation in extinct members of the Tracheophyta. It should be more widely recognized, in my opinion, that the presence or absence or *degree* of development of anastomoses in any given system of dichotomous venation has phylogenetic significance in addition to its diagnostic importance for purposes of identification and classification. The same viewpoint is justified, I believe, with reference to the occurrence of dichotomous venation and sporadic anastomoses in the leaves of certain living seed plants. An excellent illustration is provided by Arnott's (1959) discovery of various types of anastomoses in the dichotomous venation of such a "living fossil" as *Ginkgo biloba.* Napp-Zinn (1966, p. 166) in his review of leaf anatomy in gymnosperms points out that anastomoses also occur in the dichotomous venation of two living genera of cycads (e.g. *Stangeria* and *Macrozamia*). In a study of leaf venation in *Zamia* now in progress, I have found striking examples of anastomoses entirely comparable, *in a morphological sense,* to the Types I and II vein unions which occur in the leaves of both *Kingdonia* (Foster 1959, Foster & Arnott 1960) and *Circaeaster* (Foster 1966). Whether the venation patterns in these two remarkable dicotyledons represent (1) the "retention" of a condition which appeared during the early evolution of angiosperms or (2) are the result of "reversion" from a more complex vasculature, are questions which cannot be convincingly answered until future paleobotanical discoveries have clarified the origin and major trends of phylogeny of the angiosperms as a whole.

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EXPLANATION OF PLATES

PLATE I

Fig. 7. Cleared leaf showing, at left, the approximation between an unbranched vein and a branch derived from an adjacent vein-dichotomy. This type of vein approximation is represented diagrammatically in Fig. 6, × 14.

PLATE II

Figs. 8–13. Venation patterns showing intergradations between vein approximations and Type IV anastomoses. Fig. 8. "Open" marginal areole at upper left formed by convergence and abrupt divergence of two adjacent veins, × 5. Fig. 9. Vein approximation similar to one in Fig. 8 but the two veins nearly confluent, × 3.8. Fig. 10. Very close approximation between two veins forming an elongated "open" submarginal areole, × 7. Fig. 11. Leaf with a Type IV anastomosis which closely resembles the pattern of the vein approximation shown in Fig. 10, × 5.3. Fig. 12. Vein approximation forming an exceptionally small "open" submarginal areole, × 4.2. Fig. 13. Leaf with a Type IV anastomosis (lower right margin) formed by the transient union between an unbranched blindly terminating vein and the adjacent branch of a vein-dichotomy, × 4.5. *US*, unconnected vascular strand.

PLATE III

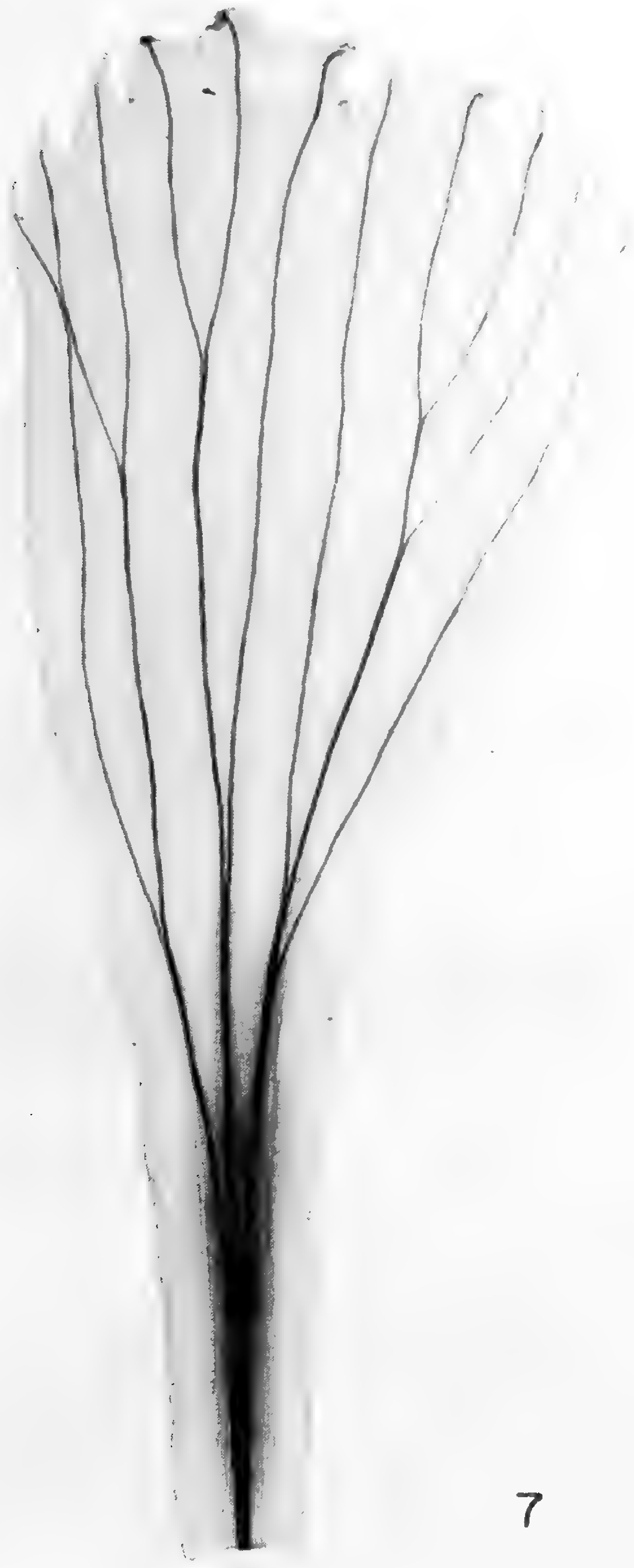
Fig. 14. Small floral bract showing, near the middle of the lamina, a striking example of a Type V anastomosis, × 32.

PLATE IV

Figs. 15–19. Fig. 15. An unusual type of an "arrested" anastomosis in which the tip of the unbranched arcuate xylem-strand at the left margin ends a few cells below the outer branch of the vein-dichotomy lying above it, × 7. FIGS. 16–19. Various examples of Type V anastomoses. FIG. 16. Primary leaf with anastomosis at right margin of lamina, × 5.5. FIG. 17. Typical adult type of foliage leaf showing a conspicuous submarginal areole, × 3.8. FIG. 18. Similar example of Type V anastomosis forming a smaller submarginal areole, × 7. FIG. 19. An example of vein union below the point of separation of the branches of a vein-dichotomy. Note blind vein-ending *between* two marginal teeth at lower left side of lamina, × 5.5. *US*, unconnected vascular strand.

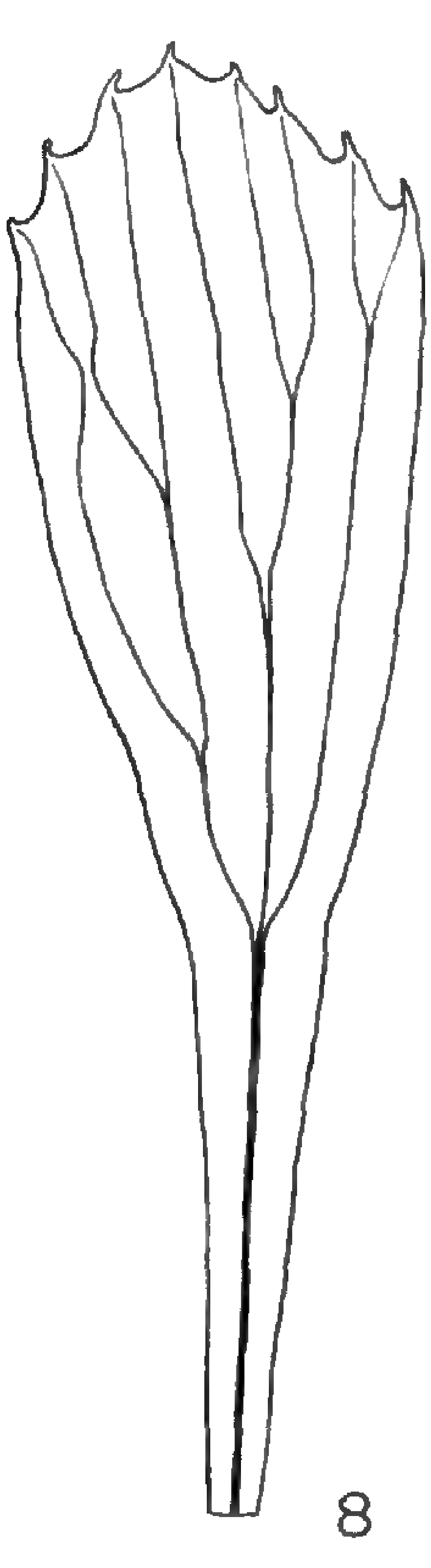
PLATE V

FIGS. 20–24. FIG. 20. Leaf illustrating approximation between marginal vein (at right) and adjacent branch of second order vein-dichotomy. This type of vein approximation is shown diagrammatically in FIG. 6, × 6. FIGS. 21–23. Various examples of Type V anastomoses morphologically related to the kind of vein approximation shown in FIG. 20. FIG. 21. Primary leaf in which a vein anastomosis produced a large marginal areole, × 4.5. FIG. 22. Floral bract with a smaller anastomosis similar in position and type to that shown in FIG. 21, × 7. FIG. 23. Conspicuous Type V anastomosis in upper central region of lamina, × 5.5. FIG. 24. Leaf with very uncommon type of vein approximation (at left margin) in which the branches of a single vein-dichotomy converge and then separate without xylem-fusion, × 4.8. *rt*, rudimentary marginal tooth; *US*, unconnected vascular strand.



FOSTER, CIRCAEASTER

Plate II



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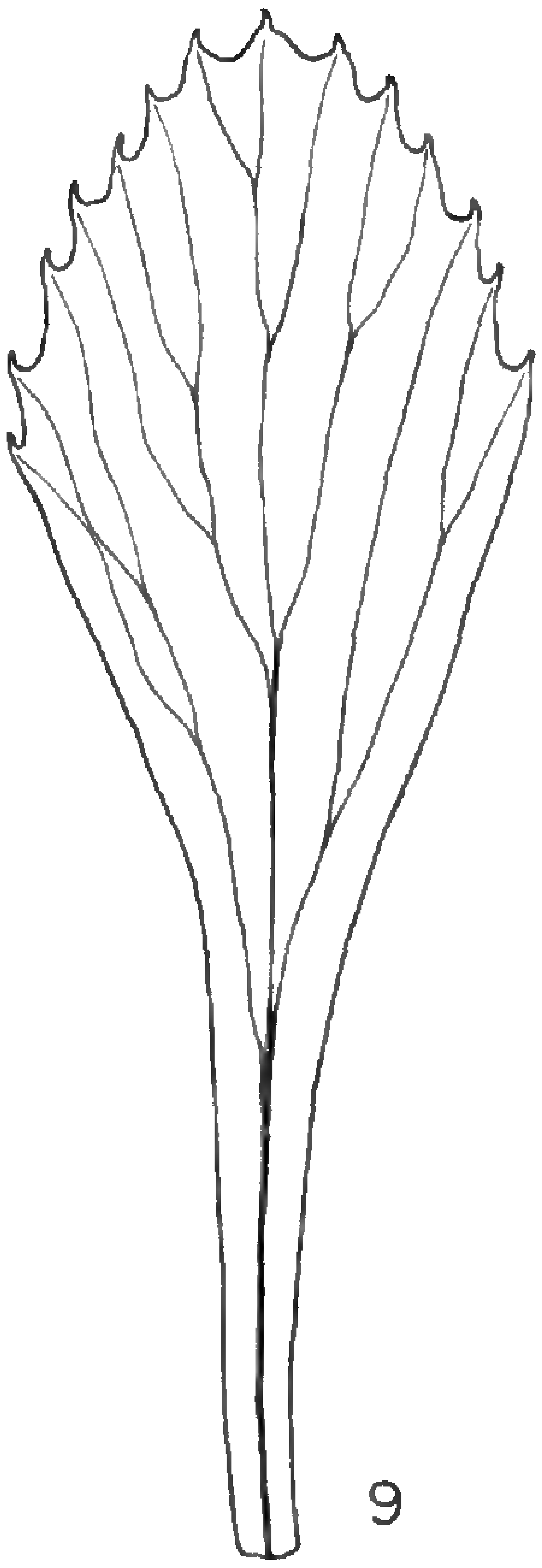

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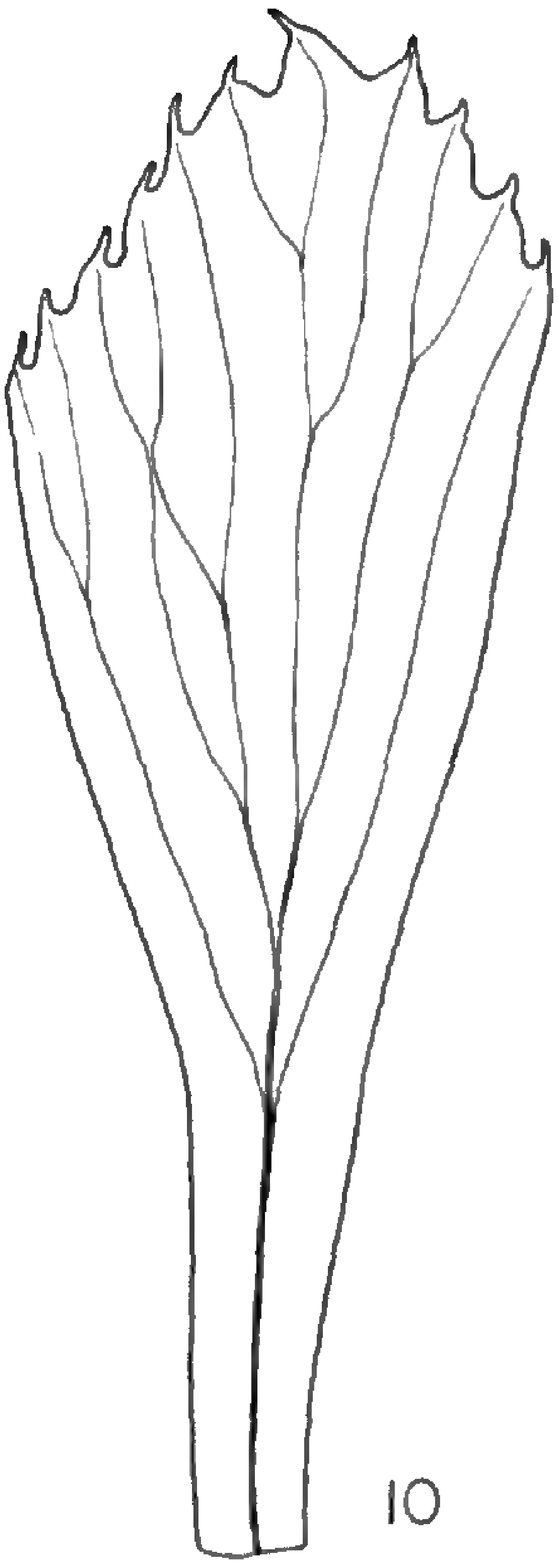

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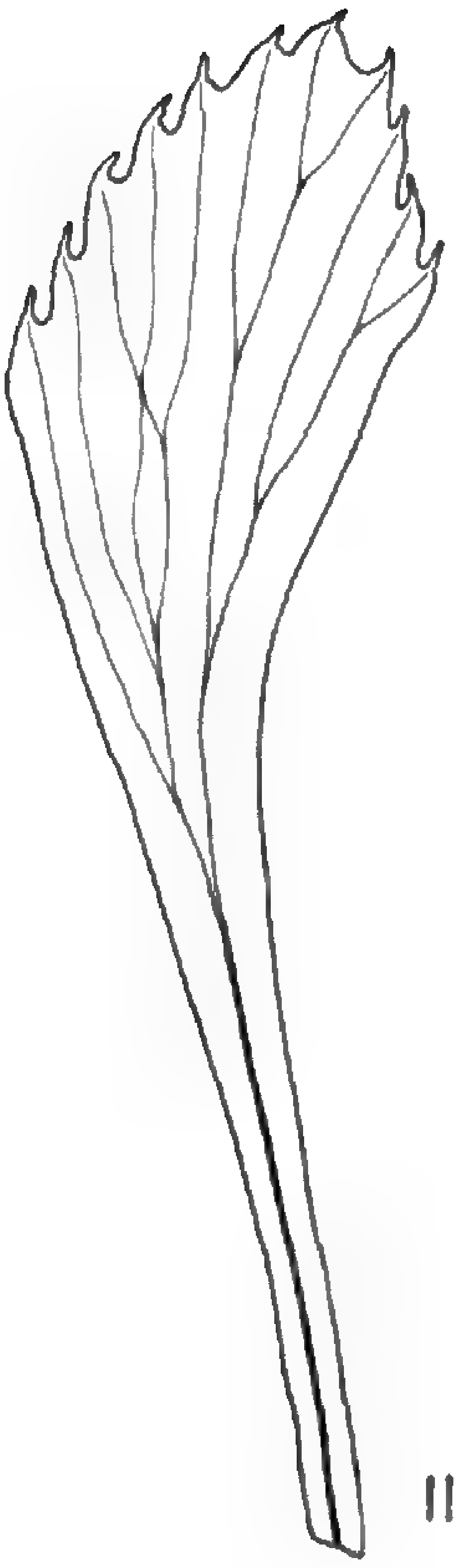

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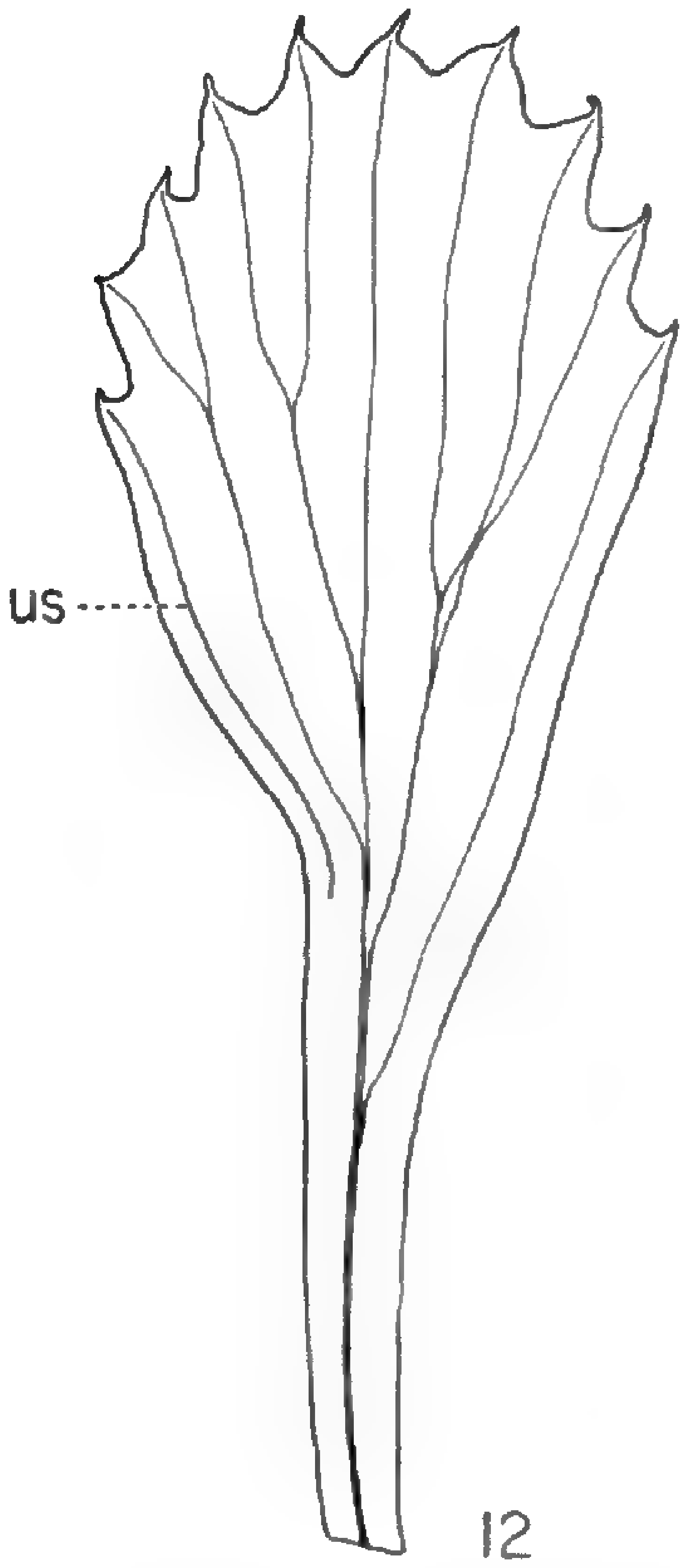

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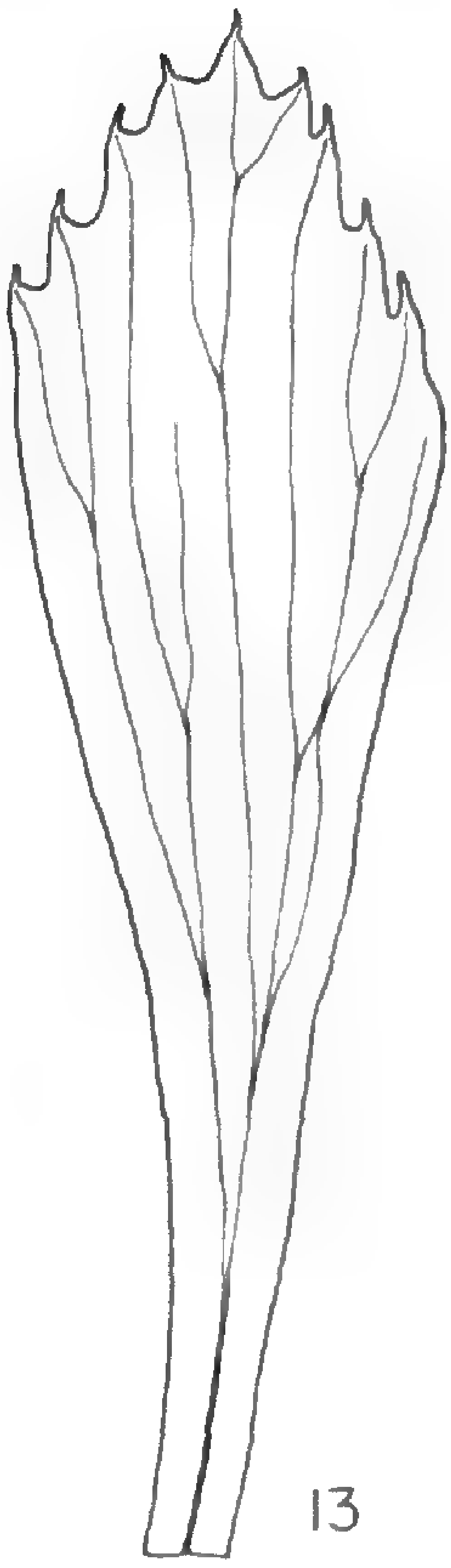

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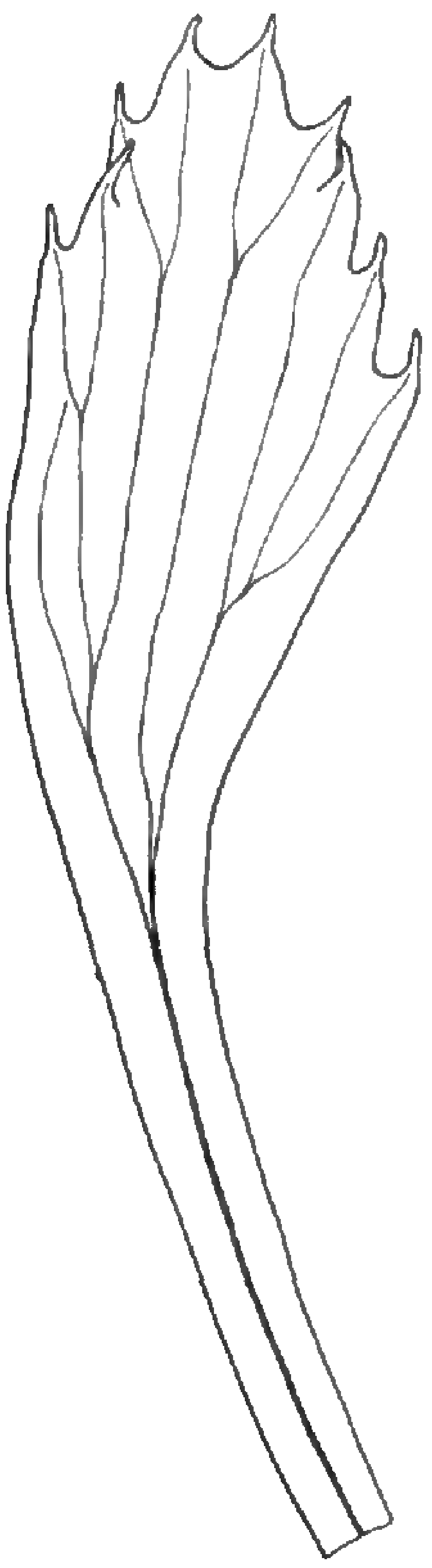
Foster, Circaeaster

Foster, Circaeaster



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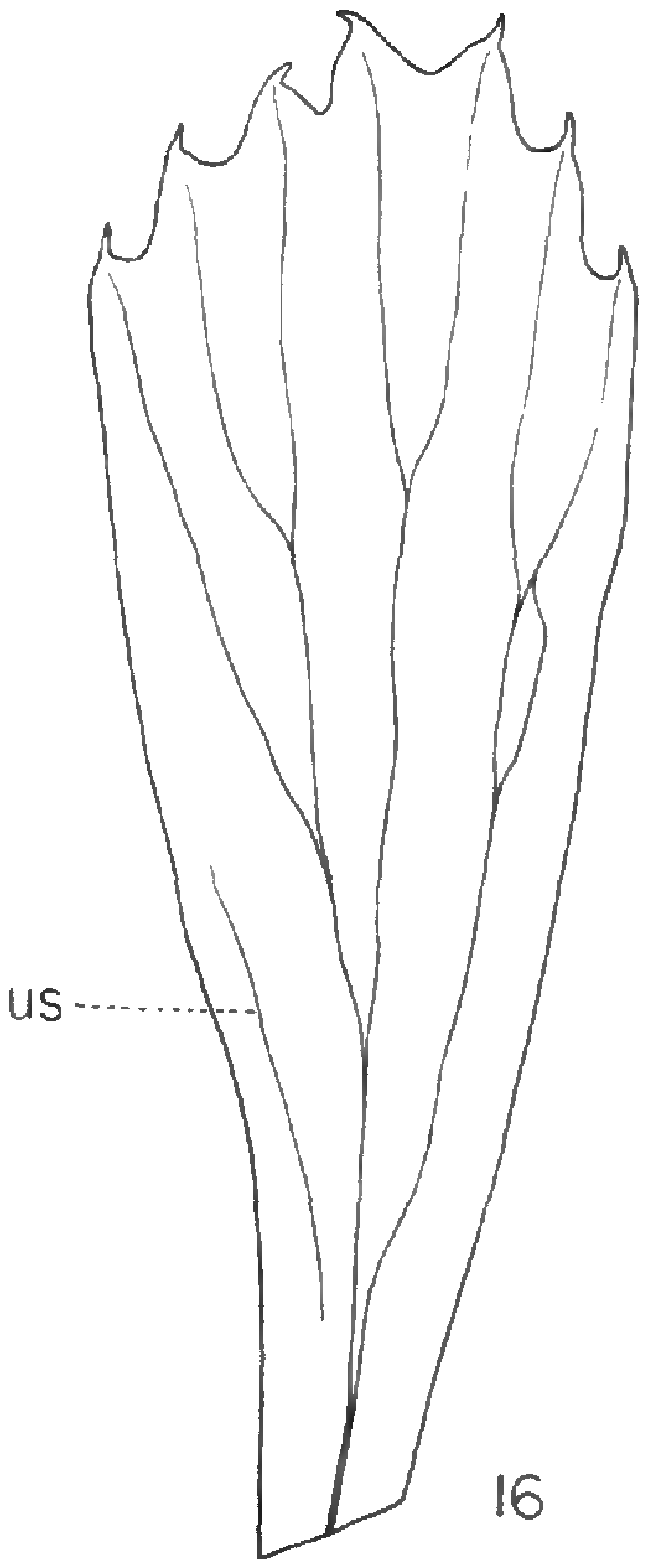

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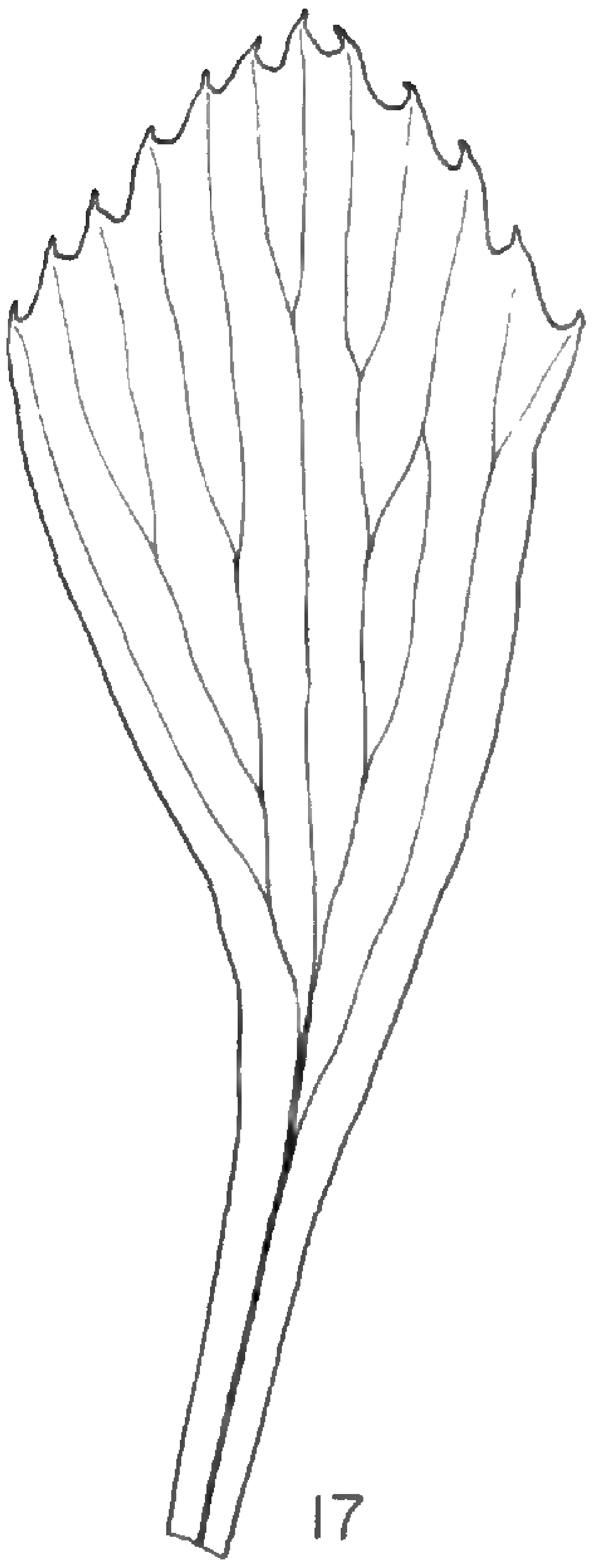

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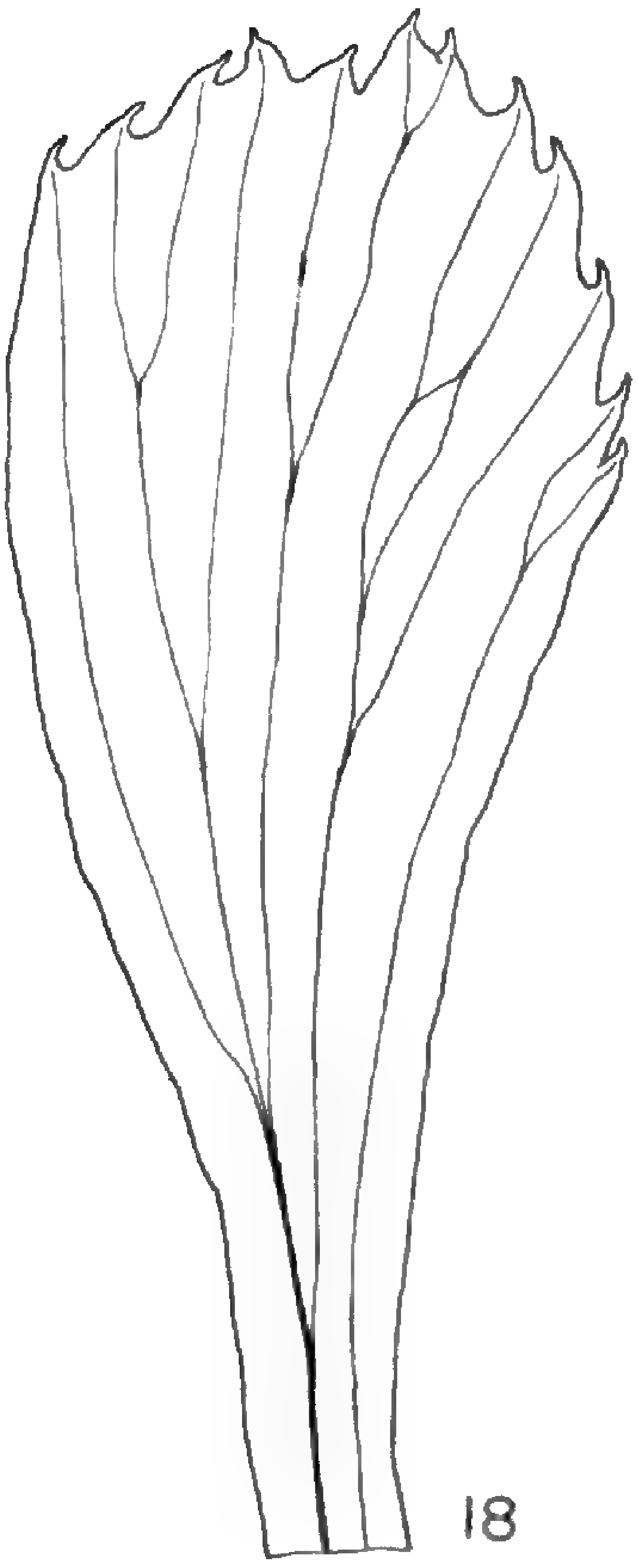

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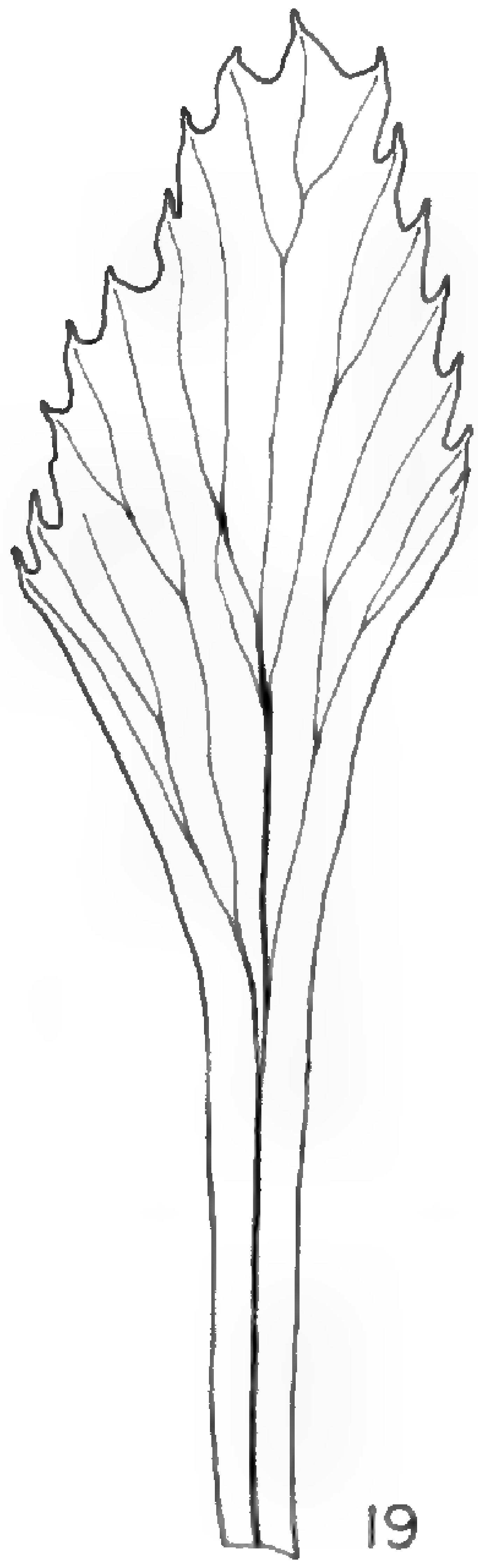

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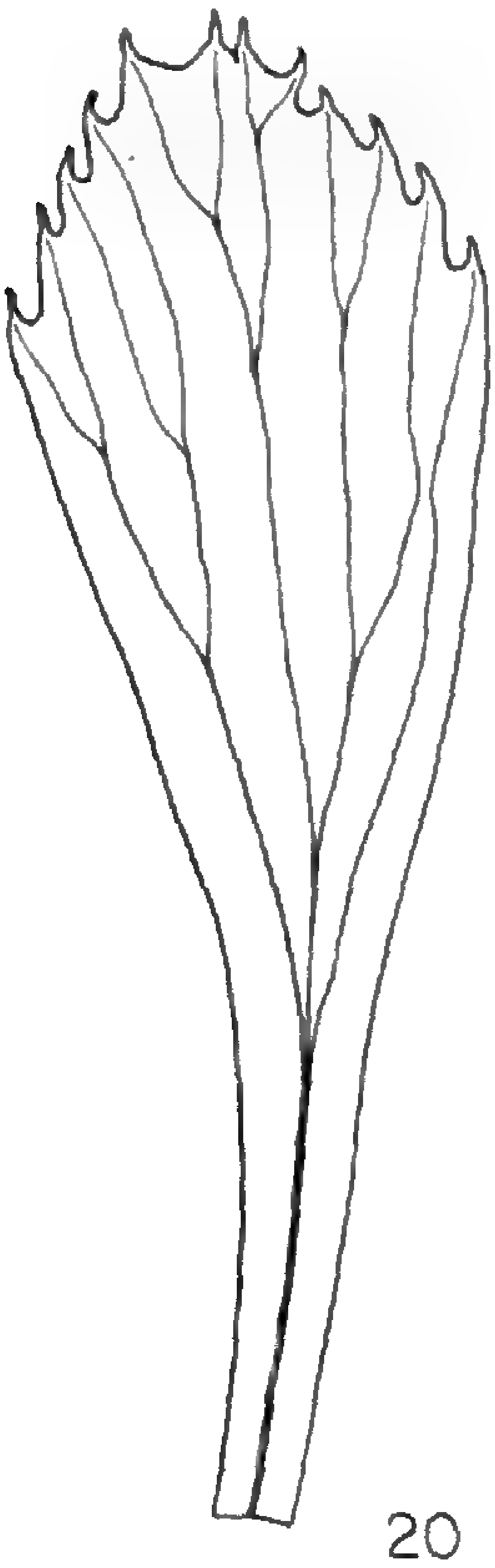
Foster, Circaeaster



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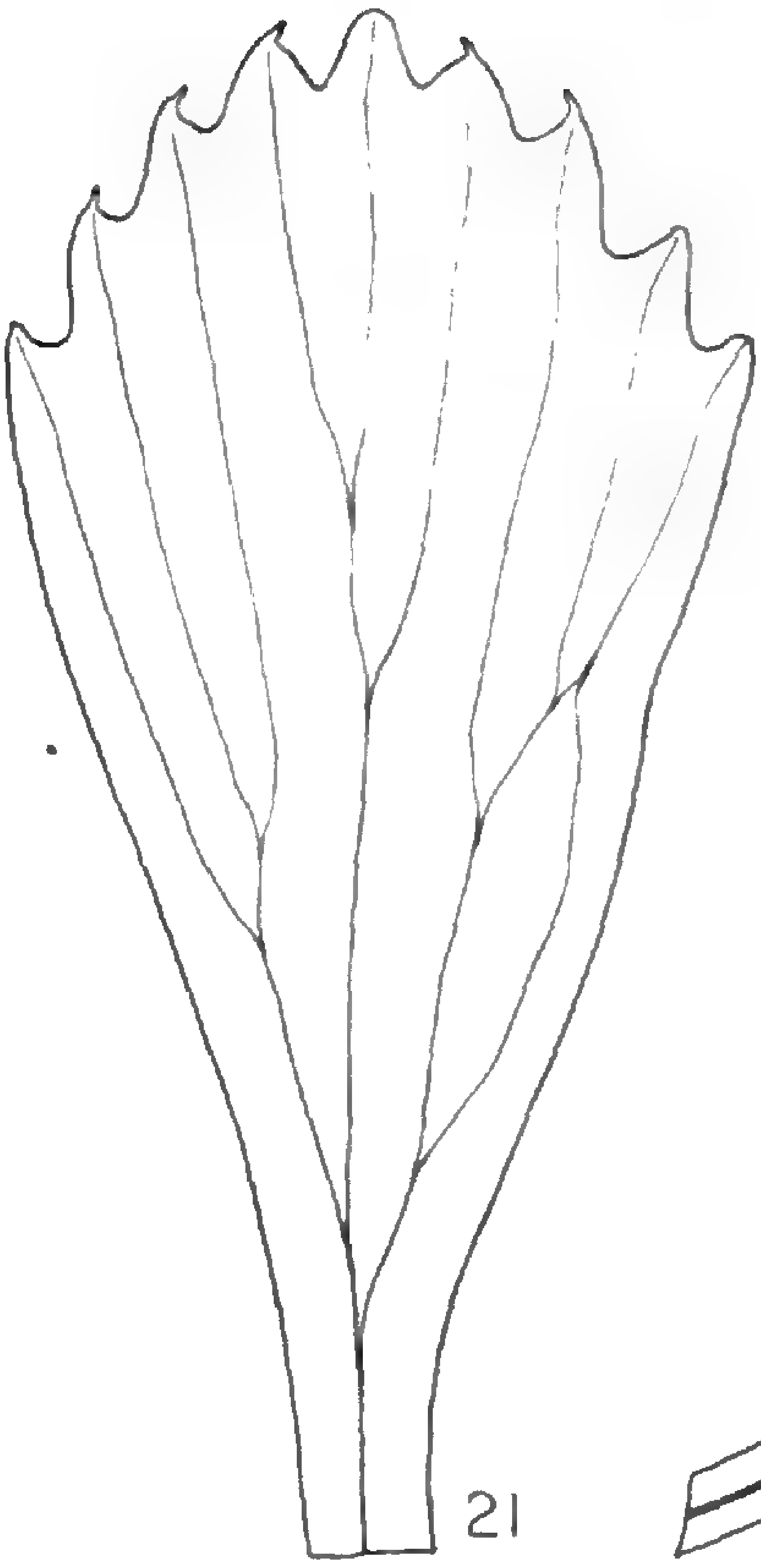

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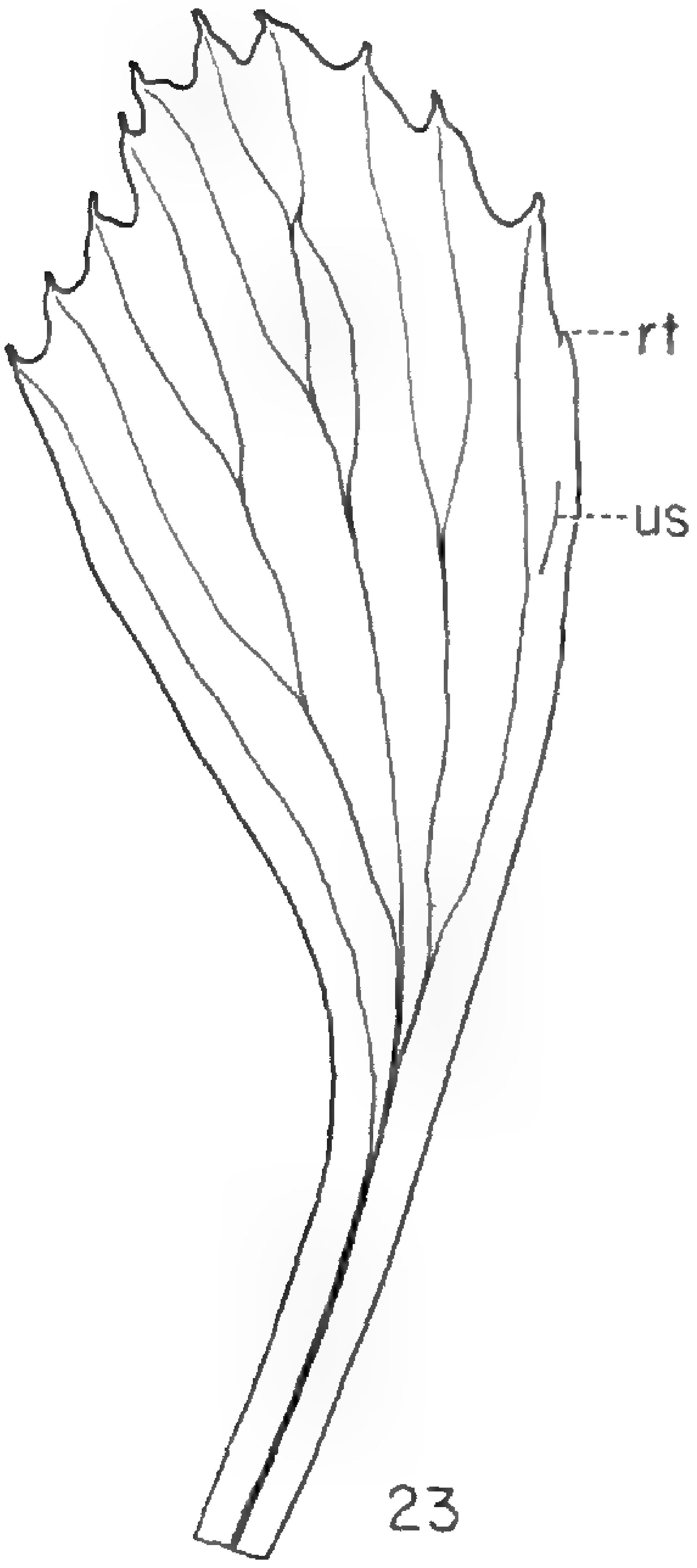

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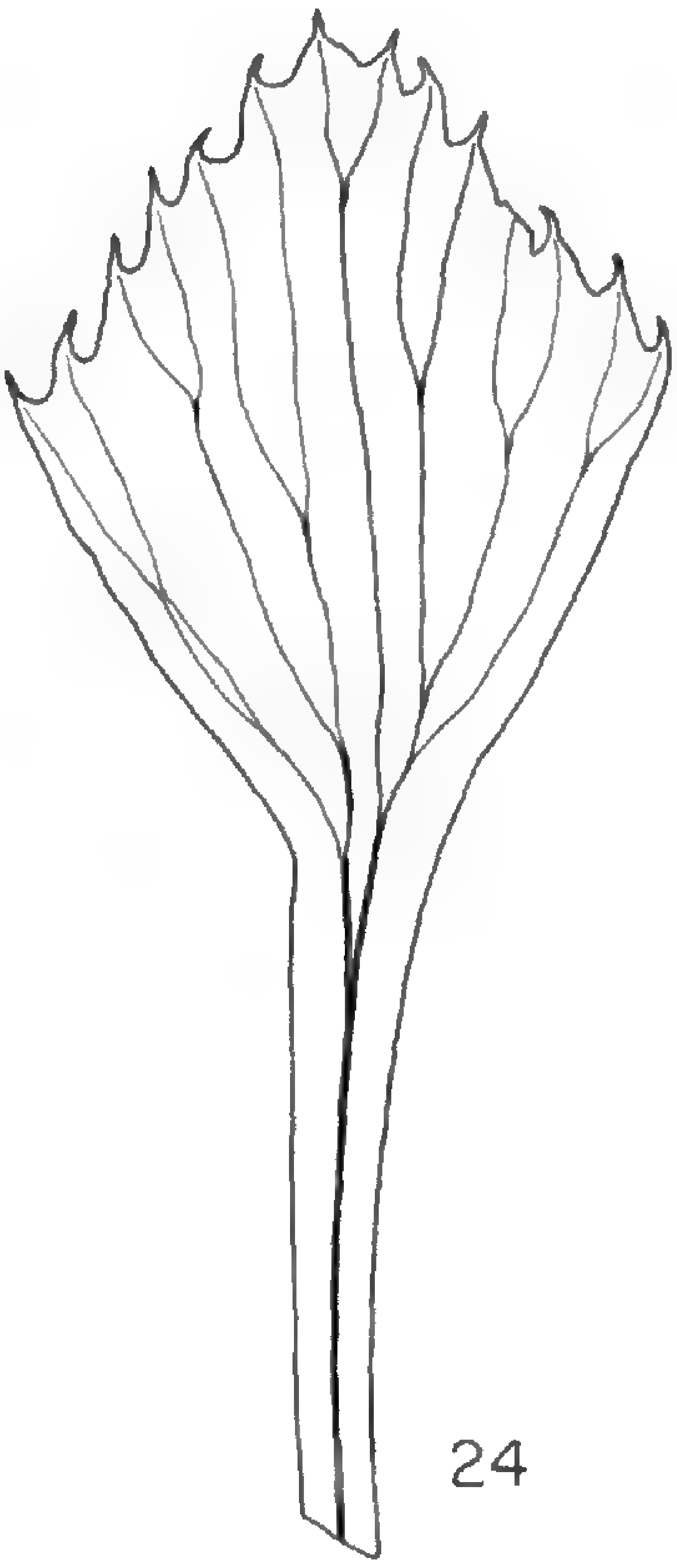

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Foster, Circaeaster

A SYNOPSIS OF THE ASIAN SPECIES OF DELPHINIUM, SENSU STRICTO *

PHILIP A. MUNZ

GROUP VII

Like Group VI, but the leaves all basal; none, or rarely one, cauline; finely dissected into laciniae mostly 1–3 mm. wide.

Not corresponding to any of the taxonomic subdivisions proposed for the genus.

KEY TO SPECIES

1. Spur not as long as the blade of the upper sepal; plants to 2.5 dm. tall.
    2. Stem strigulose in upper part; leaf blades 3–6 cm. across; sepals deep violet, minutely strigulose, 2–3 cm. long; spur 15–20 mm. long. Yunnan. .... 133. ***D. likiangense.***
    2. Stem sparsely stiff-hairy; leaf blades 2–3 cm. across; sepals pale blue, yellow-hairy, ca. 3 cm. long; spur 20–25 mm. long. Tibet. .... 130. ***D. chrysotrichum.***
1. Spur equal to or longer than blade of upper sepal.
    3. Plant not more than 1.5 dm. tall; flowers 1–3 on a stem (several in *D. souliei*); leaf blades 1–2 cm. in diameter.
        4. Spur 3 cm. long; sepals greenish purple; upper petals sordid yellow. Sikang. .... 132. ***D. hui.***
        4. Spur 2–2.4 cm. long; sepals blue to purplish blue; petals bluish. Szechwan.
            5. Flowers mostly several in an elongate raceme; pubescence spreading. .... 138. ***D. souliei.***
            5. Flowers solitary at end of scape; pubescence retrorse. .... 137. ***D. sino-scaposum.***
    3. Plant taller; flowers often more numerous; leaves larger.
        6. Axis of inflorescence and the pedicels quite glabrous except for a few hairs just below the flowers.
            7. Sepals about 20 mm. long; spur 25 mm. long; petals bluish. Yunnan. (Treated under Group VI). .... 82. ***D. autumnale.***
            7. Sepals 14–16 mm. long; spur 19–21 mm. long; petals black. Szechwan. .... 131. ***D. erlangshanicum.***
        6. Axis of inflorescence and the pedicels more generally pubescent.
            8. Upper sepal 23–24 mm. long; spur 27 mm. long. Szechwan. .... 136. ***D. saxatile.***
            8. Upper sepal 12–20 mm. long.
                9. Bracteoles well below the flower.
                    10. Upper petals entire at the tip; leaf laciniae 2–3 mm. wide. Yunnan. .... 135. ***D. pycnocentrum.***

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* Continued from volume 48, p. 545.

10. Upper petals 2-toothed; leaf laciniae 1 mm. wide. Szechwan. .... 138. *D. souliei.*

9. Bracteoles almost against the flower; upper petal emarginate at tip.
   11. Sepals 11–14 mm. long; spur 19–24 mm. long; petals blue.
      12. Upper petals emarginate at tip; follicles pubescent. Yunnan. .... 134. *D. pycnocentroides.*
      12. Upper petals entire at tip; follicles glabrous. Tibet. .... 140. *D. thibeticum.*
   11. Sepals 15–18 mm. long; spur 14–20 mm. long; upper petals yellowish. Shensi. .... 139. *D. taipaicum.*

130. **Delphinium chrysotrichum** (sphalm. *chrysotricum*) Finet & Gagnep. Bull. Soc. Bot. France **51**: 488. *pl. vii, B.* 1904. FIG. 12, A.

Delphinium chrysotrichum var. *pygmaeum* Ostenfeld in Hedin, Southern Tibet 6(3): 79. *pls. 1, 2.* 1922. (A list of flowering plants from inner Asia collected by Dr. Sven Hedin [compiled by Ostenfeld & Paulsen]).

Low, to 1.5 dm. tall, subprostrate, divaricately branched, sparsely stiff-pubescent above, subglabrous below, striate; leaves all radical; petioles ca. 5 cm. long, dilated at base; the hairy blades to 3 cm. in diameter, roundish, 3-parted into cuneate segments, the 2 lateral 2-lobed, the middle one 3-lobed, the lobes 3–5-toothed at the apices, obtuse, mucronate; flowers 1–2 on a branch; bracts pubescent, ca. 1 cm. long, petioled, 3-parted into narrow lobes; pedicels 2–7 cm. long, pubescent; bracteoles 2, pubescent, lance-oblong, obtuse, ca. 1 cm. long, placed near the middle of the pedicel; flowers pale blue, yellow-hairy without; upper sepal broad-ovate, 25–30 mm. long, obtuse, the spur straight or slightly curved, 20–25 mm. long, 6 mm. wide at base, obtuse; lateral sepals elliptic, 25 mm. by 12 mm., pubescent, emarginate-truncate at tip; lower sepals 25 mm. by 14 mm., obtuse; upper petals with the limb almost straight, glabrous, emarginate at apex, 15–17 mm. long, the spur 20–22 mm. long; lower petals oblique, the limb oblong, 7 mm. by 6 mm., 2-lobed over half its length, bearded over most of lower part, sparsely short ciliate, the claw 6–7 mm. long; stamens glabrous; follicles 3, bearded.

TYPE: Tibet, prov. Batang, Zambala, Aug., 1903, *Soulié 3039* (P); seen.

ILLUSTRATION. Var. *pygmaeum* OSTENFELD in Ostenf. & Paulsen, List Fl. Pl. Inner Asia. *pl. 1, 2.* 1922.

EXAMPLES SEEN. **Tibet oriental:** Yargong, Batang province, *Soulié 3904* (P), *3905* (P).

131. **Delphinium erlangshanicum** W. T. Wang, Acta Bot. Sinica **10**: 86. 1962.

About 3 dm. tall; leaves about 4, basal, long petioled, glabrous; blades broadly rounded or round-ovate, 6.5–9 cm. wide, the ultimate lobules linear, 1.5–2.5 mm. wide, revolute, entire or 1-lobuled; petioles 14–18 cm.

long, broad-vaginate at base; scapes erect, 3 dm. tall, retrorsely crisped-pilose and with looser yellow hairs intermixed, racemiferous above the middle; racemes ca. 6-flowered, lax; lower bracts 22 mm. long, lanceolate, the upper 13–16 mm. long; pedicels 2–6 cm. long, suberect, slightly incurved; bracteoles near the flowers, lanceolate, 10–11 mm. long, 1.6–1.8 mm. wide, puberulent; flowers suberect, blue; sepals ovate or elliptic-ovate, puberulent, 14–16 mm. long; spur 19–21 mm. long, subulate, 3.5–4 mm. wide at base, strongly decurved; upper petals black, bifid into lanceolate lobes, loosely ciliate; lower petals black, the limb narrow-elliptic, bifid to below the middle into narrow lanceolate lobes, silky villous above the base; stamens glabrous; carpels 3, densely puberulent.

TYPE: Erlangshan, Tienchuan, Szechwan, *W. K. Hu* no. *37800* (PE), not seen; photograph (E) seen.

132. **Delphinium hui** Chen, Bull. Fan Mem. Inst. Biol. Peiping (n.s.) 1: 173. 1948.

Stem 3–3.5 cm. long, with long dense hairs; leaves all radical, long petioled, deeply 3-partite, 1.5 cm. long, 2 cm. wide, the parts 3-lobed, cuneate, the lobes ovate-acute, densely pubescent above, long-pilose beneath; peduncles 3 cm. long, long white-villous; flower horizontal, solitary, greenish purple; sepals round-ovate, the upper and 2 lower prolonged into a short tip, the 2 lateral rhombic-rounded, densely pilose without, sparsely so within, ciliate on margin; spur 3 cm. long, straight or somewhat decurved, densely hairy; upper petals sordid yellow, the laminae 6 mm. long, ovate, acute, the spur almost as long as the sepal spur; lower petals bluish yellow, the laminae oblong-ovate, apically bifid, pilose and ciliate; stamens 5 mm. long, the filaments ciliate; carpels 3, glabrous with styles 6 mm. long.

TYPE: S. Sikang, Konkaling, Chandoye, at 4500 m., *T. T. Yü 13101*, Aug. 31, 1937 (PE?), not seen. Described as having the general appearance of a violet-colored pansy.

133. **Delphinium likiangense** Franchet, Bull. Soc. Philom. Paris VIII. **5**: 180. 1893. FIG. 12, B, C.

Delphinium oliganthum Franchet, Pl. Delavay. 1: 29. *pl. 8.* 1899; not Boiss., 1867.

Perennial from a creeping woody rhizome, the stem subglabrous, simple. 1–2.5 (–5) dm. tall, strigulose in upper part; leaves basal, or sometimes also 1 above; petioles 5–12 cm. long, slender, glabrous, dilated at base; leaf blades 3–6 cm. wide, subglabrous, thickish in texture, divided nearly or quite to the base into 5 segments which are in turn deeply divided into subobtuse linear lobes 2–3 mm. wide; flowers 1–3–5 on long pedicels, the bractlets lanceolate, commonly 1.5–2 cm. long, 3–5 mm. wide, placed just below the sepals; sepals deep violet, broad, minutely strigulose; upper sepal 2–3 cm. long, 1.5–2 cm. wide, broadly ovate, obtuse, the spur

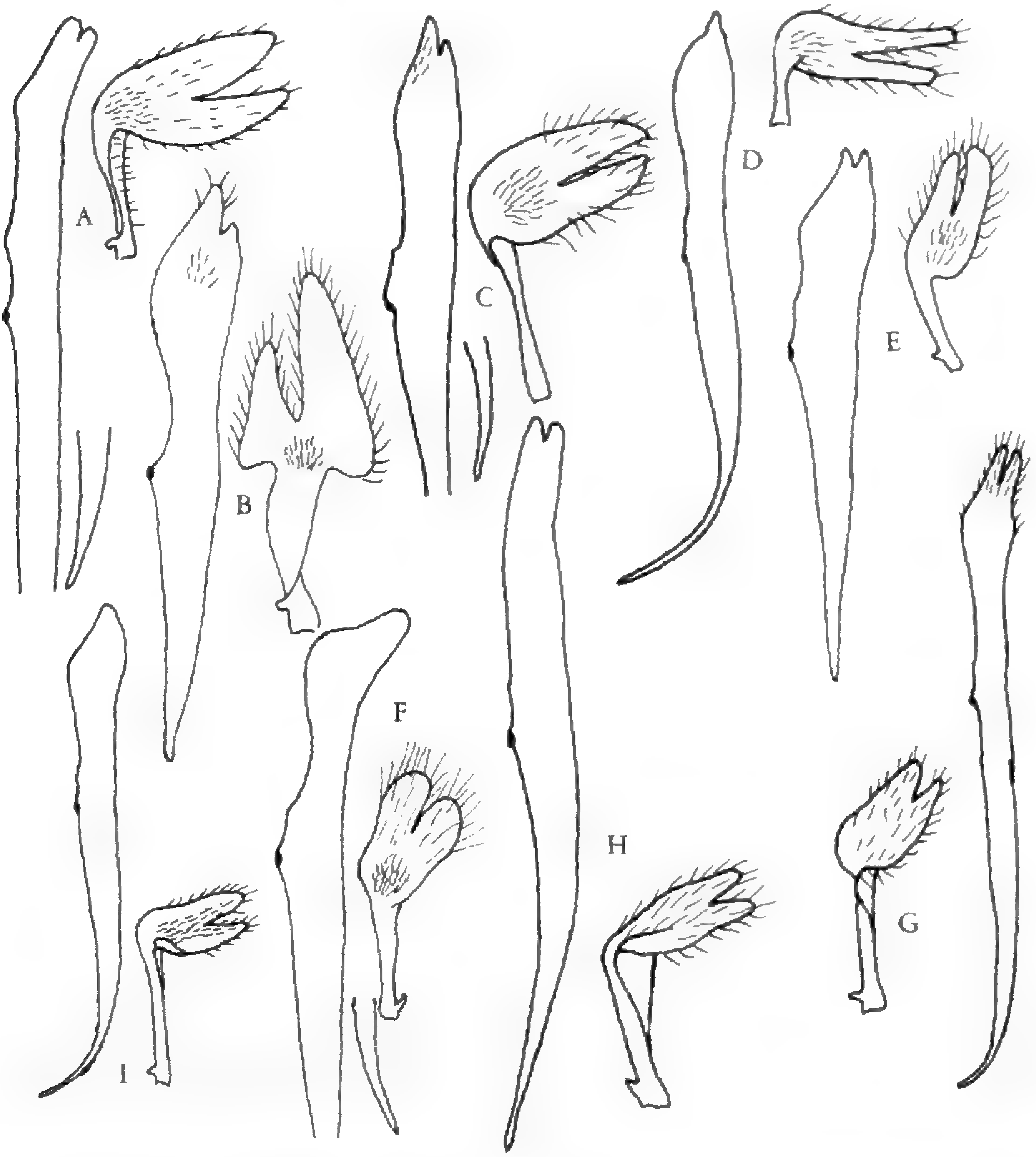

FIGURE 12. **Delphinium,** GROUP VII. Petals, the upper spurred, the lower clawed. A. *D. chrysotrichum*; blade of upper petal 15 mm. long, spur 22 mm.; blade of lower petal 7 mm. long, claw 7 mm.; drawn from *Soulié* 3039 (P). B. *D. likiangense*; blade of upper petal 15 mm. long, spur 15 mm.; blade of lower petal 10 mm. long, claw 7.5 mm.; drawn from *Delavay 2201* TYPE (P). C. *D. likiangense*; blade of upper petal 15 mm. long, spur 23 mm.; blade of lower petal 10 mm. long, claw 7 mm.; drawn from *Schneider 3251* (GH). D. *D. pycnocentroides*; blade of upper petal 11 mm. long, spur 19 mm.; blade of lower petal 8 mm. long, claw 5 mm.; drawn from *Rock 17319* (US). E. *D. pycnocentroides*; blade of upper petal 10 mm. long, spur 16 mm.; blade of lower petal 7 mm. long, claw 5 mm.; drawn from *Forrest 6643* (P). F. *D. pycnocentrum*; blade of upper petal 12 mm. long, spur 22 mm.; blade of lower petal 6 mm. long, claw 5 mm.; drawn from *Delavay 4220* (P). G. *D. souliei*; blade of upper petal 14 mm. long, spur 21 mm. long; blade of lower petal 6 mm. long, claw 8 mm.; drawn from *Soulié 2388* (NY). H. *D. souliei*; blade of upper petal 16 mm. long, spur 21 mm.; blade of lower petal 6.5 mm. long, claw 9 mm.; drawn from *Harry Smith 4048* (NY). I. *D. thibeticum*; blade of upper petal 10 mm. long, spur 18 mm.; blade of lower petal 5 mm. long, claw 6 mm.; drawn from *Soulié 3049* (P).

straight, horizontal, 15–20 mm. long, ca. 5 mm. wide at the base, narrowed to an acute point; lateral sepals 18–22 mm. long, 14–15 mm. wide, rounded at the tip; lower sepals 25–30 mm. long, 15–20 mm. wide, pointed; upper petals blue, the laminae almost straight, unequally 2-toothed, often with a few short hairs and ca. 15 mm. long, narrow, the spur 16–20 mm. long, straight; lower petals with a claw 6–7 mm. long, the lamina narrowly oblong-ovate, bearded, ca. 10 mm. long, cleft into 2 lance-oblong lobes ca. 5 mm. long; stamens 8–10 mm. long, the filaments slightly ciliate; anthers dark, 1 mm. long; follicles 3, finely hairy, 12–14 mm. long, 5 mm. wide, the styles an additional 1.5 mm.; seeds gray-brown, subglobose, 2–2.5 mm. long, longitudinally winged at the angles.

TYPE: Yunnan, on calcareous hills of Likiang, Suee-chan, at 4000 m., *Delavay 2484* and *2201*. At Paris number *2201* is designated as TYPE and has the parts dissected and drawn.

ILLUSTRATIONS. Plantae Delavayanae 1: *pl. 8*. 1889 as ***D. oliganthum***; Gardeners' Chronicle III. **60**: 128. 151. 1916.

DISTRIBUTION. About 3200 to 4600 m., in Yunnan, apparently largely in the Likiang or Lichiang Snow Range.

EXAMPLES. *C. Schneider 3251, 2928, 3774*; *G. Forrest 11360, 11052, 11203, 22291, 16949, 3768, 6634, 6483, 2903, 15322, 15170*; *Rock 25330, 24920, 24914, 17332, 6111, 10665, 10792, 10409, 11413, 11435, 5242, 9867*; *Ching 30572*.

134. **Delphinium pycnocentroides** W. T. Wang, Acta Bot. Sinica **10**: 163–164. 1962. FIG. 12, D, E.

Delphinium thibeticum Finet & Gagnep. var. ***schizophyllum*** Hand.-Mazz. Symb. Sinicae **7**: 275. 1931. Based on *Handel-Mazzetti 4100* from near Lidjiang (Lichiang) (W), not seen; but his no. *7671* was also cited, and that I have seen (E, GH).

Stem 3–8 dm. tall, 2–4.5 mm. thick at base, terete, densely retrorse-strigulose, sometimes glabrous below, simple or rarely 1-branched; basal leaves ca. 3, long petioled, the leaf blades suborbicular or round-reniform, 8–12 (–20) cm. wide, cordate, trisect, the middle segment rhombic-obovate, cuneate at base, petiolulate, twice subpinnately parted, the ultimate lobes lance-linear, 1.4–5 mm. wide, slightly revolute; lateral segments obliquely flabellate, twice as wide as the middle one, narrow-cuneate at base or sometimes petiolulate, unequally 2-parted, the upper parts like those of the middle segment, but more or less oblique; petioles 8–18 (–24) cm. long, glabrous, narrow-vaginate; cauline leaf 1, smaller than basal; racemes, elongate, narrow, 5–many-flowered, lax; pedicels 2–6 cm. long, divergent, densely strigulose and with few spreading yellow glandular hairs; bracteoles next to the flower, lanceolate, 6.5–11 mm. long, 1.2–1.6 mm. wide, purplish blue, ciliate; sepals elliptic-ovate or -obovate, purplish blue, 12–14 mm. long, puberulent; spur 19–24 mm. long, cylindric-subulate or subulate, 2–3 mm. thick at base, obtuse, straight or strongly decurved; upper petals blue, emarginate or bilobulate, glabrous; lower petals blue, the laminae narrow-elliptic, bifid into 2 obtusish lance-deltoid lobes below the middle, long-ciliate, yellow bearded at base; filaments loosely ciliate to glabrous; follicles 3, spreading-pubescent, 12–14 mm. long, the styles an additional 2.5 mm.; seeds obovate-triquetrous, 1.5–2.5 mm. long, brown, winged on the angles.

TYPE: From Yunnan, *K. M. Feng 9033*, Aug. 15, 1942 (PE?), not seen.

RANGE. In Yunnan, especially about the Lichiang Range, at elevations of 3500 to 4500 m.

EXAMPLES. *Forrest 6533*; *Rock 17338, 10657, 17319, 10813, 6135, 5787, 10670*; *C. Schneider 2278*; *Handel-Mazzetti 7671*; *T. T. Yü 13822*; *K. M. Feng 2125*; *R. C. Ching 30566.*

Wang described also var. ***latisectum*** (Acta Bot. Sinica **10**: 164) with hairs of stems spreading; leaf segments broader; based on *C. W. Wang 66226*, which I have referred to *D. tatsienense.*

135. **Delphinium pycnocentrum** Franchet, Bull. Soc. Bot. France **33**: 379. 1886. FIG. 12, F.

Delphinium lankongense Franchet, Bull. Soc. Bot. France **33**: 378. 1886. Based on *Delavay* no. *1844*, Oct. 12, 1885, Mt. Hee-chan-men (Lankong) (P, UC), both seen.

Delphinium pycnocentrum var. *lankongense* (Franchet) Huth, Bot. Jahrb. **20**: 465. 1895.

Perennial, from a rather woody root; stem erect, mostly simple, 2–9 dm. tall, subglabrous below to strigose or spreading-pubescent with rather long fine hairs, more densely strigose and pubescent above, the spreading hairs more or less enlarged and yellowish at the base; leaves basal, the petioles often purplish, 1–3 dm. long, subglabrous to strigulose and spreading-hairy, strongly dilated at the base; blades to 12 cm. in diameter, rounded-pentagonal in outline, 5-parted to the base, then deeply incised into numerous lance-linear lobes 2–4 mm. wide, sharply acute, subglabrous to ciliate; inflorescence racemose, few to many flowered, secund, peduncled, to 3 dm. long, strigose and with spreading hairs pustulate at the base; bracts entire to trifid, erect, 1–4 cm. long, mostly lanceolate; pedicels strict, appressed, 1–6 cm. long; bracteoles linear to linear-lanceolate, situated well below the flower; calyx bluish purple, pubescent; upper sepal oblong-obovate, 15 mm. long, 10 mm. wide, ending in an apiculate tip, the spur 25–28 mm. long, somewhat decurved, 3 mm. wide at the base, gradually narrowed to a finely pointed tip; lateral sepals rhombic-ovate, 14 mm. long, 9 mm. wide, obtuse, pubescent along midvein; lower sepals asymmetrically obovate, 13 mm. long, 6 mm. wide, obtuse, pubescent; upper petals blue, the blade somewhat oblique, 11 mm. long, 4 mm. wide, rounded, entire at tip, the spur 25 mm. long; lower petals bluish, the limb obovate-oblong, 7 mm. long, 5 mm. wide, cleft from 2 to 4.5 mm., bearded and ciliate, the claw 5 mm. long; stamens 7–7.5 mm. long, glabrous; anthers dark, 1.5 mm. long; follicles 3, somewhat pubescent to subglabrous, erect, 15–18 mm. long, ca. 4 mm. thick, the styles an additional 3.5 mm.

TYPE: Yunnan, in silvis montis Yang-in-chan, prope Lankong, alt. 3000 m.; *Delavay 993*, Oct. 8, 1884 (holotype P, isotype K); both seen.

Another collection referable to this species is from Yunnan, "au col de Huchan-men," *Delavay 4220* (P).

136. **Delphinium saxatile** W. T. Wang, Acta Phytotax. Sinica **6**: 367. 1957.

Perennial, scapose, the leaves all basal; leaf blades broadly cordate-pentagonal in outline, 2.5–7 cm. long, 3.5–7.5 cm. wide, 5-fid into obovate parts with cuneate base and 3–5 deep lance-linear lobes, these apiculate, loosely hirsute, ciliate, to ca. 5 mm. wide; petioles 6–15 cm. long, hirsute, canaliculate below; stem 2-flowered; bracts leaflike, smaller, the petiole ca. 1.5 cm. long; pedicel to 12 cm. long; bracteoles near its middle, linear, 5 mm. long, ciliate; flowers deep blue, pubescent, the sepals acuminate, ovate-oblong, the upper and lateral 23–24 mm. long, 9–10 mm. wide; spur 27 mm. long, straight or decurved, 3–4 mm. wide at base; lower sepals 28 mm. long, 8.5 mm. wide; upper petals about half as long as the sepals, the blades oblique-truncate, emarginate, ciliate, the spur 25 mm. long; lower petals 12.5 mm. long, the blade bifid to below the middle into 2 ovate-triangular lobes rounded at the apex and ciliate, the laminae yellow bearded near the base, claw ca. 6 mm. long, appendiculate; stamens glabrous, 7 mm. long; carpels 3, velutinous.

TYPE: Szechwan, Pao-hsing-hsien; Kuo-pa-yan, at 2100 m., Aug. 8, 1933. *T. H. Tü 4366* (PE), not seen; photograph (E), seen.

137. **Delphinium sino-scaposum** W. T. Wang, Acta Bot. Sinica **10**: 165. 1962.

Delphinium scaposum W. T. Wang, Acta Phytotax. Sinica **6**: 364. 1957, not Greene, 1881.

Plant 11–16.5 cm. high; leaves all basal, glabrous, long petioled (4–13 cm.); laminae broadly reniform, 1.5–3.5 cm. long, 2–6 cm. wide, trisect, the middle segment broadly rhombic-obovate, basally cuneate-attenuate, 3-parted to below the middle, the ultimate divisions to 3.5 mm. wide; petioles 2–10 cm. long, vaginate; scapes 1-flowered, 9–16 cm. high, retrorse-pubescent; bracts sparsely pilose or trifid, 1.5–1.8 cm. long, the lobes lanceolate or the whole entire; flower purplish blue; pedicel 3–6 cm. long; bracteoles near the flower, lanceolate, 11 mm. long, subglabrous; sepals broadly elliptic, obtuse, 16.5 mm. long, 12 mm. wide, pubescent; spur 22–24 mm. long, 3 mm. thick at base, declinate; upper petals slightly shorter than sepals, upper abruptly narrowed above the middle, emarginate at apex, ciliate, spur as long as sepal spur; lower petals 16 mm. long, the limb divided to the lower third, loosely silky, as long as the claw which is appendaged; stamens glabrous, 7 mm. long; carpels 3, sparsely short-silky.

TYPE: Szechwan, *T. H. Tü 3606* (PE?), not seen; photograph (E), seen.

No specimens available. The author of *Delphinium sino-scaposum* says it resembles *D. likiangense* but has 1-flowered scapes; upper petals emarginate and ciliate, lower not yellow bearded; carpels loosely silky.

138. **Delphinium souliei** Franchet, Bull. Soc. Philom. Paris VIII. 5: 172. 1893. FIG. 12, G, H.

Delphinium paludicola Ulbr. Notizbl. Bot. Gart. Berlin 12: 357. 1935. Based on *H. Stevens 87*, holotype (F), isotype (NY), seen; from Szechwan, Tachienlu to Sachou, via Mouping.

Stems 1–4 dm. tall, slender, erect, finely hairy or pilose, simple; leaves in a basal cluster, the petioles very slender, 2–15 cm. long, subglabrous, vaginate and purplish at base; blades pale green, 1–2 cm. across, unequally many partite, the segments 2–3 times divided into linear lobules 1–2 mm. wide with revolute margins and prominent midvein beneath; flowers mostly 2–15, in a simple elongate raceme; lower bracts frequently vaginate at base, then with few linear lobes, the upper lanceolate, often purple, 1–2 cm. long; pedicels erect, pilose, 3–7 cm. long; bracteoles lance-linear, opposite, about the middle of the pedicel or above; sepals blue, the upper 15–20 mm. long, acutish, pilose, the spur slightly curved, 20–30 mm. long, ca. 5 mm. wide near the base, very gradually narrowed to the blunt tip; lateral sepals oblong-ovate, 14–15 mm. long, 7–8 mm. wide; lower sepals elliptic-ovate, 14–17 mm. long, 7 mm. wide, with an acutish prolongation at the tip; upper petals pale blue, the blade almost straight, 14–16 mm. long, deeply notched to shallowly bilobed, the spur 21 mm. long; lower petals tinged with blue, the blade oblong, sparsely bearded, 6–6.5 mm. long, bifid for ca. 2 mm., the claw broad, 8–9 mm. long; stamens glabrous, 6–7 mm. long; anthers dark, 1–1.5 mm. long; follicles 3, hairy when young, ca. 12 mm. long, reticulate-veined; seeds fuscous, broadly winged, scarcely 1 mm. long.

TYPE: Szechwan, "lieux secs a Tizou, Tché-to-chan, environs de Tatsien-lou," Sept.–Oct., 1891, *R. P. Soulié 364* (P); seen.

DISTRIBUTION. In Szechwan and Sikang, 3500 to 4000 m.

REPRESENTATIVE COLLECTIONS. **Szechwan:** *Mousset 27*; *Soulié 2388*; *E. H. Wilson 4689, 3092, 3092a*; *Harry Smith 4048.* **Sikang:** *Harry Smith 11732, 12056.* Apparently *D. paludicola* was described for taller plants of *Delphinium souliei*.

139. **Delphinium taipaicum** W. T. Wang, Acta Bot. Sinica 10: 164–165. 1962.

Stem ca. 22 cm. tall, 3 mm. thick at base, retrorsely silky-pilose or glabrescent, basal leaves ca. 2, long petioled, the blades pentagonal-reniform, 5–8 cm. wide, trisect, the middle segments sessile, cuneate, trifid to middle, the middle lobes obovate-oblanceolate, trilobulate or entire, the lateral unequally bifid, the lobules ovate, obtusely mucronate, ultimate divisions lanceolate, densely strigulose beneath, loosely villous above; petioles 7–14 cm. long, loosely retrorse-pilose, narrowly vaginate; racemes 2–4-flowered, 4–7.5 cm. long; lower bracts trisect, short vaginate-petiolate, the segments trifid or entire, the others oblong-ovate or lanceolate, 14–16 mm. long; pedicels divergent, 1.5–4 cm. long, densely retrorse-pilose; bracteoles to 2 mm. distant from the sepals, oblong-ovate, 9–12 mm. long, 3–3.5 mm. wide, obtusish, loosely puberulent; sepals purplish, obovate, 15–18 mm. long, loosely puberulent; spur 14–20 mm. long, cylindric-subulate or subulate, slightly decurved; upper petals yellowish, glabrous, emarginate; lower petals purplish, the limb yellow bearded, obovate–elliptic, bilobulate to 1/4 its length, loosely ciliate, claw shorter than limb, appendiculate; stamens glabrous; carpels 3, villous, becoming 15 mm. long; seeds obovoid-triquetrous, 2 mm. long, dark brown, winged on angles.

TYPE: Shensi, Tai-pai-shan, Pa-sian-tai, 3900 m., Sept. 15, 1939, *T. N. Liou & P. C. Tsoong 986* (PE), not seen; photograph (E), seen.

I have had no material of this species which the author differentiates from *Delphinium thibeticum* in its trisect leaves and densely villous carpels; and from *D. pycnocentrum* in the wider laciniae of the leaves, densely retrorse-pilose pedicels, and bilobed lower petals.

140. **Delphinium thibeticum** Finet & Gagnep. Bull. Soc. Bot. France **51**: 489. 1904. FIG. 12, I.

Delphinium thibeticum var. *subintegrum* Finet & Gagnep. Bull. Soc. Bot. France **51**: 489. 1904. Based on *Soulié 3044*, E. Tibet, between Zambal & Yargong, (P); seen.

Perennial, 6–10 dm. tall, from rather woody roots; stem slender, leafless or with 1 leaf, mostly simple, subglabrous or with scattered retrorse hairs, these becoming more numerous upward and strigulose in the inflorescence; leaves 5–7; petioles slender, to 12 or 15 cm. long, dilated at base; blades sparsely pubescent below, glabrous above, 5–10 cm. in diameter, broader than long, divided almost to base into narrowly cuneate segments, these 3-parted to about the middle and each part with 2–3 lance-oblong lobules to ca. 1 cm. long, 3–4 mm. wide, mucronate; inflorescence a simple, rather lax, many flowered raceme or with 1 or 2 smaller branches; bracts mostly entire, lance-oblong, 7–10 mm. long; pedicels ascending to suberect, strigulose, 1.5–5 cm. long; bracteoles subtending the flower, 4–5 mm. long, lance-oblong; flowers deep blue, rather loosely short-pubescent; upper sepals oblong-ovate, 11 mm. long, 7 mm. wide, apiculate, the spreading-decurved spur 20–22 mm. long, 2.5 mm. wide at the base, slender; other sepals ca. 11 mm. by 6 mm., elliptic-obovate, obtuse; petals bluish, the upper lamina rather straight, 100 mm. long, 3 mm. wide, entire at the glabrous tip, the spur 19–20 mm. long; lower laminae rather narrow-oblong, 5 mm. long, 2.5 mm. wide, short bearded from the middle out, short-ciliate, bifid 1/3 its length into lanceolate lobes, claw 6 mm. long, appendiculate; stamens glabrous; carpels 3, becoming ca. 12 mm. long, the styles an additional 3 mm.

TYPE: Eastern Tibet, Batang province, Yargong, *Soulié 3049* (P); seen.
COLLECTIONS SEEN. **Yargong:** *Soulié 3893* and *3894*.

GROUP VIII

Heavy-rooted perennials. Leaves with the ultimate divisions lanceolate to ovate, mostly over 5 mm. broad. Sepals not persistent and membranous. Petals blue or paler, not almost black. Spur usually not strongly curved.

This is a purely artificial group, not corresponding to any of the taxonomic divisions of the genus.

KEY TO SPECIES

1. Spur obviously longer than the blade of the upper sepal.
  2. Stem and axis of inflorescence glabrous.
    3. Lamina of upper petal ca. 7 mm. long. Siberia. . . 163. *D. laxiflorum.*
    3. Lamina of upper petal 9–12 mm. long. China.
      4. Upper sepal 14–15 mm. long.
        5. Bracteoles paired near the summit of the pedicel, sometimes a third one farther down; blade of upper petal emarginate; stem angled, fistulose. Yunnan. . . . . 152. *D. georgii.*
        5. Bracteoles 2, near the middle of the pedicel; blade of upper petal erose or entire; stem not angled or fistulose. Szechwan.
          6. Stem white-hirsute below; carpels glabrous; spur often strongly curved. . . . . 162. *D. laxicymosum.*
          6. Stem glabrous below; carpels pilose; spur mostly nearly straight. . . . . 169. *D. mitzugense.*
      4. Upper sepal 10–11 mm. long.
        7. Bracteoles 3–5 mm. long; carpels glabrous.
          8. Lower petal blade ca. 5 mm. wide; racemes few flowered; petioles 6–9 cm. long. Szechwan, Yunnan. . . . . 154. *D. glabricaule.*
          8. Lower petal blade ca. 3 mm. wide; racemes many flowered; petioles longer. Shansi. . . . . 153. *D. giraldii.*
        7. Bracteoles 10–12 mm. long; carpels silky. Szechwan. (This species treated in Group VI). . . . . 118. *D. sutchuense.*
  2. Stem and axis of inflorescence, or at least the latter, pubescent.
    9. Pubescence of stem and inflorescence appressed or nearly so.
      10. Lamina of upper sepal 8–10 mm. long; sepals strigulose; carpels glabrous.
        11. Leaf segments petiolulate; petioles somewhat vaginate at base. . . . . 183. *D. trifoliolatum.*
        11. Leaf segments sessile; petioles not vaginate. . . . . 180. *D. sungpanense.*

10. Lamina of upper sepal 12–18 mm. long; carpels more or less pubescent.

12. Bracteoles 10–18 mm. long, near the base of the pedicels; sepals yellow-spotted at base on back; spur slightly uncinate at apex. Tibet. . . . . 149. *D. davidii.*

12. Bracteoles linear, 5–10 mm. long; sepals not so spotted; spur blunt at apex.

13. Upper petal rounded and entire at apex; flowers pale blue, the spur 18–22 mm. long. Sikang, Szechwan. . . . . 173. *C. pachycentrum.*

13. Upper petal truncate and minutely bilobed at apex.

14. Flowers violet, the spur 25–32 mm. long. Northwest Yunnan. . . . . 184. *D. umbrosum.*

14. Flowers intense blue, the spur 18 mm. long. Bokhara. . . . . 165. *D. lipskii.*

9. Pubescence of stem and inflorescence spreading.

15. Inflorescence with some hairs yellow and glandular.

16. Upper sepal blade 18–20 mm. long; lower petal blade quite glabrous. Asia Media. . . . . 159. *D. knorringianum.*

16. Upper sepal blade 10–15 mm. long; lower petals bearded.

17. Limb of lower petal 8–11 mm. long, oblong, cleft to about 3 or 4 mm. Yunnan, Szechwan. . . . . 150. *D. delavayii.*

17. Limb of lower petal mostly 4–5 mm. long.

18. Bracteoles ca. 7–13 mm. long.

19. Stem subglabrous; bracteoles in upper third of pedicel. Szechwan. . . . . 170. *D. muliense.*

19. Stem spreading-hairy; bracteoles subtending the flowers. Himalaya. . . . . 151. *D. drepanocentrum.*

18. Bracteoles shorter or, if as long, then the stems obviously spreading hairy.

20. The bracteoles 2–3 mm. long, near or above the middle of the pedicel; spur 20–22 mm. long; upper sepal 12 mm. long. Tibet. . . . . 177. *D. sherriffii.*

20. The bracteoles mostly 5–7 mm. long.

21. Blades of lower cauline leaves 7–12 cm. in diameter; petioles vaginate at base; bracteoles in upper fourth of pedicel.

22. Lower petal laminae divided two-thirds their length; sepals lilac in color. . . . . 164. *D. lilacinum.*

22. Lower petal laminae divided one-fourth their length; sepals dark blue. . . . . 174. *D. pogonanthum.*

21. Blades of lower cauline leaves 4–7 cm. in diameter; petioles not vaginate at base; bracteoles mostly lower on the pedicel.

23. Sepals minutely puberulent on both

sides; upper petals blue; carpels puberulent. Szechwan. . . . . 175. *D. pseudo-campylocentrum.*

23. Sepals loosely puberulent to subglabrous on the outside, glabrous within; upper petals yellowish; carpels glabrous. Honan. . . 157. *D. honanense.*

15. Inflorescence lacking yellow glandular hairs.
    - 24. Sepals glabrous, the upper ca. 12 mm. long, spur ca. 15 mm. long. Bokhara. . . . . 182. *D. ternatum.*
    - 24. Sepals with hairs.
        - 25. The sepals with very fine puberulence.
            - 26. Bracteoles 6–8 mm. long, subtending the flower; leaves crowded near the base of the stem. Tibet. (Treated in Group VII). . . . . . 140. *D. thibeticum.*
            - 26. Bracteoles smaller, a little below the flower; leaves up and down the stem. Yunnan. 181. *D. taliense.*
        - 25. The sepals with coarser hairs. Yunnan to Tibet.
            - 27. Blade of lower petal 6–7 mm. long; sepal spur about 20 mm. long. . . . . 174. *D. pogonanthum.*
            - 27. Blade of lower petal 7–10 mm. long; sepal spur 18–28 mm. long. . . . . 156. *D. hirticaule.*

1. Spur not or scarcely longer than the blade of the upper sepal.
    - 28. The spur considerably shorter than the blade of the upper sepal. Eastern India. . . . . 167. *D. malabaricum.*
    - 28. The spur about as long as the blade of the upper sepal.
        - 29. Sepals subglabrous.
            - 30. Bracteoles 4–5 mm. long; leaf blades to 20 cm. broad; flowers in short racemes. Northern Iran. (Treated in Group VI). . . . . 101. *D. lanigerum.*
            - 30. Bracteoles about 2 mm. long.
                - 31. Leaf blades to 15 cm. broad; flowers in an open panicle, pale blue. China. . . . . 179. *D. sparsiflorum.*
                - 31. Leaf blades to 5 cm. broad; flowers in racemes, blue. Iran. (Treated in Group IV). . . . . 46. *D. saniculifolium.*
        - 29. Sepals pubescent.
            - 32. Stem glabrous or nearly so.
                - 33. Sepals with cornute appendages at tip 1–2 mm. long.
                    - 34. Ultimate leaf segments 5–8 mm. wide; upper petals entire, blue. Western China. 146. *D. ceratophorum.*
                    - 34. Ultimate leaf segments 2–4 mm. wide; upper petals emarginate, yellow. Tibet. . . 145. *D. ceratophoroides.*
                - 33. Sepals lacking cornute terminal appendages. Siberia. . . . . 147. *D. cyananthum.*
            - 32. Stem pubescent.
                - 35. Inflorescence lacking glandular hairs.
                    - 36. The inflorescence with spreading hairs; upper sepals ca. 12 mm. long. Caucasus. . . . . . 172. *D. osseticum.*
                    - 36. The inflorescence with more or less appressed hairs.
                        - 37. Upper sepal blade ca. 10 mm. long; lower petal blade entire, not bifid. Szechwan. . . . . 173. *D. pachycentrum.*

37. Upper sepal blade longer.

38. Blade of upper sepal 20 mm. long.

39. Upper sepal ca. 8 mm. wide, acuminate; petals violet. Szechwan. .... 160. *D. lancisepalum.*

39. Upper sepal 10–13 mm. wide, obtuse; petals very dark. Caucasus. .... 148. *D. dasycarpum.*

38. Blade of upper sepal mostly 13–16 mm. long, not acuminate.

40. Ultimate leaf divisions long-acuminate; blade of lower petal rounded, ca. 12 mm. by 10 mm. Tibet. .... 141. *D. acuminatissimum.*

40. Ultimate leaf divisions not long-acuminate.

41. Upper petal lamina entire; entire plant gray-strigulose; spur more or less uncinate at apex. Ural Mts. .... 185. *D. uralense.*

41. Upper petal laminae 2-toothed.

42. Flowers light blue; laminae of lower petal more or less obovate, with broad lobes; carpels strigose. Siam. .... 178. *D. siamense.*

42. Flowers deeper blue to violet or purple.

43. Bracteoles near the middle of the pedicel; sepals densely pubescent, deep blue, 13–15 mm. long. Nepal, Bhutan. .... 143. *D. altissimum.*

43. Bracteoles near the flower.

44. Sepals minutely strigulose, rich purple to deep maroon. Bhutan, Nepal. .... 166. *D. ludlowii.*

44. Sepals blue-violet to blue with some white. China. .... 171. *D. orthocentrum.*

35. Inflorescence with some glandular hairs.

45. Upper petals bidentate at tip.

46. Blade of lower petal ca. 10 mm. long; bracteoles subtending the flower. Himalaya. .... 176. *D. scabriflorum.*

46. Blade of lower petals ca. 5 mm. long; bracteoles near the middle of the pedicel. Tibet. .... 155. *D. gyalanum.*

45. Upper petals entire at tip.
  47. Bracteoles somewhat below the flower.
    48. Spur 5 mm. thick near the base, incurved; lower petals with acute lobes. Tibet. .... 161. *D. lasiocarpum.*
    48. Spur 2.5 mm. thick; lower petals with obtuse lobes. Lake Marka-kul. . . 142. *D. altaicum.*
  47. Bracteoles against the flower.
    49. Limb of lower petal ca. 5 mm. long, very short-bearded. Yunnan. .... 168. *D. micropetalum.*
    49. Limb of lower petal ca. 10 mm. long, with long hairs.
      50. Inflorescence a crowded, many-flowered raceme; bracteoles 5–6 mm. long. Tibet. .... 158. *D. kingianum.*
      50. Inflorescence lax, with few to several flowers; bracteoles to 1 cm. long. Kamchatka. ...... 144. *D. brachycentrum.*

141. **Delphinium acuminatissimum** W. T. Wang, Acta Bot. Sinica **10**: 138. 1962. FIG. 13, B.

About 1 m. tall, smooth, purplish and glabrous above, simple, equally and densely leafy; midcauline leaves with limb broad-pentagonal, about 6–8 cm. long, 8–10 cm. wide, cordate at base, tripartite to 3 or 4 mm. above the base, the middle part broadly rhombic, long-acuminate or subcaudate-acuminate, trifid to below the middle, the secondary lobes broadly lanceolate, few toothed or incised-lobulate; the lateral parts broadly obliquely flabellate, bifid to beyond the middle, the upper secondary lobes like those of the middle part, unequally bifid, crisped-puberulent; petioles as long as the laminae, not vaginate; upper leaves gradually smaller; racemes 8.5–12 cm. long, 8–10-flowered; lower bracts leaflike, the middle trifid, upper linear; pedicels 2–6 cm. long, divergent, retrorse-puberulent toward the tip; bracteoles near the flower, linear, 7–12.5 mm. long, puberulent; sepals blue, the upper ovate-elliptic, others oblong, 14–17 mm. long, crisped-puberulent; spur 11–14 mm. long, 4 mm. wide at the base, subulate-cylindric, obtuse, straight, or slightly decurved; upper petals blue or partly yellowish, glabrous, oblique, triangular, subobtuse; lower petals blue, the limb slightly shorter than the claw or subequal, obovate or broadly elliptic, 6–10 mm. wide, rounded at apex, entire to emarginate, short-ciliate, yellow bearded near base; stamens glabrous; carpels 5, glabrous.

TYPE: Tibet, Lung-tze, Aug. 20, 1960, *K. N. Fu 1146* (PE), not seen; photo. (E), seen.

Other specimens apparently referable here, from Tibet, Raleing, 5000 m., Aug. 26, 1924, no collector given (E); Karola, Aug. 28, 1927, *F.M.B.* (E); Trakan La, Char Chu, *Ludlow & Sherriff 1987* (BM).

142. **Delphinium altaicum** Nevski in Komarov, Fl. U.S.S.R. 7: 161, 726. 1937. FIG. 13, C.

Delphinium dictyocarpum var. *pubiflorum* Trautv., Bull. Soc. Nat. Mosc. 33: 81. 1860; teste Regel, on sheet at Kew, collected by *Ludwig* in Siberia altaica.

Delphinium elatum L. var. *pubiflorum* (Trautv.) Huth, Bot. Jahrb. 20: 399. 1895.

Stem 8–10 dm. high, tinged violet below and short-strigulose, somewhat pubescent and glandular above; leaves glabrous or nearly so above, short-pubescent on nerves beneath, round-cordate or -reniform, to 2 dm. broad, sometimes subcuneate at base, palmatifid almost to base into 5 or 7 narrow-rhombic remote segments which are unequally pinnatifid into rather few divergent sharply pointed lance-ovate to lanceolate lobules 5–25 mm. long; petioles to 1 dm. or more long, not vaginate at base; racemes simple, somewhat dense, 1–2 dm. long, the axis densely short-pilose with spreading hairs; bracts linear, pubescent, ca. 10 mm. long; pedicels divergent, 1–2 cm. long, densely pubescent; bracteoles linear-filiform, 4–7 mm. long, 0.5 mm. wide, densely glandular-pubescent, located in upper part of pedicel; sepals bluish, more or less glandular-pubescent, ovate or elliptic-ovate, the upper sepal ca. 15 mm. long, 10 mm. wide, subacuminate-recurved; spur 1.5–2 cm. long, to 2.5 mm. thick, obtusely acuminate, incurved below the apex; lateral sepals obovate, 14 mm. long, 8 mm. wide, obtuse; lower sepals elliptic, 12 mm. long, 7 mm. wide; upper petals blue, the lamina almost straight, 11 mm. long, 2.5 mm. wide, bearded and ciliate, bifid about half way into oblong lobes, the claw 6 mm. long, appendiculate; stamens 6–7 mm. long; anthers dark; follicles 3, densely glandular-pilose.

TYPE: near Lake Marka-kul, Altai Mts., Siberia, *B. Keller*, Aug. 4, 1908 (LE), seen.

143. **Delphinium altissimum** Wall. Cat. no. 4718. 1830, ***nomen***; Plantae Asiaticae Rariores 2: 25. *pl. 128.* 1831. FIG. 13, D.

Delphinium altissimum subsp. *wallichii* var. *nipalensis* Brühl in Brühl & King, Ann. Bot. Gard. Calc. 5: 101. 1896. Based on Nepal, *Wallich*; an 1819 specimen seen at BM. Possibly also var. *phallutensis* Brühl, *loc. cit.*, of which I have not been able to see authentic material.

Perennial from a fleshy branching or simple elongate root; stem 1–1.5 m. tall, terete, strigulose, simple below, somewhat branched above, remotely leafy; lower petioles to 3 dm. long, slightly vaginate, the upper shorter; leaf blades cordate-pentagonal in outline, to 15 cm. across, palmately 5-partite to 1 or 2 cm. from the base, the segments broadly cuneate-obovate, 3-lobed or with additional short lobes or large coarse broad teeth, acute, subglabrous above, pubescent beneath on veins; uppermost leaves trifid; inflorescence strigose with rather long white hairs, a many-flowered central rather dense raceme and some additional lax few-flowered branches below it; bracts lanceolate to linear (or the lowest

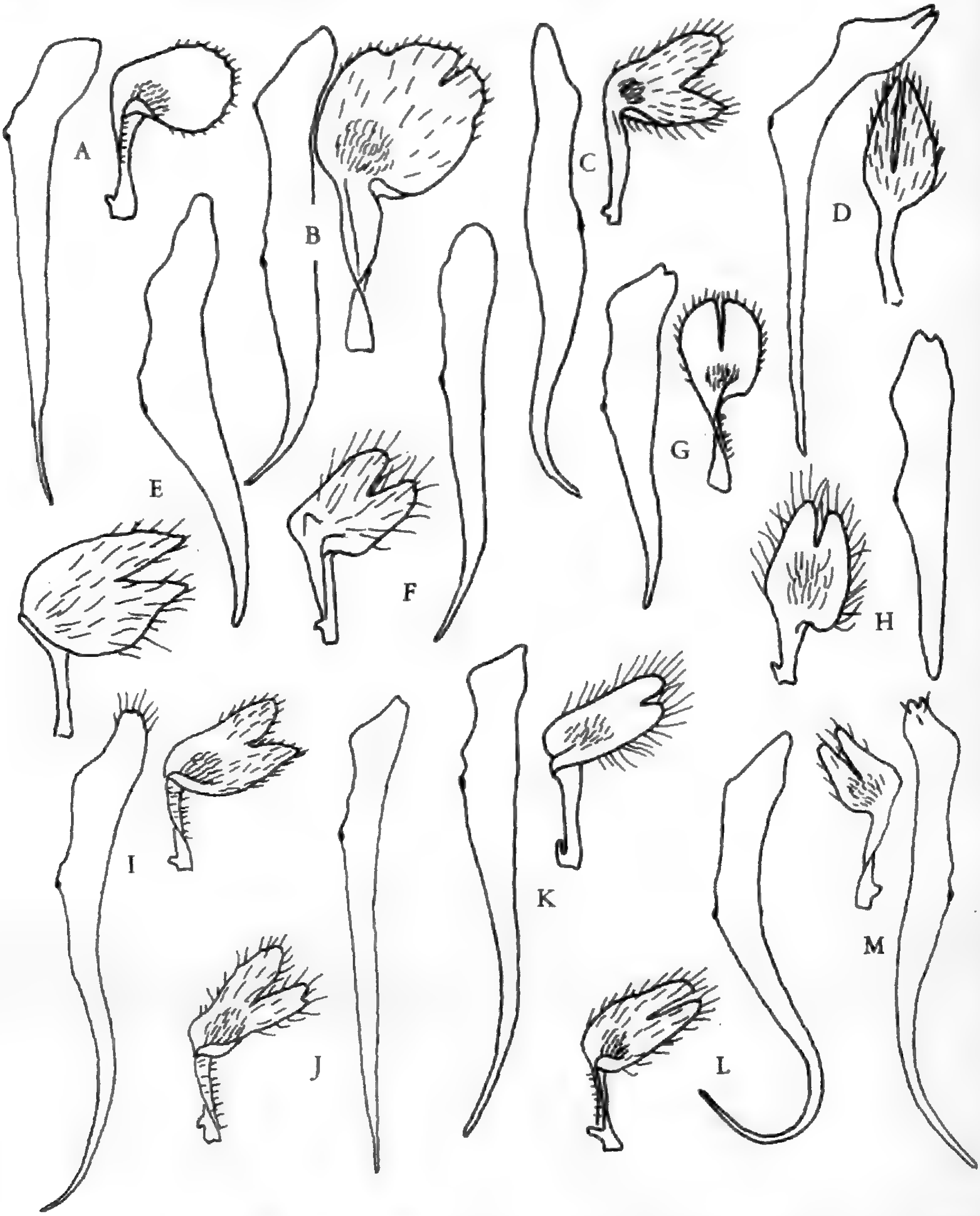

FIGURE 13. **Delphinium,** GROUP VIII. Petals, the upper spurred, the lower clawed. A. *D. sordidecaerulescens* of Group VI; blade of upper petal 14 mm. long, spur 13 mm.; blade of lower petal 7 mm. long, claw 6 mm.; drawn from *Harry Smith 3983* TYPE (UPS). B. *D. acuminatissimum* of Group VIII; blade of upper petal 14 mm. long, spur 13 mm.; blade of lower petal 9 mm. long, claw 8 mm.; drawn from Ralieng, Tibet (E). C. *D. altaicum* of Group VIII; blade of upper petal 11 mm. long, spur 15 mm.; blade of lower petal 6.5 mm. long, claw 6 mm.; drawn from *Keller*, TYPE (LE). D. *D. altissimum*; blade of upper petal 12 mm. long, spur 18 mm.; blade of lower petal 7 mm. long, claw 5 mm.; drawn from *Ludlow & Sherriff 8496* (BM). E. *D. brachycentrum*; blade of upper petal 12 mm. long, spur 14 mm.; blade of lower petal 10 mm. long, claw 5 mm.; drawn from *Eschscholtz* TYPE (LE). F. *D. ceratophorum*; blade of upper petal 9 mm. long, spur 15 mm.; blade of lower petal 7 mm. long, claw 5 mm.; drawn from *Rock 17321* (GH). G. *D. cyananthum*; blade of upper petal 9 mm. long, spur 13 mm.; blade of lower petal 5 mm. long, claw 5 mm.; drawn

foliose and 2–3 cm. long, the upper sometimes serrate, pubescent, to ca. 1.5 cm. long; pedicels 1–2(–5) cm. long, divaricate, with 2 linear or lanceolate bracteoles near the middle, these 4–5 mm. long; sepals deep blue, densely pubescent; upper sepal ovate, acute, 13–15 mm. long, 5 mm. wide, the spur 20–22 mm. long, 4 mm. wide at base, slightly curved; lateral sepals oblong-obovate, 15 mm. long, 10 mm. wide, obtuse; lower sepals oblong-obovate, 15 mm. long, 8 mm. wide; petals light purple, the upper blades somewhat oblique, bidentate at apex, 11 mm. long, the spur 17–18 mm. long; lower petals with a blade 6 mm. by 3 mm., deeply bilobed into lanceolate lobes, the claw 7 mm. long; stamens 8–9 mm. long, glabrous; anthers rounded-oblong, 1 mm. long; follicles 3, pilose, cylindrical, divergent, 12 mm. by 3 mm., the beak an additional 2.5 mm.; seeds obovoid, not winged or scaly, round in cross section.

TYPE: "Crescit in sylvis montanis Nepaliae," a *Wallich* specimen from Nepal seen at BM, probably authentic material.

RANGE. Growing in old fields, stony jungle, etc., 1500–2500 m., Bhutan and Nepal and possibly Assam.

EXAMPLES: **Bhutan:** *Ludlow & Sherriff 3496, 3558*; *Cooper & Bulley 2556, 2008*. **Nepal:** *Wigram 99*; *Lall Dhwoj* in 1928; *Colom 282*; *Ludlow & Sherriff 298*. **Assam:** *Kingdon Ward 14015*.

144. **Delphinium brachycentrum** Ledeb. Fl. Rossica 1: 60. 1841.
FIG. 13, E.

Delphinium stenosepalum Turcz. Bull. Soc. Nat. Mosc. **27**(2): 278. 1854. Type, Tigil, *Turczaninow* (LE); seen.

Delphinium maydellianum Trautv. Act. Horti Petrop. **6**: 7. 1879. Type, Terra Tschukschorum, *G. Maydell* Aug. 8, 1869 (LE); seen.

Delphinium cheilanthum Fisch. subsp. *brachycentrum* (Ledeb.) Huth, Bot. Jahrb. **20**: 345. 1895.

Perennial from fibrous roots, the stem 1.5–7 dm. tall, ashy pubescent to subglabrous, 4–5 mm. thick, simple or few branched, leafy; lower leaves on slender petioles to ca. 1 dm. long and more or less vaginate at the base, the blades mostly wider than long, 5–12 cm. wide, 3–5-parted into subcuneate parts 1–3 or more cm. wide, these in turn coarsely few-toothed or -lobed, subglabrous to soft-pubescent above, more pubescent, often whitish,

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from *Schrenck* TYPE (LE). H. *D. dasycarpum*; blade of upper petal 9 mm. long, spur 10 mm.; blade of lower petal 6 mm. long, claw 4 mm.; drawn from *Prescott* in 1851 (PHIL). I. *D. davidii*; blade of upper petal 9 mm. long, spur 20 mm.; blade of lower petal 6 mm. long, claw 5 mm.; drawn from *David* TYPE (P). J. *D. delavayi*; blade of upper petal 8 mm. long, spur 17 mm.; blade of lower petal 7.5 mm. long, claw 5 mm.; drawn from *Delavay 74* (P). K. *D. delavayi*; blade of upper petal 9 mm. long, spur 19 mm.; blade of lower petal 7 mm. long, claw 6.5 mm.; drawn from *C. W. Wang 71376* (A). L. *D. drepanocentrum*; blade of upper petal 9 mm. long, spur 20 mm.; blade of lower petal 6.5 mm. long, claw 5 mm.; drawn from *Dhwoj 0191* (BM). M. *D. georgei*; blade of upper petal 10 mm. long, spur 18 mm.; blade of lower petal 5 mm. long, claw 5 mm.; drawn from *Forrest 11353* TYPE (E).

beneath; cauline leaves gradually reduced up the stem; flowers few to several in rather lax racemes; bracts trifid into lanceolate lobes and to 6 cm. long, or the upper entire, linear, 1–3 cm. long; pedicels ascending-arcuate, 2–8 cm. long; bracteoles setaceous, to 1 cm. long, a pair near the flower, often an additional one below; sepals deep blue, with a darker spot near the apex, villous, subacuminate; upper sepal 15–25 mm. long, 5–8 mm. wide, the spur somewhat curved, 15–20 mm. long, 3–4 mm. wide at the base, pointed; lateral sepals 16–24 mm. long, 5–9 mm. wide; lower sepals 18–28 mm. long, 6–8 mm. wide; upper petals bluish at tip, the lamina almost straight, 12 mm. long, entire, the spur 13–15 mm. long; lower petals blue, the claw 5 mm. long, the ovate-elliptic blade 10 mm. long, bearded, divided ca. 3 mm.; stamens glabrous; anthers dark, 1.2 mm. long; follicles 3, hairy.

TYPE: Kamtschatka, *Eschscholtz* (LE); seen, very densely pubescent.

Ranging from the Lena-Kolyma district to Chuch Peninsula, south to Kamtchatka, Bering Island, and Northern Kuriles according to Hultén, the last area named being in America.

From Kamtchatka I have seen among other specimens: *Komarov 3896*; *Peters* in 1831; *Eyerdam 2*; *Hultén 733, 638.*

145. **Delphinium ceratophoroides** W. T. Wang, Acta Bot. Sinica **10**: 158. 1962.

Stems erect, ca. 3 dm. tall, 2.5 mm. thick below, smooth, glabrous, simple or one branched, with ca. 3 leaves; basal or lower cauline leaves withered by anthesis, the other cauline leaves long petioled and with broadly pentagonal blades, 2.5–4 cm. long, 3.6–7 cm. wide, cordate, 3-parted to 2 mm. above the base, the primary median parts broadly obovate-rhombic, narrow-cuneate at base, 3-parted to middle, the secondary middle parts broadly rhombic, divided into ultimate lobules 2–4 mm. wide, primary lateral parts broadly obliquely flabellate, bifid to three-fourths their length, all densely strigulose beneath, somewhat hirtellous above; petioles 5–11.5 cm. long; racemes 3–11 cm. long, lax; lower bracts trifid or linear, the others linear; pedicels 4–5.5 cm. long, divergent, glabrous, bibracteolate in upper part; bracteoles remote from flower, linear, 5–10 mm. long, puberulent; sepals blue, elliptic, 18–22 mm. long, strigulose, short-corniculate, spur 25 mm. long, subulate, 3 mm. thick basally, decurved at right angle to the obtuse, yellowish, glabrous, emarginate upper petals; lower petals blue, the limb suboblong, bifid to slightly beyond the middle, the base yellow bearded, claw ca. as long as limb, appendaged; filaments loosely ciliate; carpels 3, densely hirtellous.

TYPE: Tibet, Tsa-wa-rung, Aug., 1935, *C. W. Wang 65706* (PE), not seen; photo. (E), seen. No material available for this species. *Delphinium ceratophoroides* was described as near *D. ceratophorum*, but the stems 3-leaved, glabrous; leaves more deeply divided, the basal ones gone by anthesis; sepal-tips shorter.

146. **Delphinium ceratophorum** Franchet, Bull. Soc. Bot. France **33**: 377. 1886. FIG. 13, F.

? *Delphinium ceratophorum* var. *hirsutum* W. T. Wang, Acta Bot. Sinica **10**: 158. 1962.

Perennial from an elongate rhizome with fibrous coating; stem subscapose, slender, 2–9 dm. tall, mostly glabrous except for the few hairs at the base and above, simple or slightly branched; leaves largely basal or nearly so, on slender petioles 5–15 cm. long, these scattered hairy, or sparsely retrorse-strigose or glabrous, more or less dilated at the base, the blades roundish in outline, 3–12 cm. across, divided almost to the base into 3 or 5 cuneate obovate parts which are somewhat hairy and variously incised into lanceolate or ovate, acute to obtuse divisions 5–8 mm. wide; cauline leaves few, simpler; racemes 1 to few, lax, mostly 3–7-flowered; bracts linear to sublanceolate, or 3-parted into linear lobes, 5–15 mm. long; pedicels arched-ascending, 2–6 cm. long; bracteoles linear or wider, 5–8 mm. long and near the summit of the pedicel; sepals purplish blue, callous-cornute below the apex, the upper sepal ovate, 18–20 mm. long, 8–10 mm. wide, coarse-pubescent, the spur decurved, 20–22 mm. long, 3.5 mm. wide at the base, coarse-pubescent, attenuate to a narrow tip; lateral sepals broadly elliptic, 20 mm. by 11 mm., the cornute appendages to 2 mm. long; lower sepals broadly elliptic, 18–20 mm. long; upper petals blue or bluish at the tip, straight, narrow, the limb 9 mm. long, entire, the spur ca. 15 mm. long; lower petals blue, the claw 5–5.5 mm. long, the bearded lamina ca. 7 mm. long, 5 mm. wide, cleft for 2 mm. and with a prominent appendage at the base; stamens 5–6 mm. long, glabrous; anthers dark, 1.3 mm. long; carpels 3, hairy.

TYPE: Yunnan, "in monte Hee-Chan-Men; inter dumeta, alt. 3200 m.," *Delavay 967* (P, K) seen, the K specimen in a type folder. But another *Delavay* number, *1845*, from Lao-kouan-tsoui, below San-yn-kay, at 2500 m., is marked TYPE at (P), has dissection drawings, and probably should be taken as the holotype.

REPRESENTATIVE SPECIMENS. **Yunnan:** *Rock 17321, 4746, 10737, 22852, 23080*; *Ching 21392*; *Schneider 3459*; *Forrest 10967, 6403, 6568, 2763*. **S. W. Szechwan:** *Rock 23992*.

147. **Delphinium cyananthum** Nevski in Komarov, Fl. U.S.S.R. 7: 160. 725. 1937. FIG. 13, G.

Stems 7.5–10 dm. tall, glabrous, or slightly pilose at times below the inflorescence; petioles glabrous except on the ciliate margins or strigulose, the lower to 15 cm. long; leaves round-cordate, the lower to 15 cm. broad, palmatisect almost to the base, the segments rhombic, the base entire for 2–3 cm., then biternately incised, glabrous above and beneath or pubescent on veins beneath, ciliate-pilose on margins; raceme branched, dense, many flowered, the flowers light blue; bracts to 1 cm. or longer, subsetaceous; pedicels commonly ca. 1 cm. long, adpressed to divaricate, densely pilose;

bracteoles linear-subulate or sometimes almost linear-lanceolate, densely pilose, 1.5–5 mm. long, placed just below the flower; sepals strigulose and pubescent, densely puberulent at tips, ovate, obtuse, 10–11 mm. long, 4–8 mm. wide, spur 11–13 mm. long, to 3 mm. thick near the base; petals pale, the upper emarginate, almost straight, the lamina 9 mm. long, spur 13 mm.; lower petal 2-cleft, bearded, the lamina oblong-rounded, 5 mm. long, claw 5 mm. long; stamens ciliate; carpels 3, densely pubescent.

TYPE: Songoria, Tentek River, *Schrenk* (LE); seen.

A specimen from **Irkutsk:** distr. Balagansk, by *Kryschtofowitsch* in 1908 (UC) seems to belong here.

148. **Delphinium dasycarpum** Stev. ex DC. Syst. 1: 547. 1817. FIG. 13, H.

Delphinium speciosum var. *dasycarpum* Rupr. Flora Caucausi 36, 287. 1869.

Stem 5–10 dm. tall, erect, striate, simple, pubescent; petioles pubescent, not dilated at base; leaf blades pubescent, 5-lobed, the lobes lanceolate, subtrifid, incised-dentate at apex, the upper leaves cuneate at base, the lower subcordate; raceme simple, pubescent, scarcely elongate; flowers a beautiful blue; axis and pedicels soft-pubescent; bracts one-third as long as the pedicels, linear-subulate; bracteoles linear-subulate; sepals subvillous, 20–25 mm. long, 9–13 mm. wide, oval; spur straight, 18–20 mm. long; petals dark, the 2 upper with emarginate lamina ca. 9 mm. long, spur 10 mm. or more; the lower deeply bifid, the ovate lamina 6 mm., the claw 4 mm. long; follicles 3, densely hairy.

TYPE: "hab. circa Nartsanam in Caucaso cisalpino," *Steven* (G?), not seen.

A specimen apparently belonging here is Caucasus, *Prescott* in 1851 (PHIL).

149. **Delphinium davidii** Franchet, Bull. Soc. Philom. Paris VIII. 5: 179. 1893. FIG. 13, I.

Delphinium longipes Franchet, Nouv. Arch. Mus. Paris II. 8: 191, 192. 1886, not Moris, 1837.
Delphinium grandiflorum L. var. *davidii* (Franchet) Brühl in Brühl & King, Ann. Bot. Gard. Calc. 5: 98. 1896.

Perennial from a slender rhizome; stem slender, 3–4 dm. tall, setulose with spreading or appressed hairs, branching from base; basal leaves with petioles to 2.5 dm. long, slender, sparsely pilose; blades 5–8 cm. in diameter, pale above, glaucescent beneath, rounded-pentagonal in outline, tripartite into segments cuneate and entire below, trifid to the middle with oblong-ovate lobules to 15 mm. long and 5–8 mm. wide; cauline leaves shorter petioled, the uppermost 3–5-parted into entire linear segments; flowers solitary to few, corymbose-racemose; bracts like reduced leaves, to 3 cm. long; pedicels 6–10 cm. long, retrorse-strigulose; bracteoles divided to entire, 10–18 mm. long, placed well below the middle of the pedicel; sepals dilute blue, strigose, with yellow spots at base on back; the sepals 15–20 mm. long, ovate, 10–12 mm. wide, obtuse to rounded at the tip, spur linear-subulate, decurved-spreading to slightly uncinate at apex, 20–26 mm. long; lamina of upper petal somewhat hairy at apex, slightly fuscous, almost straight, 9 mm. long, entire; that of lower petal pale blue, oblong-ovate, short-bilobed, bearded, short-ciliate, 6 mm. long, claw 5.5 mm. long; stamens glabrous; follicles 3, hirsute.

TYPE: Tibet, "Prov. de Moupin, in lapidosis," *David,* July, 1869, (P); seen. The above citation probably is in western Szechwan. A collection by *E. H. Wilson, 4690,* from western Szechwan, seems to belong to this species, which is unusual in having the bracteoles near the base of the pedicels and was long thought to lack them.

150. **Delphinium delavayi** Franchet, Bull. Soc. Bot. France 33: 379. 1886. FIG. 13, J. K.

Delphinium delavayi var. *acuminatum* Franchet, Bull. Soc. Bot. France 33: 380. 1886. From meadows near Mt. Yengtze-hay, near Lankong, 3000 m., *Delavay 1846* (P, K); seen. Leaves much incised.

Delphinium delavayi forma *aureum* W. T. Wang, Acta Bot. Sinica 10: 144. 1962. Isotype (A), seen, *T. T. Yü 12548.*

Delphinium trichophorum var. *brevistylum* f. *brevungue* Lévl. Repert. Sp. Nov. 7: 102. 1909. Type number from San Chan, *Ten 579* (E); seen.

Perennial from a rather woody fibrous root system, the stem 5–10 dm. tall, usually simple, leafy throughout, spreading-hirsute or -pubescent, or the hairs more or less retrorse, many in the inflorescence enlarged and yellow at the base; lower leaves with petioles 3–20 cm. long, dilated at base, somewhat hairy, the blade divided almost to the base into 5 or 7 segments that are broadly cuneate, slightly incised or to about half way, then coarsely ovate toothed or sometimes more pointed, the laminae 3–10 cm. wide, not as long, mostly quite pubescent, paler beneath than above; upper leaves gradually reduced, shorter petioled, the uppermost often trisect; raceme rather dense, often many flowered; lower bracts foliaceous, trilobed, to 2 cm. long, the middle ones mostly lanceolate, entire, 1–2 cm. long, the uppermost linear; pedicels ascending-erect, 1–3 cm. long, hairy; bracteoles linear to lanceolate, subopposite near the flower, 4–10 mm. long; flowers mostly bluish violet to rich purple, pubescent; upper sepal broadly ovate, 15 mm. by 10 mm., obtusely rounded at apex, the spur decurved, 20 mm. long, 3 mm. wide at base; lateral sepals elliptic-oblong, 15 mm. by 7 mm., truncate rounded at apex; lower sepals 14–16 mm. by 9 mm., ovate-oblong, obtuse; upper petals bluish, the lamina almost straight, 10–12 mm. long, entire, spur 16–18 mm. long; lower petals with a claw 6 mm. long, blade sparsely short bearded, elliptic-oblong, 10–11 mm. long, cleft ca. 3 mm.; stamens subequal, subglabrous, 6–7 mm. long; anthers dark, 1.5 mm. long; follicles 3, somewhat hairy, reticulate veined, erect and closely parallel, 2–3 cm. long, 4–5 mm. wide, the style an additional

3–4 mm.; seeds brownish, 1.5 mm. long, densely covered with lamellate scales.

TYPE: Yunnan, San Kong to the north of Tali, Nov. 8, 1883, *Delavay 22,* holotype (P), isotype (K), photo. (BH), all seen. Two other sheets at P (*Delavay 74* and *1847*) are also labeled TYPE.

DISTRIBUTION. About 2700 to 4500 m., Yunnan and Szechwan and eastern Tibet.

REPRESENTATIVE SPECIMENS SEEN. **Yunnan:** *Maire 6367, 7449*; *Forrest 2861, 2963, 6319, 28587*; *Rock 4404, 5786, 5799, 5828, 5030, 4849, 5806, 5298, 5768, 6093, 5936, 6149, 9914, 6177, 9474, 18519, 5167, 10634, 11483*; *Schneider 2143, 3576*; *Ten 69*; *Yü 22461, 14367, 15543*; *Delavay 4109*; *Henry 9668A, 9668*; *Ching 21456*; *Tsai 53738*; *Feng 2461, 217, 1697*. **Szechwan:** *Rock 18324, 24190*; *Fang 2944*; *Peng 145*; *E. H. Wilson 3090.*

√ 151. **Delphinium drepanocentrum** (Brühl) Munz, comb. nov.

FIG. 13, L.

Delphinium altissimum var. *drepanocentrum* Brühl ex Huth, Bot. Jahrb. **20:** 419. 1895 and subsp. *drepanocentrum* Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5:** 101. 1896.

Delphinium umbrosum Hand.-Mazz. subsp. *drepanocentrum* (Brühl) Chowdhury ex Mukerjee, Bull. Bot. Surv. India **2:** 293–5. 1961.

Perennial from rather a woody base, 4–6 dm. high, the stem simple or nearly so, spreading, and long- and soft-hairy with more or less brownish hairs throughout, often with more or less purplish epidermis, leafy; lowest leaves gone by anthesis, cauline with petioles 5–20 cm. long, somewhat dilated at base, soft-hairy; blades 3- or mostly 5-lobed to 1–2 cm. from the base, with rather long hairs above and on veins beneath, somewhat pentagonal in outline, 5–10 cm. broad, with a rather deep basal sinus, the lobes broad-rhombic, cuneate below, with rather shallow and ovate teeth 2–5 mm. deep and even broader, or sometimes shallowly 3-lobulate, then toothed, the teeth mucronate; leaves gradually reduced upward, the uppermost becoming trifoliolate bracts 2–3 cm. long; inflorescence a secund, 5- to 20-flowered raceme 1–3 dm. long, more or less retrorse-hairy and apparently glandular; upper bracts linear to lance-elliptic, 1–2 cm. long; pedicels erect, 1–4 cm. long; bracteoles oblong-linear, ca. 1 mm. wide, 7–8 mm. long, subtending the flower; sepals mauve to dull purple, with rather coarse appressed hairs; upper sepal ovate, 12–13 mm. long, 8 mm. wide, obtuse, the spur curved into a half circle or merely decurved-spreading, 20–22 mm. long, 2.5 mm. wide at base, narrowed into a very slender tip; lateral sepals elliptic-oblong, 12–13 mm. long, 5–6 mm. wide, rounded-truncate at apex; lower sepals asymmetrically oblong-elliptic, 10–11 mm. long, 5 mm. wide, rounded at tip; petals bluish, the lamina of the upper slightly oblique, 9 mm. long, 2.5 mm. wide, glabrous, pointed, subentire, the very slender spur 20 mm. long; lower lamina oblong, 6.5 by 3 mm., bifid for about 4 mm. into 2 linear-oblong, bearded lobes, the claw 5 mm. long; stamens ca. 5 mm. long, glabrous; anthers dark, 0.8 mm. long;

follicles 3, 15–18 mm. long, 3 mm. wide, somewhat hairy, the style 2 mm. long; seeds obovoid angled, scarcely 1 mm. long, with transverse rows of brownish scales.

TYPE: W. Sikkim, near Wallanchun, King's collectors. Not seen.

RANGE. Growing on open and brushy slopes, 3500 m. to 5500 m., mostly in Nepal.

REPRESENTATIVE SPECIMENS. *Lall Dhwoj 0641, 0191*; *Stainton*, July 27, 1956, *1142, 1144*.

152. **Delphinium georgei** Comber, Notes Bot. Gard. Edinb. **18**: 236. 1934. FIG. 13, M.

Stem 9–13 dm. tall, erect, fistulose, angled, glabrous, purplish-glaucescent, 6 mm. thick at the base; basal leaves gone by anthesis, cauline numerous, sparsely pubescent, yellowish above when dry, whitish beneath, the lower blades to 8 cm. long, 15 cm. wide, 5-fid into rhombic-cuneate segments, the interior 3-lobulate, the outer 2-lobulate, the lobules unequally and coarsely crenate-dentate, apiculate; upper leaves smaller; lower cauline petioles 12–16 cm. long, slightly vaginate; inflorescence lax, few branched or simple, about 20-flowered and 3 dm. long, the slender axis glabrous, striate; bracts linear-lanceolate, 5–10 mm. long; pedicels slender, 2–6 cm. long, divergent; bracteoles 2, subulate, inconspicuous, subopposite, near the summit of the pedicels, 2–3 mm. long and with a third subulate one 7–8 mm. long toward the base of the pedicel; upper sepal purplish blue, strigose, 15 mm. long, 10 mm. wide, ovate, acutish, the spur 22 mm. long, subulate, subfalcate, 2.5–3 mm. thick near the base; lateral sepals oblanceolate, 17 mm. long, 5 mm. wide, pubescent only along the central nerve; lower sepals subelliptic, 20 mm. long, 6 mm. wide, strigose; upper petals glabrous, the blade 10 mm. long, slightly oblique, truncate, emarginate, rarely sparsely setose, spur subfalcate; lower laminae oblique, 5 mm. by 3 mm., bilobed, with divergent lance-oblong lobes 3 mm. long, white-ciliate at apex, yellow bearded at middle, claw 6 mm. long, sparsely ciliate, appendaged; filaments 5–6 mm. long; anthers 1.5 mm. long; carpels 3, glabrous or slightly setose.

TYPE: Yunnan, on the Tong Shan in the Yangtse Bend, at 3600 to 3900 m., Sept., 1913, *G. Forrest 11353* (E), seen.

SPECIMENS SEEN. **Kansu:** *Farrer 159*. **Yunnan:** *Yü 14490*; *Cavalerie 7871*; *Maire 2128*; *K. M. Feng 2272, 2742*; *Rock 10539*.

153. **Delphinium giraldii** Diels, Bot. Jahrb. 36. Beibl. **82**: 39. 1905; Hand.-Mazz. Acta Hort. Gothob. **13**: 54. 1939. FIG. 14, A.

Perennial, to 1 m. or so tall; stem glabrous; leaf blades to 22 cm. broad, 3-parted into subpetiolulate parts, the median part 2–3-lobed, the lateral parts 2-lobed at 1–2.5 cm. above the base into irregularly pinnatifid-incised, ovate or broadly rhombic-acute lobes, their ultimate divisions broadly to narrowly ovate or subtriangular, acute, strigose above and beneath; lower petioles very long; inflorescence pyramidal with lax lateral racemes and elongate many-flowered terminal raceme, glabrous; bracts and bracteoles minute, lance-linear, 3–5 mm. long, somewhat strigulose, the bracteoles near the flower; pedicels divaricate, rather short; sepals puberulous without, apparently pale blue-violet; upper sepal round-ovate, 10 mm. by 9 mm., subapiculate, the spur straight, ca. 20 mm. long, 4 mm. wide at base, subacute; lateral sepals elliptic, 9 mm. by 5 mm., rounded-truncate at apex, puberulent especially along midrib and on margin; lower sepals asymmetrically elliptic-oblanceolate, obtuse, 10 mm. by 4.5 mm.; petals pale, the upper lamina scarcely oblique, shallowly 2-toothed, glabrous, 9 mm. long, the spur 20 mm. long; lower laminae oblong, oblique, 5 mm. by 3 mm., divided over halfway into 2 lance-oblong, ciliate lobes, with a small patch of beard near base of blade, claw 5 mm. long; stamens 5–6 mm. long, glabrous; anthers dark, oblong, 1 mm. long; follicles 3, glabrous; seeds squamate.

TYPE: Shansi, mountains of Tsin-ling Shan, *Giraldi* (B), not seen. At UC and at K (in type cover) is probably authentic material from northern Shansi (Schensi), *Rev. Jos. Giraldi*, Aug. 4, 1897, but without collection number.

154. **Delphinium glabricaule** W. T. Wang, Acta Bot. Sinica **10**: 154. 1962. FIG. 14, B.

Stem 7 dm. tall, ca. 8 mm. in diameter at the base, glabrous, branched, equally foliose; lower cauline leaves long petioled, the blades broadly pentagonal-cordate, 5–6 cm. long, 7–8 cm. wide, trisect to base or 0.5–1 mm. above, the middle division sessile, broadly rhombic, cuneate, entire below middle, trifid above into rhombic-ovate middle parts and oblique lateral ones, ultimately divided into few-toothed lobules, loosely strigulose on both sides along the nerves; the petioles 6–9 cm. long, glabrous, not vaginate; racemes ca. 36 cm. long, 8-flowered, lax, with glabrous axis; lower bracts lanceolate, ca. 4 cm. long, 5.5 mm. wide, others smaller, linear; pedicels glabrous, 4–9 cm. long, somewhat arcuate curved, divergent, bibracteolate above the middle; bracteoles 4–5 mm. long, linear; sepals blue, broadly obovate, 11 mm. long, puberulent, the spur 18–20 mm. long, subulate, spirally decurved at middle or below; upper petals blue, the laminae glabrous, emarginate, slightly oblique, 11 mm. long; lower petals blue, the laminae 6 mm. long, bifid into lance-triangular short-ciliate lobes and yellow bearded at the base, claw 6 mm. long stamens glabrous; carpels 3, glabrous.

TYPE: Szechwan, Hsio-chin, July 23, 1958, *H. S. Chang & Y. H. Jen 6099* (PE), not seen; photo (E), seen.

I refer here, from Szechwan, *Rock 16830* and *18121*; from **Yunnan,** *R. C. Ching 2141.*

Wang says that *Delphinium glabricaule* is near *D. sungpanense*, but has leaf segments not acuminate, the spur spirally decurved, and the filaments glabrous.

155. **Delphinium gyalanum** Marquand & Airy-Shaw, Jour. Linn. Soc. Bot. **48**: 156. 1929. FIG. 14, C.

? *D. dictyocarpum* DC. subsp. *tibeticum* P. Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 100. 1896. Described as from "Southern Tibet, between the northern frontier of Sikhim and Lhassa," with two varieties *glandulosum* and *cinereum*, but no collectors named. A specimen loaned me from Gyangtse, July–Sept., 1904, *Capt. H. J. Walton* (CAL), is labeled "var. tibeticum" and seems to be glandular.

Stem erect, to 2 or 2.5 m. high, glabrescent, purplish, striate, more pubescent and glandular in the inflorescence; lower petioles to 5 dm. long, sparsely pubescent or villous, somewhat vaginate at base; lower laminae subreniform in outline, 18–30 cm. in diameter, 5- or 7-lobed to the middle or below, the lobes cuneate, 4–10 cm. wide, 3-lobulate with sharp angular sinuses, then shallowly divided into acute uneven lanceolate teeth 1–5 mm. long and 1–4 mm. wide; upper leaves palmately incised-dentate, short petioled, glabrescent except for the rows of short hairs along the veins beneath; inflorescence loosely panicled, many flowered, to 3 dm. long, the racemes lax, with spreading yellow glandular hairs and somewhat appressed, non-glandular white ones; bracts linear to lanceolate, entire, 1–2 cm. long, 1–4 mm. wide, pubescent; pedicels 3–8 cm. long, arched-ascending; bracteoles near middle of pedicel, linear-oblong, 9–10 mm. long; sepals deep blue, to violet or pale mauve, pubescent, the upper sepal ovate, 16–17 mm. long, 9–10 mm. wide, subobtuse, the spur straight or slightly decurved, 18–22 mm. long, 3 mm. wide at base, obtuse; lateral sepals obovate, 19 mm. by 12 mm., with a truncate-obtuse prolongation at apex; lower sepals similar, but more acute; upper petals bluish, the limb lanceolate, shallowly bidentate, 10 mm. long, 4–5 mm. wide, the spur 15–16 mm. long; lower laminae ovate, 5 mm. by 3 mm., yellow bearded at base, bifid into lanceolate hairy lobes 3 mm. long, the claw 5 mm. long; stamens 5–6 mm. long; anthers dark, 1 mm. long; follicles 3, densely pilose to subglabrous, 8–12 mm. by 4–5 mm., the styles an additional 4 mm. long; seeds dark, angled-obovoid, squamate, ca. 1.2 mm. long.

TYPE: Southeastern Tibet, in shady thickets on exposed flank of valley, gorge of the Tsang-po near Gyala, 2700 m., July 21, 1924, *F. Kingdon Ward 5969* (K) seen; isotype (E), seen.

REPRESENTATIVE EXAMPLES: **Southeastern Tibet:** *Ludlow, Sherriff & Taylor 5329, 5824, 5701, 4849, 6250*; *Kingdon Ward 12031*; *Ludlow & Sherriff 2777, 8789, 9893, 8781, 1942, 2461, 2421, 9632, 11108, 528*; *F. Spencer Chapman 187, 201*; *Hingston 367, 408*; *H. J. Walton 106*; *H. M. Stewart* in 1907; *L. A. Waddell* in 1904.

156. **Delphinium hirticaule** Franchet, Jour. Bot. Morot **8**: 275. 1894. FIG. 14, D.

Delphinium hirticaule var. *micranthum* Finet & Gagnep. Bull. Soc. Bot. France **51**: 485. 1905. Based on *Farges 630 bis*, pro parte, with lamina of lower petal deeply divided.

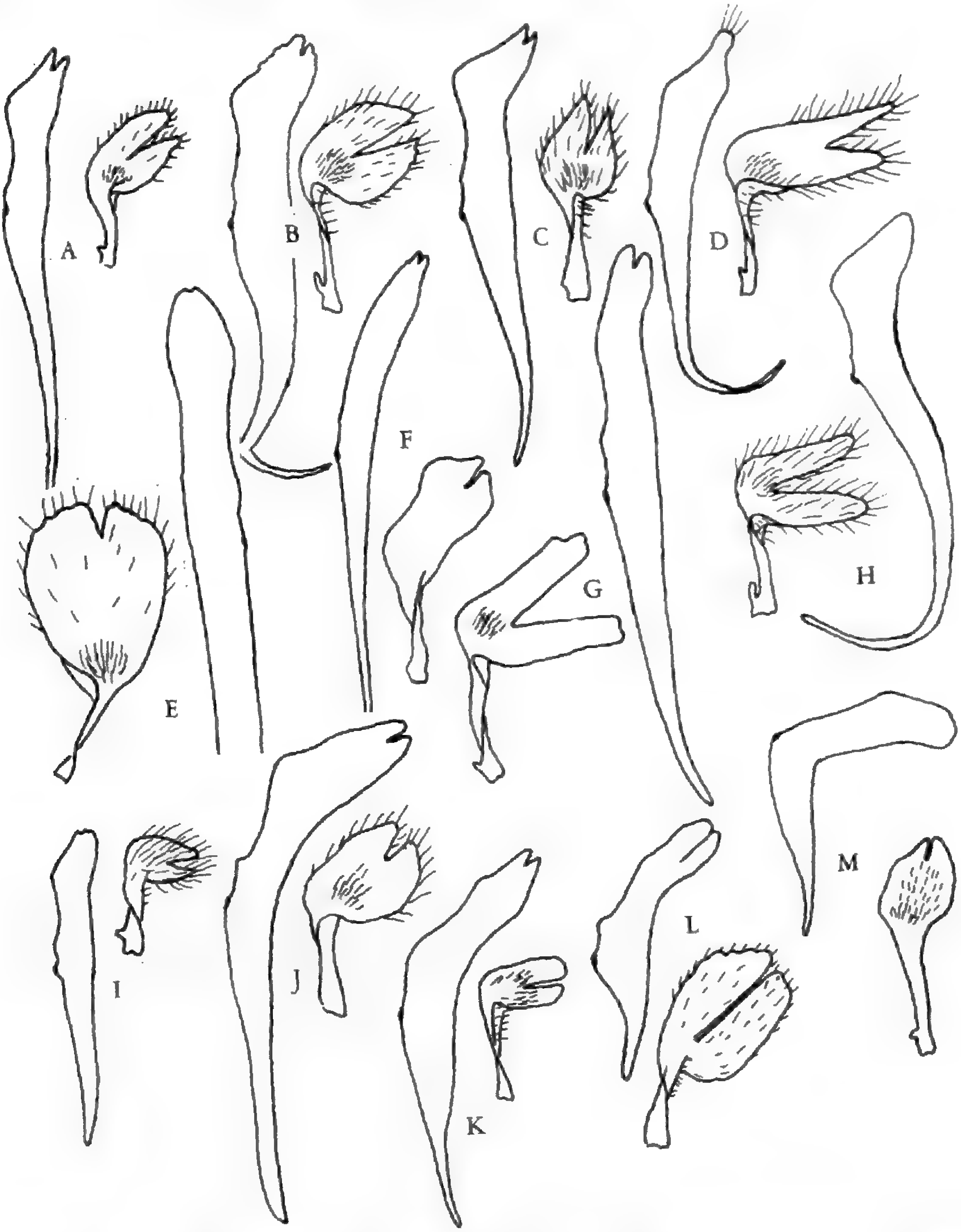

FIGURE 14. **Delphinium**, GROUP VIII. Petals, the upper spurred, the lower clawed. A. *D. giraldii*; blade of upper petal 9 mm. long, spur 20 mm.; blade of lower petal 5 mm. long, claw 5 mm.; drawn from *Giraldi* in 1897 (UC). B. *D. glabricaule*; blade of upper petal 11 mm. long, spur 18 mm.; blade of lower petal 6.5 mm. long, claw 6 mm.; drawn from *Rock 16830* (US). C. *D. gyalanum*; blade of upper petal 11 mm. long, spur 16 mm.; blade of lower petal 5 mm. long, claw 5 mm.; drawn from *Ludlow, Sherriff & Taylor 5329* (BM). D. *D. hirticaule*; blade of upper petal 11 mm. long, spur 16 mm.; blade of lower petal 9 mm. long, claw 6 mm.; drawn from *Maire 6367* (UC). E. *D. kingianum*; blade of upper petal 14 mm. long, spur 20 mm.; blade of lower petal 10 mm. long, claw 5 mm.; drawn from *Ludlow & Sherriff 527* (E). F. *D. knorringianum*; blade of upper petal 14 mm. long, spur 22 mm.; blade of lower petal 7 mm. long, claw 6 mm.; drawn from *Knorring 368* TYPE (LE). G. *D. lancisepalum*; blade of upper petal 15 mm. long, spur 19 mm.; blade of lower petal 9 mm. long,

Delphinium coelestinum Franchet, Jour. Bot. Morot **8:** 276. 1894. Type, *Farges 630 ter* (P) with lower petals deeply divided. Seen.

Delphinium hirticaule var. *coelestinum* (Franchet) Finet & Gagnep. Bull. Soc. Bot. France **51:** 486. 1905.

Perennial from a fibrous root; stem simple or branched above, 3–10 dm. tall, somewhat spreading hairy below, glabrous to densely hairy above; leaves largely basal, the petioles slender, sparsely setose, 5–12 cm. long, slightly dilated at the base; blades round-pentagonal in outline, 2–8 cm. in diameter, sparsely setulose on both surfaces, 5-parted to near the base into cuneate-obovate segments to ca. 3 cm. wide, these 3- or more lobed or toothed, the ultimate lobes lance-oblong to ovate, rounded, mostly 3–7 mm. wide; flowers few in an open raceme, or with 1–2 lower branches; bracts mostly simple, 8–12 mm. long, linear to lance-linear; pedicels subglabrous or more or less setulose, mostly 1–4 cm. long, ascending; bracteoles linear to lance-linear, to ca. 1 cm. long and placed near the flower; sepals deep blue, with short stiff hairs; upper sepal ovate, 15–17 mm. long, 7–9 mm. wide, subacute, the spur horizontal, somewhat decurved, 18–23 mm. long, 3 mm. wide at the base, gradually narrowed to a subacute point; lateral sepals oblong-obovate, 15–20 mm. long, 8–10 mm. wide, rounded at apex, with median line of hair; lower sepals 16–20 mm. long, 7–9 mm. wide, obtuse, more generally pubescent; upper petals pale, the laminae almost straight, entire, 11–13 mm. long, more or less setose at tip, the spur 10–20 mm. long; lower petals bluish, the blade oblique, rounded or deeply lobed at the apex, 7 mm. by 5 mm., with a basal patch of bearding and ciliate on margin; stamens 7–8 mm. long, glabrous; anthers dark, 1.5 mm. long; follicles 3, sparsely pilose, 10–17 mm. long, 3 mm. wide, erect, the styles an additional 2.5 mm. long; seeds brown, 3-angled, lamellate on all sides, ca. 1.8 mm. long.

TYPE: Szechwan, district of Tchen-kéou-tin, *Farges 630 bis* (P) seen, some sheets with this number having lower petals more deeply divided than others; same true of specimens at (K).

SPECIMENS SEEN: **Szechwan:** *Rock 18205*; *T. L. Tai 101803*. **Yunnan:** *Feng 2841*; *Maire 6367*; *Ching 21945*; *Rock 5167, 6305, 17317*; *Schneider 1867*. Much material that has been referred here belongs to *D. ceratophorum*.

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claw 6.5 mm.; drawn from *Harry Smith 11248* (NY). H. *D. laxicymosum*; blade of upper petal 11 mm. long, spur 27 mm.; blade of lower petal 7 mm. long, claw 6 mm.; drawn from *F. T. Wang 21767* (A). I. *D. laxiflorum*; blade of upper petal 7 mm. long, spur 10 mm.; blade of lower petal 4 mm. long, claw 4 mm.; drawn from *Burdakova* in 1931 (NY). J. *D. lipskii*; blade of upper petal 13 mm. long, spur 19 mm.; blade of lower petal 6 mm. long, claw 5 mm.; drawn from *Korshinsky* TYPE (LE). K. *D. ludlowii*; blade of upper petal 10 mm. long, spur 12 mm.; blade of lower petal 4.5 mm. long, claw 5 mm.; drawn from *Ludlow & Sherriff 894* (E). L. *D. malabaricum*; blade of upper petal 10 mm. long, spur 7 mm.; blade of lower petal 7 mm. long, claw 5 mm.; drawn from *Santapau 11552* (MO). M. *D. micropetalum*; blade of upper petal 9 mm. long, spur 12 mm.; blade of lower petal 5 mm. long, claw 6.5 mm.; drawn from *Yü 20783* (E).

157. **Delphinium honanense** W. T. Wang, Acta Bot. Sinica **10**: 146. 1962.

Stems 5–6 dm. tall, 5–6 mm. thick at base, angled, glabrous, simple, equally leafy; lower and middle cauline leaves with rather long petioles, the blades 6–7 cm. long, 7–10 cm. wide, cordate, tripartite rather deeply, the middle part broadly rhombic, acute or short-acuminate, entire in lower half, above the middle unequally ovate-dentate or indistinctly 3-lobulate, the lateral parts bifid to below the middle, the upper lobes much as in the middle part, loosely strigose beneath or glabrescent, with stiffer hairs above; petioles 1.5–2 times as long as blades, loosely hirsute, not vaginate; upper leaves reduced; racemes 8–11 cm. long, ca. 10-flowered; lower bracts trifid, others lance-linear to linear, 8–17 mm. long; pedicels 1–2.5 cm. long, obliquely spreading, with white and yellow-glandular hairs; bracteoles near the middle of the pedicels, linear, 5–8 mm. long, puberulent; sepals purple, elliptic- to narrow-ovate, 15–16 mm. long, loosely puberulent to subglabrous; spur 20–21 mm. long, subulate, 3 mm. wide at base, slightly decurved; upper petals yellowish, glabrous, emarginate or bilobulate; lower petals blue, the limb bifid into obtuse triangular lobes to beyond the middle, ciliate, yellow bearded near base, claw subequal, short-appendiculate; stamens glabrous; carpels 3, glabrous.

TYPE: Honan, Sichia, May 14, 1959, Honan Exped. no. 534 (PE), not seen; photo. (E), seen.

Said to be near *D. hirticaule*, but stems glabrous, parts of leaves less divided. I have seen no material I could refer here.

158. **Delphinium kingianum** Brühl ex Huth, Bot. Jahrb. **20**: 469. 1895; Brühl, Ann. Bot. Gard. Calc. **5**: 108. 1896, *pro synon.*
FIG. 14, E.

Delphinium pachycentrum ssp. *tsangensis* vars. *dasycarpa* and *lasiocarpa* Brühl, *loc. cit.* 108 — according to Wang, Acta Bot. Sinica **10**: 138. 1962.
Delphinium kingianum var. *leiocarpum* Brühl ex Huth, *loc. cit.*
? *Delphinium kingianum* var. *eglandulosum* Wang, *loc. cit.*

From a thick central fibrous root, stems in clumps, 3–4 dm. tall, 3–5 mm. thick, subglabrous below, densely spreading-pubescent upward with yellow glandular hairs, densely leafy, the cauline leaves 3–10 cm. across, subglabrous above, paler and more strigose beneath, palmatifid almost to base into narrow-cuneate segments which are sharply lobed about half way, then with sharp lanceolate teeth 2–10 mm. long, 1–3 mm. wide; petioles slender, 2–5 cm. long, scarcely widened at base; inflorescence a crowded many flowered raceme to ca. 1 dm. long, densely glandular-pubescent; lower bracts reduced leaves, upper lance-linear, 6–10 mm. long; pedicels 1–4 cm. long, arched-ascending; bracteoles lance-linear, acuminate, 5–6 mm. long, subtending the flower; sepals purplish blue, white-villous, the upper lance-ovate, 20 mm. by 10 mm., rounded-obtuse, the spur 20–22 mm. long, 3 mm. wide at base, quite sharply pointed; lateral sepals oblong, 22 mm. by 8 mm., rounded at tip; lower sepals oblong, 22 mm. by 7 mm., narrower at tip; upper petals bluish, the laminae almost straight, 14 mm. long, 3 mm. wide, entire, rounded at tip, the spur 19–20 mm. long; lower petals with an obovate lamina 12 mm. by 8 mm., deeply emarginate, bearded at base, sparsely so above, claw 5 mm. long, appendiculate; stamens 6–7 mm. long; carpels 5, pubescent to almost glabrous.

TYPE: Between the northern frontier of Sikkim and Lhassa, King's collector. Not seen.

REPRESENTATIVE SPECIMENS: **Tibet:** *Ludlow & Sherriff 527, 855*; *B. J. Gould 508*; *L. A. Waddell*, Sept. 5, 1904.

159. **Delphinium knorringianum** B. Fedtsch. Jour. Roy. Hort. Soc. **61**: 196, 197, *fig. 43.* 1936. FIG. 14, F.

Perennial from an elongate root, the stems ascending to suberect, 3.5–4.5 dm. tall, more or less branched above, with short stiff spreading hairs below and glandular in the inflorescence; leaves mostly basal, with petioles 8–12 cm. long, slightly dilated below; blades 4–5 cm. broad, more or less pentagonal, 5-parted, the parts cuneate toward base, indistinctly 5-lobed at apex, the lobes oblong-ovate, more or less rounded at tip, to 7 mm. wide; stem leaves reduced, the upper subsessile, with entire broadly linear lobes; inflorescence with one to few spreading branches and bristly glandular-hairy, each branch subcorymbose, with 3–5 blue-purple flowers; lower bracts 3–5-parted; pedicels 3–7 cm. long, divaricate; bracteoles 2, linear, ca. 4 mm. long, near the middle of the pedicel; upper sepal subglabrous to glandular-pubescent, ovate, 17–18 mm. long, 11 mm. wide, obtuse, the spur straight, 21–22 mm. long, bilobed at tip, the lobes divergent; lateral sepals broadly ovate, 22 mm. by 12 mm., pubescent; lower sepals pubescent, 22 mm. by 12 mm., ovate; petals pale, blue purple, the upper with elongate-elliptic limb, clawed, bidentate, glabrous, ca. 14 mm. long, the spur 19–20 mm. long; lower petals with elongate-linear limb, rounded at top, bidentate, 6 mm. long, narrowed gradually into a claw 7 mm. long; follicles 2–3, densely pubescent.

TYPE: Asia Media, Kirghistan, Osh district, sources of Akhbura River (Alai Range), July, 1913, *O. E. Knorring 368* (LE); seen. Illustrated in original description. No other material seen.

160. **Delphinium lancisepalum** Hand.-Mazz. Acta Horti Gothob. 13: 55. *fig. 2a.* 1939. FIG. 14, G.

Delphinium pachycentrum Hemsl. var. *lancisepalum* (Hand.-Mazz.) W. T. Wang, Acta Bot. Sinica **10**: 140. 1962 and var. *pseudo-lancisepalum*. Wang. *loc. cit.*

Stem 2–5 dm. tall, 3–4 mm. thick, simple or with few short sterile branches, white-strigulose, densely and equally leafy to inflorescence; petioles mostly 3–6 cm. long, slender, more or less strigulose, dilated at base; blades cordate-orbicular in outline, mostly 4–9 cm. in diameter, minutely strigulose on both the upper green and lower pale surfaces, trifid almost to base, the 2 lateral segments deeply bifid, the 5 parts thus created rhombic-lanceolate to -ovate, trilobed to about the middle then deeply toothed, the teeth lance-oblong to ovate, 2–4 mm. wide, acute; inflorescence a dense raceme, 5–12-flowered, with dense retrorse pubescence; lower bracts leafy, upper linear, filiform, 1–1.2 cm. long; pedicels 1.5–5 cm. long, almost erect; bracteoles filiform, 10–12 mm. long, next to the flower; sepals blue to pinkish, somewhat strigulose and ciliate, the upper lance-ovate, 19–20 mm. long, 8 mm. wide, acuminate, the spur almost straight, 20–23 mm. long; lateral sepals lance-ovate, 20–22 mm. long, 8 mm. wide, acute; lower sepals with about the same dimension, more acuminate; upper petals deep violet, the laminae almost straight, deeply retuse, 15 mm. long, glabrous, the spur 19 mm. long; lower petals with laminae 9 mm. long, 7.5 mm. wide, with a small basal patch of bristly hairs and 2 gaping oblong lobes 4–5 mm. long, claw 6.5 mm. long; stamens 7–8 mm. long, quite broad in lower part, glabrous or ciliate; anthers dark, oblong, 1.2–1.4 mm. long; follicles 3, hairy.

TYPE: Sikang, district Kangting (Tachienlu), Ta-pao-shan, 4500 m., Aug. 20, 1934, *Harry Smith 11248* (W?), not seen; isotypes (A, BM, MO, NY), seen.

COLLECTIONS SEEN: **Szechwan:** *Legendre 1563*; *H. Li 78175*.

161. **Delphinium lasiocarpum** Tamura, Acta Phytotax. & Geobot. Kyoto **15**: 196. 1954.

Stem striate, sparsely recurved-pilose or subglabrous; cauline leaves short petioled, the blades reniform, 6 cm. long, 12 cm. wide, curved-pilose on veins of both sides, tripartite, the middle segment pinnatifid, the lateral bifid, the lobes unequally pinnatifid and the lower incised; inflorescence many flowered, paniculately branched, yellow-villous above; lower bracts 3-parted or trifid, the upper linear; pedicels to 5 cm. long, with opposite bracteoles above the middle; flowers blue, 2.5 cm. in diameter, the spur longer than the sepals, to 20 mm. long, 5 mm. wide at base, slightly curved; upper petals glabrous, 25 mm. long, with incurved spur 7–8 mm. long; lower petals bifid or lobed, white bearded, the lobes acute or obtuse; follicles 3, villous, 10 mm. long without the style, this 4–5 mm. long; seeds smooth, winged.

TYPE: Tibet near Lhasa, Panchogan, *103900* (KYO); not seen. I have been unable to borrow any material of this species, so can offer only a translation of the original description. The author thinks it related to *Delphinium altissimum*.

162. **Delphinium laxicymosum** W. T. Wang, Acta Bot. Sinica 10: 148. 1962.
FIG. 14, H.

Stem 5–7.5 dm. tall, ca. 4 mm. thick at base, loosely white-hirsute below, glabrous above, branched, equally foliose; lower cauline and middle leaves longish petioled, the blades broadly pentagonal, 4–8 cm. long, 6–12.5 cm. wide, cordate, 3-parted almost to base, the middle part rhombic, the lateral obliquely triangular-ovate, all lobulate and toothed, loosely strigulose on both surfaces; petioles 1.5 to 2 times the laminae, loosely hirsute; upper cauline leaves reduced; flowers in 3–5-flowered corymbiform clusters; lower bracts to 3 cm. long, trifid to entire, upper subfiliform; pedicels 2–7 cm. long, glabrous, divergent; bracteoles near the middle of the pedicel, filiform, 2–2.5 mm. long, 0.2 mm. wide; sepals intense blue, elliptic-obovate or elliptic, 14 mm. long, puberulent, the spur 23–25 mm. long, subulate, slightly to much decurved; upper petals yellowish, 11 mm. long; lower blue, 6 mm. long, bifid to slightly below the middle into lance-oblong obtuse lobes, long-ciliate, yellow bearded near base, claw 6 mm. long, short-appendiculate; stamens glabrous; carpels 3, glabrous.

TYPE: Szechwan, north of Wen-chuan Hsien, 3100 m., July 20, 1930, *F. T. Wang 21767* isotype (A), seen.

Another collection probably to be referred here is Tsé-Kou, *Abbé Monbeig* (UC).

Wang said his proposed species, ***Delphinium laxicymosum***, is near *D. potaninii*, but with stem and petioles hirsute and inflorescence more cymose.

163. **Delphinium laxiflorum** DC. Syst. 1: 360. 1817. FIG. 14, I.

Delphinium villosum Stev. ex DC. var. *laxiflorum* (DC.) Huth, Bot. Jahrb. **20**: 412. 1895.

? *Delphinium elatum* var. *anomalum* Kunth ex Huth, *loc. cit.* 399. From the Altai Mts. and with light colored petals, hence not *D. elatum*.

Delphinium amoenum Stev. ex DC. Syst. **1**: 546. 1817. Placed in synonymy here by Nevski in Komarov, Fl. U.S.S.R. **7**: 158. 1937. I have not seen authentic material.

Said to be vegetatively like *Delphinium dyctiocarpum* DC. (Group IX), i.e. 6–15 dm. tall, robust, quite glabrous, large leaved, the lower petioles to 2 dm. long; leaf blades rounded, pentagonal in outline, the upper ca. 4 cm., the lower 15 cm. broad, 3-, 5-, or 7-parted to within 1 or 2 cm. of the base, the parts not deeply laciniate; inflorescence a dense raceme or open panicle, many flowered; bracts mostly entire; pedicels 1–3 cm. long; bracteoles linear, 3–7 mm. long, well below the flower; sepals violet-blue, glabrous, 10–12 mm. long, spur 12–20 mm. long; petals blue, or the upper whitish, the upper erose or scarcely bidentate, the laminae 7 mm. long, spur 10 mm.; lower petals pale blue, the laminae 4 mm. long, 2-lobed, bearded, the claw 4 mm. long; ovary apparently glabrous to pubescent.

TYPE: "Hab. in Sibiria (hortul.)" (G? not seen). A specimen loaned from Leningrad as "D. dictyocarpum D. Altai, 1826, Herb. Ledebour" has blue petals and seems to be authentic material of *D. laxiflorum*.

Some other specimens apparently referable here are all Siberian and differ from *D. dyctiocarpum* in not having almost black petals.

Siberia: Semipalatinsk, *Krylov & Sergievskaya* in 1929 (NY); *Karelin & Kiri-*

loff in 1840 (MO). Altai borealis, *Erastova* in 1909 (BM); *V. Burdakova* in 1931 (NY); *Chaffanjon 1019* (P).

164. **Delphinium lilacinum** Hand.-Mazz. Symb. Sinicae 7: 277. 1931.

Delphinium handelianum W. T. Wang, Acta Phytotax. Sinica **6**: 365. 1957.

Rhizome very short, the roots slender; stem 5–6 dm. tall, striate, hairy, equally leafy, weakly branched almost from base; leaves pentagonal, 7–12 cm. in diameter, 5-fid to three-fourths or seven-eighths their length, the divisions rhombic-ovate, the margins rarely contiguous, deeply incised, then coarsely crenate, green on both surfaces, sparsely strigose above, reticulate veined beneath; petioles one and one-half times as long as the middle laminae, the upper half as long, more or less vaginate, sparsely hirsute; racemes terminal on stems and branches, to 14-flowered, densely and retrorsely white-strigulose and somewhat yellow-hirsute; lower bract 3-parted, others entire, upper subulate-lanceolate, half as long as pedicels or the uppermost as long; pedicels divergent, 1–5 cm. long; bracteoles in upper fourth of pedicel, lance-linear, ca. 5 mm. long, ciliate; sepals lilac, broadly ovate, rounded at apex, sinuate-attenuate, white strigulose and yellow-hispid, densely ciliolate; spur about twice as long as blade, attenuate; petals about equal to sepals, the upper 3 mm. wide, with 2 linear lobes 1.5 mm. long; lower petals with lamina equaling claw, 3 mm. wide, cut into 2 narrow lobes for two-thirds its length, ciliate and long white-bearded; stamens 6 mm. long; anthers brown, oblong, 1 mm. long; carpels 3, sparsely white-strigose.

TYPE: Beyendjing (Peyentsin), Yunnan, forests near Guti, Aug. 29, 1919, *Ten 1292* (PE?); not seen. The only collection that I have seen which seems to me possibly representing this species is *Cavalierie 2936* (E), also from Yunnan. This proposed species, *Delphinium lilacinum*, may be too close to *D. pogonanthum*.

165. **Delphinium lipskii** Korsh. Bull. Acad. Pétersb. V. **9**: 402. 1898. FIG. 14, J.

Rhizome woody, elongate; stems erect, 6–7.5 dm. tall, cinereous-pubescent below, glabrous in the inflorescence, openly branched above; leaves grayish pubescent beneath, glabrous above, 4–5 cm. wide, the lower broadly reniform, trisect almost to the base, the segments sessile, the lateral 2-parted almost to base, all segments 3-lobed into entire or incised lobules (these oblong, 4–10 mm. long, 3–6 mm. wide); parts of the upper leaves lanceolate, entire; bracts all entire, lance-linear, 4–5 mm. long; pedicels glabrous, 3–4.5 cm. long; bracteoles 2–3, minute, at middle of pedicel or below; upper sepal ca. 14 mm. by 7 mm., apiculate, intense blue, spur 18 mm. long, 3.5 mm. wide at base, spreading, subcylindric, blunt; lateral sepals oblong-elliptic, 14 mm. by 8 mm., rounded; lower sepals 14 mm. by 6 mm., apiculate; upper petals pale blue, oblique, the laminae ca. 13 mm. by 4 mm., shallowly incised, the spur ca. 19 mm. long; lower petals blue, the round-obovate laminae 6 mm. long, 4 mm. wide, deeply incised, white-hairy, the claw 5 mm. long; stamens 7–8 mm. long, ciliate; anthers yellow, 1 mm. long; follicles 3, hirsute, 14–20 mm. long, with blue styles an additional 2 mm. long.

TYPE: Buchara (Bokhara), Darwaz, near Chumbau River, between Sary-dasch and Kala-i-chum, 1300 to 1600 m., June, 1897, *Korshinsky* (LE), seen; photo. (A), seen.

166. **Delphinium ludlowii** Munz, sp. nov. FIG. 14, K.

Delphinium ludlowianum Chowdhury ex Mukerjee, Bull. Bot. Surv. India **2**: 293–296. 1960; *nomen.*

About 1 m. tall, the stems sparingly and minutely strigulose, more densely so in the inflorescence, rather slender, remotely leafy; cauline leaves pentagonal-reniform in outline, green above, paler beneath, strigulose on both surfaces, to about 12 cm. broad, 5-fid to about 1 cm. from base, the segments cuneate-rhombic, incised about halfway to the midrib into 3 broad lobes, these shallowly and evenly rather coarsely toothed, the teeth lance-oblong, mostly 3–5 mm. long, 2–3 mm. wide, mucronate; petioles to ca. 12 cm. long, slender, subglabrous, slightly vaginate at base; leaves gradually reduced toward the inflorescence into leafy bracts; inflorescence mostly a lax 6–12-flowered raceme 1–2.5 dm. long, closely strigulose; upper bracts petiolate, lanceolate, 1–2.5 cm. long, 2–6 mm. wide; pedicels arched, 1–5 cm. long; bractlets subtending the flower, subspatulate, 4–6 mm. long; sepals rich purple to pale maroon, minutely strigulose; the upper sepal oblong-ovate, 13–15 mm. long, 11–12 mm. wide, with an extended blunt tip, the spur spreading, 12–15 mm. long, 4.5 mm. wide at base, rather abruptly narrowed to an acute tip; lateral sepals oblong-obovate, 12 mm. by 8 mm., subtruncate; lower sepals 13 mm. by 6–7 mm., rather pointed; petals bluish, the upper laminae strongly oblique, 10 mm. long, 2.5 mm. wide, glabrous, bidentate, the spur 11–13 mm. long; lower laminae oblique, oblong, 5 mm. by 2.5 mm., divided almost halfway into 2 oblong lobes, subglabrous except near the central base, the claw 5 mm. long; stamens 5–6 mm. long, glabrous; anthers dark, oblong, 1 mm. long; follicles 3, divergent, glabrous, 12–13 mm. by 3 mm., the styles an additional 2.5 mm. long; seeds angled.

Caules ca. 1 m. alti, minute strigulosi, tenues, remote foliosi; folia caulium pentagono-reniformia, supra viridia, infra pallida, 6–12 cm. lata. 5-fida, segmentibus cuneato-rhombeis, incisis, dentatis; petioli 6–12 cm. longi, tenues, subglabri; inflorescentia cum 6–12 floribus, laxa, 1–2.5 dm. longa, strigulosa; bracteae superiores petiolatae, lanceolatae, 10–25 mm. longae, 2–6 mm. latae; pedicelli 1–5 cm. longi; bracteolae subter florem, subspatulatae, 4–6 mm. longae; sepala purpurea vel purpureo-rubra, strigulosa, 12–13 mm. longa, 4–7 mm. lata, calcar 12–15 mm. longum, base 4.5 mm. latum; petala subcaerulea, laminae superiores obliquae, 10 mm. longae, 2.5 mm. latae, glabrae, bidentatae; laminae inferiores obliquae, oblongae, 5 mm. longae, 2.5 mm. latae, bilobatae, base barbatae, unguis 5 mm. longus; stamina glabra; antherae oblongae, 1 mm. longae; folliculi 3, divergentes, glabri, 12–13 mm. longi; styli 2.5 mm. longi; semina angulata.

TYPE: Northeastern Bhutan, Trashiyangsi, 3300 m., Aug. 28, 1934, among stones in dense jungle, *Ludlow & Sherriff 894* (BM); isotype, (E).

OTHER NUMBERS SEEN. **Bhutan:** Singhi Dzong, Khoma Chu, *Ludlow & Sherriff 470* (BM, E); Me La, *Ludlow & Sherriff 368* (BM, E); Trashiyangsi, *Ludlow & Sherriff 1008* (BM); Singhi Kusted, *Cooper* for *Bulley, 4322* (BM); Bamthang, *Ludlow & Sherriff 16972* (BM); Rudo La, *Ludlow & Sherriff 20978* (BM); Dur Chu, *Ludlow & Sherriff 19485* (BM).

One of my great pleasures when working at the British Museum of Natural History in 1965 was to become acquainted with Mr. Frank Ludlow, whose extensive collection from the Himalaya and Tibet have been of great value in this study, and I am delighted to name this species for him! ***Delphinium ludlowii*** seems close to ***D. altissimum***, but has more evenly toothed leaves, bracteoles nearer the flower, and sepals more minutely pubescent.

Instead of using the name ***Delphinium ludlowianum*** which Chowdhury wrote on some herbarium sheets in Great Britain, and which Mukerjee listed in the Bull. Bot. Surv. India **2**: 293–6. 1960, without description, I feel that I should employ a different epithet. I have had no contact with Dr. Chowdhury to learn whether he wished his name published, and have been unable to ascertain his whereabouts. I am, therefore, using the name ***Delphinium ludlowii*** for my new species.

167. **Delphinium malabaricum** (Huth) Munz, comb. nov. FIG. 14, L.

Delphinium dasycaulon Fresen. var. *malabaricum* Huth, Bot. Jahrb. **20**: 435. 1895.

Perennial from a woody cylindrical rhizome; stem 3–10 dm. tall, rather slender, glabrous to retrorse-pubescent below, strigose in the inflorescence, simple to few branched above, remotely few leaved; lower petioles 1–2.5 dm. long, glabrous to somewhat pubescent, strongly vaginate at base, the few cauline petioles reduced, the upper very short; lower leaf blades more or less reniform in outline, 3–10 cm. broad, glabrous or nearly so above, with few to many stiff hairs on the margin, and along veins beneath, 5- or 7-fid to 1/3 or 1/2 their length, the broad cuneate-obovate segments mostly bifid, then coarsely toothed with broad entire or toothed teeth with mucronate tips, middle cauline leaves more deeply divided, the segments entire to 3-toothed or more; inflorescence a series of 1 to few rather dense, several to many flowered racemes; lower bracts leafy, trifid, to 2 or 4 cm. long, upper linear, entire, 6–10 mm. long; pedicels divergent, 5–20 mm. long, strigose; bracteoles subulate, near middle or base of pedicel; sepals bright blue, with a white subterminal spot, strigose to subglabrous; upper sepal ovate, 10–14 mm. long, 5–7 mm. wide, the spur subconic, 7–9 mm. long, 3–4 mm. wide at base, rather obtuse; lateral sepals elliptic-obovate, truncate-rounded at apex, 13–16 mm. long, 7–9 mm. wide; lower sepals narrowly obovate, 11–13 mm. long, 5–7 mm. wide; upper petals pale, the laminae glabrous, slightly oblique, ca. 10 mm. long, with 2 terminal round-tipped lobes ca. 2.5 mm. long, the spur 7 mm. long; lower laminae blue, round-oblong, 7 mm. by 5 mm., divided to near the base, short-ciliate and strigulose, the claw 5 mm. long; stamens 6–7 mm. long, ciliate; anthers bluish, almost round, less than 1 mm. long; follicles 3, strigulose, divergent, perhaps 10 mm. long, the styles an additional 3 mm.

TYPE: The only collection cited by Huth which is, therefore, the type, is, E. India, Malabar Concan, *Stocks*, cited from G, B, W, LE . I have seen none of these, but have seen the collections from GH and P. I suggest the Geneva specimen as the holotype, the others as isotypes.

Apparently a species of the Western Ghats in India and quite distinct from the Ethiopian *Delphinium dasycaulon* in its non villous stems, longer bracts, glabrous upper petals, etc.

MATERIAL SEEN. Khandala, *Santapau 11551* and *11552* (MO); Purandhar, *Santapau 13868* and *13869* (MO); Iooner, Deccan, *Stocks* (K); Bombay, *Dalzell* (K); *Ghanta* (K).

168. **Delphinium micropetalum** Finet & Gagnep. Bull. Soc. Bot. France **51**: 479. 1905. FIG. 14, M.

Delphinium micropetalum subsp. *confusum* Choudhury ex Mukerjee, Bull. Bot. Surv. India **2**: 293–296. 1960; *nomen.*

Delphinium jugorum Hand.-Mazz. Symb. Sinicae **7**: 273. 1931. Based on *Handel-Mazzetti 9712* from Mekong-Salwin Divide, n.w. Yunnan (W). Not seen, but the published figures are like those of *D. micropetalum.* Put into synonymy also by W. T. Wang, Acta Bot. Sinica **10**: 142. 1962.

Stem striate, 4.5–10 dm. tall, simple or sparsely branched above, thick, retrorsely hirtellous, with 3–4 equally spaced leaves, or leafless above; leaves suborbicular in outline, rather stiff-strigose above and beneath, the lower cauline the largest, 11–14 cm. in diameter, trifid to 1 cm. from the base, all parts broadly rhombic-obovate, obtuse, trifid, coarsely and irregularly narrowly cuneate, dentate and incised, the teeth subovate, 1–5 mm. long and almost as wide; lower petioles 3–4 times as long as the blades, vaginate; racemes densely 8–13-flowered, those on the branches reduced, the axis white-strigose and with yellow glandular hairs; lower bracts foliaceous, petioled, dilated at base, 3–5-lobed, 1–2 cm. long; the others oblong-lanceolate, entire; pedicels 1.5–5 cm. long, divergent; bracteoles puberulent, lance-linear, 10–12 mm. long, just below the flower; sepals intensely blue, upper sepal ovate, 14 mm. by 8 mm., the spur 12–14 mm. long, 3.5 mm. wide at the base; lateral sepals oblong, 16 mm. by 8 mm., subtruncate; lower sepals asymmetrically obovate, 18 mm. by 12 mm., broad at apex; lamina of upper petals yellowish, at right angles to the spur, 9 mm. long, 3.5 mm. wide, obtuse or emarginate, the spur 12 mm. long; lower laminae 5 mm. by 3 mm., oblique, oblong, bifid one-fourth its length, the lobes obtuse, short hairy below the middle, claw 6.5 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, oblong; carpels 3, puberulent, to 10 mm. long, the style an additional 3 mm.

TYPE: Western Yunnan, Tsé-Kou, April 1895, *Soulié 1098* (P); seen.

SPECIMENS SEEN. 3300–4400 m. **Southeastern Tibet:** *Rock 22401, 22402, 22373.* **Yunnan:** Yü *20783, 20639, 20369, 22320*; *Forrest 221*; *Tsai 58069.* **Burma:** Chawchi Pass, *Farrer 1867, 1156*; *Forrest 27516, 27225, 25091*; *Lepcha 865.*

169. **Delphinium mitzugense** Ulbr. Notizbl. Bot. Gart. Berlin **12**: 358. 1935. FIG. 15, A.

Delphinium taliense Franch. var. *glabrum* W. T. Wang, Acta Bot. Sinica **10**: 159. 1962. Based on same type as *D. mitzugense.*

? *Delphinium taliense* var. *pubipes* Wang, *loc. cit.* I have not seen cited material.

Stem 10–12 dm. high, erect, stout, glabrous and glaucous below with some red, more or less bluish and glaucous above, branched above, with few remote leaves; basal leaves gone by anthesis, the lower cauline with petioles 1.5–2 dm. long, stout, glabrous, vaginate, the upper shorter and more slender; blades rounded in outline, the lower 10–13 cm. in diameter, scattered-strigose above and beneath, paler beneath, palmately 7-fid to 1 cm. or less from the base, the segments subcuneate-obovate, mostly 3-lobed distally, each lobe divided into 2–3 smaller, oblong, acute to obtuse mucronulate divisions 2–5 mm. wide, the uppermost leaves divided into 5 lanceolate entire segments; inflorescence few branched, paniculate, glabrous, lax; bracts subulate, 8–15 mm. long, bluish; pedicels slender, ascending, 2–5 cm. long, blue; bracteoles subulate, 5–8 mm. long, placed near the middle of the pedicel; sepals blue, somewhat strigulose; the upper sepal ovate, 13–15 mm. long, 7 mm. wide, obtuse, the spur horizontal-decurved, 20–25 mm. long, 4 mm. wide at base, subcylindric, the tip ca. 1.5 mm. wide; lateral sepals 15 mm. long, 8 mm. wide, rounded-truncate, strigose on median nerve; lower sepals subelliptic, 14 mm. long, 6 mm. wide, obtuse; petals bluish, the upper laminae slightly oblique, spatulate, erose, 9 mm. long, the spur 20 mm. long; lower laminae oblique, oblong-obovate, 7–8 mm. long, deeply cleft into lance-oblong lobes, yellow-bearded at base of lamina, the remainder with long white hairs and ciliate, claw 5 mm. long; stamens 4–6 mm. long, moderately dilated below, glabrous; anthers bluish, 1 mm. long; carpels 3, pilose.

TYPE: Southwestern Szechwan, Muli, Mt. Mitzuga, 4300 m., *J. F. Rock 18317*, holotype (B?), not seen; isotypes (GH, US), seen.

Another collection is Szechwan, Huei-li Hsien, *T. T. Yü 1598* (GH). Since Wang reduced *D. mitzugense* to varietal status under *D. taliense*, he must have considered the two very close, but the latter has a much wider lamina of the lower petal, and an emarginate upper petal.

170. **Delphinium muliense** W. T. Wang, Acta Phytotax. Sinica **6**: 365. 1957. FIG. 15, B.

Delphinium pachycentrum Hemsl. var. *tenuicaule* Chen, Bull. Fan Mem. Inst. Biol. Peiping (n.s.) **1**: 168. 1948. Type, *T. T. Yü 6989*, 3300 m., Muli, Kulu (PE?); not seen. Reduced to synonymy of his new species (*D. muliense*) by W. T. Wang, Acta Bot. Sinica **10**: 149. 1962.

Delphinium muliense var. *minutibracteolatum* W. T. Wang, Acta Bot. Sinica **10**: 149. 1962. Based on *T. T. Yü 14371*, which I have not seen, but the separation because of reduced bracteoles hardly seems well founded.

Perennial, 6–7 dm. tall, striate, subglabrous, slender, simple or with short sterile branches, equably leafy; basal leaves lacking at anthesis; cauline laminae pentagonal, cordate, 2.5–5.5 cm. long, 4–7 cm. wide, 3-sect, the central segment rhombic, petiolulate, trifid to its middle, lateral segments 2-parted, bifid to trifid, all parts incised into dentate lobes, strigose above, pubescent beneath on nerves; petioles 4–15 cm. long, glabrous, somewhat vaginate; raceme few to many flowered, 6–20 cm. long, retrorsely white-hairy and yellow-glandular; lower bracts leaflike, but smaller, upper lanceolate to linear, 8–14 mm. long; pedicels erect-spreading, 1–5 cm. long; bracteoles in upper third of pedicel, lanceolate to linear, 5–13 mm. long, 1–2 mm. wide; flowers bluish-purple to yellowish, the upper sepal obovate, cymbiform, 12–15 mm. long, the spur somewhat decurved, 20–25 mm. long; other sepals oblong-obovate, obtuse, 14–18 mm. long; petals bluish, the upper laminae ca. 8 mm. long, obliquely truncate, glabrous to pubescent, entire, spur 15–20 mm. long; lower laminae 5–6 mm. long, ovate, yellow bearded near base, bifid to below the middle with oblong triangular lobes strigose and ciliate, claw 4.5–5.5 mm. long, appendiculate; stamens glabrous; carpels puberulent on sutures.

TYPE: Szechwan, Muli, Ha-lin, 3500 m., July 11, 1937, *T. T. Yü 6989?*, published as 6988 (PE, A), photo. (A); photo. and isotype seen.

EXAMPLES. Seemingly agreeing with the type, Muli, *Rock 16916*. **Tibet**: Yigrong Gorge, 3300 m., *Kingdon Ward 12190*; Kongbo Prov., *Ludlow, Sherriff & Taylor 6920*; Tsanpo Valley, *Ludlow, Sherriff & Taylor 5397*; Lochen La. *Kingdon Ward 12240*; Shweli-Salwin Divide, *Forrest 11792*.

171. **Delphinium orthocentrum** Franchet, Bull. Soc. Philom. Paris VIII. **5**: 178. 1893. FIG. 15, C.

Delphinium szechuanicum Ulbr. Repert. Sp. Nov. **14**: 298. 1916. Type, West Szechwan, *E. H. Wilson 1088* (B?) not seen; isotypes (GH, US), seen.

Perennial from a woody root, the stem glabrous below, erect, simple, leafy throughout, 5–10 dm. tall, grayish in inflorescence with appressed short hairs; petioles to 1 dm. or more long, somewhat dilated at base; laminae of leaves somewhat strigulose on both sides, 1 dm. or more in diameter, deeply 5-parted, the segments broadly obovate-rhombic, broad at base, unequally incised into acute lobes, the terminal one elongate; inflorescence a rather crowded raceme with perhaps 8–20 flowers; bracts

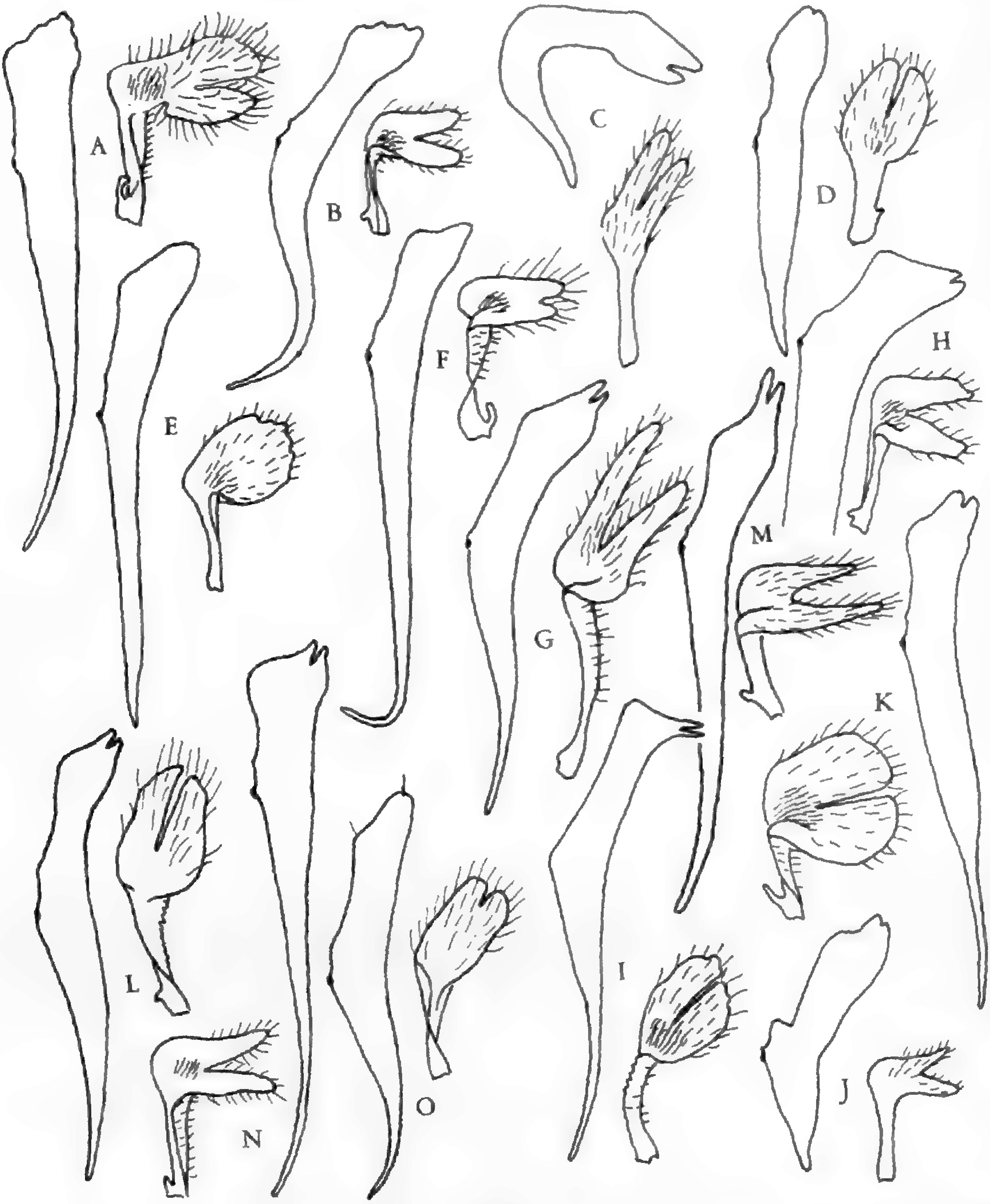

FIGURE 15. **Delphinium,** GROUP VIII. Petals, the upper spurred, the lower clawed. A. *D. mitzugense*; blade of upper petal 9 mm. long, spur 20 mm.; blade of lower petal 7 mm. long, claw 5 mm.; drawn from *Rock 18317* (US). B. *D. muliense*; blade of upper petal 8 mm. long, spur 15 mm.; blade of lower petal 5 mm. long, claw 4 mm.; drawn from *Kingdon Ward 12190* (BM). C. *D. orthocentrum*; blade of upper petal 10 mm. long, spur 11 mm.; blade of lower petal 7 mm. long, claw 6 mm.; drawn from *Harry Smith 3541* (A). D. *D. osseticum*; blade of upper petal 9 mm. long, spur 10 mm.; blade of lower petal 6 mm. long, claw 4.5 mm.; drawn from *Busch* TYPE (LE). E. *D. pachycentrum*; blade of upper petal 11 mm. long, spur 16 mm.; blade of lower petal 6 mm. long, claw 6 mm.; drawn from *Pratt 462* ISOTYPE (BM). F. *D. pogonanthum*; blade of upper petal 10 mm. long, spur 25 mm.; blade of lower petal 6 mm. long, claw 6 mm.; drawn from *Feng 2115* (A). G. *D. scabriflorum*; blade of upper petal 12 mm. long, spur 15 mm.; blade of lower petal 10 mm. long, claw 6 mm.; drawn from *Ludlow & Sherriff 3342* (BM). H. *D. sherriffii*; blade of upper

all foliaceous, lanceolate to linear, entire or few toothed, 1–5 cm. long; pedicels erect, pubescent, 2–4 cm. long; bracteoles 2–3, linear, placed from just below the flowers to near the middle of the pedicel, 10–15 mm. long; sepals blue-violet, pubescent, the upper one oblong-ovate, 15 mm. long, 6 mm. wide, obtuse, the spur erect, obtuse, 12–16 mm. long, 3.5 mm. thick at the base; lateral sepals 13 mm. by 7 mm., oblong-elliptic, pubescent along midrib, obtuse; lower sepals 15 mm. by 7 mm., pointed, pubescent; upper petals bluish, the laminae 10 mm. long, almost straight, unequally bidentate at apex, the spur thick at base, recurved, narrow at tip; lower petals bluish, the claw 6 mm. long, the bearded lamina oblong, 7 mm. long, divided ca. 4.5 mm. into lance-oblong segments; stamens 7–8 mm. long; anthers dark, 1 mm. long; follicles 3, sparsely silky.

TYPE: Szechwan, in western part, *Potanin* in 1885 (P); seen.

REPRESENTATIVE MATERIAL. **Szechwan:** *H. Smith 4200, 3541*; *E. H. Wilson 3093*; *W. P. Fang 4037, 4038, 1083.*

172. **Delphinium osseticum** N. Busch, Bull. Acad. Sci. U.S.S.R. 7: 449. 1931. FIG. 15, D.

Stem ca. 1 m. tall, more or less muricate-roughened to bristly with white spreading hairs, leafy; petioles thickly hairy, not vaginate at base; leaf blades to 1.5 dm. in diameter, deeply 5-fid into rather narrow segments, densely and softly hairy, especially on the upper surface, more or less appressed underneath where the hairs along the veins are longer, the blades pinnately shallowly laciniate or serrulate into lanceolate teeth or lobes 2–5 mm. wide, 4–15 mm. long; inflorescence rather a dense raceme, 2–5 dm. long, branched, with soft pubescence; middle and upper bracts entire, lanceolate, hairy, bluish, 15–25 mm. long; pedicels ascending or erect, 1–4 cm. long; bracteoles densely white-hairy on the back and edge, ovate, ovate-elliptic or ovate-lanceolate, acuminate, usually 7–10 mm. long, 3–5.5 mm. broad, bluish, located near the flower; sepals blue, the upper membranous, strongly veined, with long white hairs, strongly cu-

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petal 9 mm. long, spur 20 mm.; blade of lower petal 6 mm. long, claw 5 mm.; drawn from *Ludlow & Sherriff 5833* TYPE (BM). I. *D. siamense*; blade of upper petal 11 mm. long, spur 18 mm.; blade of lower petal 6 mm. long, claw 6 mm.; drawn from *Kerr 6612*, ISOTYPE (BM). J. *D. sparsiflorum*; blade of upper petal 10 mm. long, spur 7.5 mm.; blade of lower petal 4 mm. long, claw 5 mm.; drawn from *Rock 13191* (GH). K. *D. taliense*; blade of upper petal 9 mm. long, spur 22 mm.; blade of lower petal 7 mm. long, claw 5 mm.; drawn from *Bodinier & Ducloux 370* (P). L. *D. ternatum*; blade of upper petal 10 mm. long, spur 15 mm.; blade of lower petal 6.5 mm. long, claw 5.5 mm.; drawn from *Regel* at Hissar (LE). M. *D. trifoliolatum*; blade of upper petal 10 mm. long, spur 20 mm.; blade of lower petal 7 mm. long, claw 6 mm.; drawn from *Henry 7448* (GH). N. *D. umbrosum*; blade of upper petal 8 mm. long, spur 24 mm.; blade of lower petal 6 mm. long, claw 5 mm.; drawn from *Wang 69052* (A). O. *D. uralense*; blade of upper petal 10 mm. long, spur 13 mm.; blade of lower petal 5 mm. long, claw 5 mm.; drawn from *Litwinow* TYPE (LE).

cullate, 12 mm. long, 7 mm. wide, the spur 13 mm. long, 4 mm. wide at base, straight; lateral sepals 12 mm. by 8 mm., rounded-obovate; lower cucullate, 12 mm. by 5 mm.; petals pale, the upper laminae slightly oblique, 9 mm. long, emarginate, glabrous, the spur 10 mm. long; lower laminae slightly oblique, ovate, 6 mm. by 5 mm., bifid halfway into 2 round-oblong ciliate lobes, the claw broad, 4.5 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, 1.5 mm. long; carpels 3, glabrous.

TYPE: Upper borders of forest, Caucasus, eastern cis-Caucasus (Ossetia), at 1800 m., July 23, 1930, *Busch* (LE), seen.

ILLUSTRATION. Bull. Acad. Sci. U.S.S.R. 7: 451. 1931.

173. **Delphinium pachycentrum** Hemsl. Jour. Linn. Soc. Bot. 29: 301. 1892. FIG. 15, E.

Delphinium pachycentrum subsp. *hemsleyi* Brühl ex Brühl & King. Ann. Bot. Gard. Calc. **5**: 108. 1896.

Delphinium pachycentrum var. *lobatum* W. T. Wang, Acta Bot. Sinica **10**: 140. 1962.

Delphinium sertiferum Franchet, Bull. Soc. Philom. Paris VIII. **5**: 171. 1893. Type, Tatsienlu, Szechwan, *R. P. Soulié 24* (P); seen.

Perennial from a thick woody root, stem simple except at summit, 4–6 mm. thick, 3–4 dm. tall, leafy throughout; petioles slender, slightly dilated at base, strigulose, 3–10 cm. long; leaf blades divided almost to base into 3 or 5 segments (the 2 lateral then divided almost to base), rounded-pentagonal in outline, 3–10 cm. in diameter, ultimately shallowly incised or toothed, the teeth oblong-ovate or deltoid, acute; inflorescence close-pubescent, somewhat corymbiform, the lower pedicels elongate, solitary or on short suberect branches, the upper 1–5 cm. long; lower bracts reduced foliage leaves, the upper smaller; bractlets linear, 5–8 mm. long, near the flower; sepals pale blue, densely appressed-pubescent; upper sepal 14–16 mm. long, 9–10 mm. wide, ovate, acutish, the spur straight, 18–22 mm. long, 3–3.5 mm. wide at base, only slightly narrowed to a blunt end; lateral sepals 14–16 mm. long, 6–8 mm. wide, oblong-ovate, obtuse, pubescent on whole outer surface; lower sepals slightly longer, oblong; laminae of upper petals whitish yellow, straight, 13–14 mm. long, rounded and entire at apex, the spur 20–22 mm. long; lower laminae blue, almost round, 9–10 mm. long, divided 1–2 mm., hirsute at base, sparsely so otherwise, claw 8 mm. long, ciliate; stamens 7–8 mm. long, glabrous; anthers dark, 1.4 mm. long; follicles 3, densely yellow-hairy, 10–12 mm. long, 3–4 mm. wide, erect, the styles an additional 2 mm.; seeds rounded, hyaline-alate.

TYPE: Szechwan, near Ta-tsien-lou, *Pratt 462* (K), isotypes (BM, CAL, P); all seen.

OTHER COLLECTIONS. Tatsienlu, *Soulié 2379* (K, P); *Harry Smith 11051* (A, MO, NY); Mt. Konka, Konkaling, *Rock 16884* (P).

174. **Delphinium pogonanthum** Hand.-Mazz. Symb. Sinicae 7: 279. 1931. FIG. 15, F.

Stems 1–2, fistulose, 5–8 dm. tall, scattered-bristly with stiff white hairs, remotely few leaved; lower petioles 1–2 dm. long, bristly hairy, the bases broadly sheathing, upper petioles short; leaf blades broadly cordate-rounded in outline, to 1 dm. across, with scattered appressed stiff hairs, trifid to ca. 1 cm. from the base, the two lateral divisions deeply cut so as to make 5 divisions, these broadly cuneate-obovate, coarsely and deeply toothed distally, the teeth 3–8 mm. long, 3–4 mm. wide, subacute; upper leaves reduced, then passing into trifid foliose bracts 15–25 mm. long, upper bracts linear-lanceolate, entire, hairy, ca. 10 mm. long; inflorescence a lax raceme to 3.5 dm. long, or with 1–2 short racemose branches below; the axis and pedicels with spreading and retrorse, coarse, hyaline, white or yellow hairs to almost 1 mm. long; pedicels ascending, 1–5 cm. long; bracteoles 2, erect, broadly linear, 6–10 mm. long, near to or somewhat below the flower; sepals dark blue, stiff-pubescent; upper sepal broadly ovate, 13 mm. long, 10 mm. wide, obtuse, the spur horizontal, slightly decurved, ca. 20 mm. long; 3 mm. wide at the base, narrowed to a long tapering apex; lateral sepals asymmetrically elliptic-oblong, 12 mm. by 6 mm., pubescent along the midline, rounded at apex; lower sepals more pubescent, 12 mm. long, 4 mm. wide, rounded at apex; upper petal laminae bluish, almost straight, entire, glabrous, 9 mm. long, the spur 19 mm. long; lower laminae oblong, oblique, 7 mm. long, 2 mm. wide, bearded near base, long-ciliate the apex unequally shallowly 2-lobed; stamens 6–7 mm. long, glabrous; anthers dark, linear-oblong, 1.3 mm. long; follicles 3, pubescent, 10 mm. long, the style an additional 3 mm.; immature seeds with transverse tiers of scales.

TYPE: N. W. Yunnan, 3600–4025 m., southeast of Dschungdien, between Peti and Alo, Aug., 1914, no. *4576, Handel-Mazzetti*? (W?), not seen. In the original description there is a figure on p. 281 which is helpful.

Specimens to be referred here: **Yunnan:** *H. T. Tsai 57615* (A); Konkaling, Muli, 3600 m. *T. T. Yü 13270* (A, BM, E); Muli, Kulu, 3300 m., *Yü 14367* (BM, E); Haba Snow Range, *K. M. Feng 2115* (A); S. Chungtien, *Feng 1836* (A).

175. **Delphinium pseudo-campylocentrum** W. T. Wang, Acta Bot. Sinica **10**: 150. 1962.

Delphinium hirticaule Franchet var. *mollipes* Wang, Acta Bot. Sinica **10**: 146. 1962. Based on *K. H. Yang 58941*, from Wu-hsi, Szechwan, isotype (E), seen.

Root elongate, 2–5 mm. in diameter; stem ca. 4 dm. high, 4 mm. thick at base, spreading-hirsute below, glabrous above, simple or few branched above, equally foliose throughout; lower cauline leaves with broadly pentagonal blades 4–4.5 cm. long, 4.5–6.5 cm. wide, cordate at base, trisect, the middle segment 3-parted to below the middle, the lateral segments broader than the middle, 2-parted for three-fourths their length, all parts few lobuled, strigulose especially above; petioles 4.5–5.5 cm. long, not vaginate, hirsute; upper cauline leaves gradually reduced; racemes 4–9-flowered, lower bracts leaflike, 2–4 cm. long, others linear to subulate, 3–10 mm. long; pedicels 2–4 cm. long, divergent, slightly incurved, bracteolate above the middle, loosely yellow glandular-puberulent; bracteoles oblong-linear to subulate, 2–6.5 mm. long, loosely strigulose; sepals deep blue, narrowly elliptic or broadly lanceolate, 11–15 mm. long, minutely puberulent on both surfaces, the spur 17–22 mm. long, subulate, slightly decurved at apex; upper petals blue, glabrous; lower petals blue, the limb ovate, bilobed one-third to one-half the length, ciliate, yellow bearded at base; stamens glabrous; carpels 3, loosely puberulent.

TYPE: Szechwan, Tachin, 4400 m., Aug. 5, 1958, *H. Li 78358* (PE), not seen; photo. at (E) seen.

The only specimen I have seen is the one mentioned above as isotype of *D. hirticaule* var. *mollipes*.

176. **Delphinium scabriflorum** D. Don, Mem. Wernerian Soc. 3: 412. 1821. FIG. 15, G.

Delphinium carela Buch.-Ham. ex D. Don, Prod. Fl. Nepal. 195. 1825. New name for *D. scabriflorum*.

Perennial from rather a woody root; stem 6–12 dm. or more tall, rather slender, terete, more or less spreading-hairy throughout or at least above, scattered-leafy; leaves pentagonal, the blades of the lower 5–15 cm. wide, open-cordate, 5-fid to near the base or 1–2 cm. above, the segments subcuneate below, stiff-pubescent on both sides, but especially on nerves beneath, the segments incised-lobed then coarsely toothed, the lobules oblong-ovate, 2–5 or more mm. wide; petioles hairy, 1–2 dm. long, scarcely vaginate at the base; upper leaves gradually reduced; central raceme open, 8–12-flowered, with fewer-flowered branches from below; inflorescence densely short-hairy, some of the hairs glandular; lower bracts foliose, divided, to 3 cm. long, the upper simple, entire, linear to lanceolate, 1–2 cm. long; pedicels arched-spreading, densely pubescent, 1–5 cm. long; bracteoles linear, to lanceolate, 5–10 mm. long, subtending the flower; sepals blue to rich blue-violet, with rather stiff appressed hairs, the upper sepal round-ovate, 15 mm. long, 10 mm. wide, subacute, the spur 18 mm. long, 3 mm. wide at base; lateral sepals oblong-obovate, 13 mm. long, 7 mm. wide, obtuse; lower asymmetrically obovate, 15 mm. long, 8 mm. wide; petals blue, the upper laminae oblique, 12 mm. long, 3 mm. wide, glabrous, bidentate, the spur 15–16 mm. long; lower laminae oblong, 10 mm. long, 3.5 mm. wide, bifid into 2 unequal lance-oblong lobes, white-ciliate, the claw 6 mm. long, bearded; stamens 6–7 mm. long; anthers elongate, 1.5 mm. long; follicles 3, subglabrous.

TYPE: "Alpibus Nepaliae," *D. Wallich*; not seen.

RANGE. Growing on open or wooded, often somewhat rocky hillsides, mostly in Bhutan.

COLLECTIONS SEEN. Ridang near Trongsa, 2200 m., *Ludlow & Sherriff 219* (BM); valley of Khano Chu Kurted, *Cooper & Bulley 4223* (BM); Chandesi, 2500 m., *Ludlow & Sherriff 3342* (BM); Yatola ridge, Tongsa, 3200 m., *Cooper & Bulley 4114* (BM). A specimen from Burma, Chimili woods, *R.A.*, Aug. 21, 1919 (E) is near the above.

√177. **Delphinium sherriffii** Munz, sp. nov. FIG. 15, H.

Perennial, the stem 10–16 dm. tall, 7–8 mm. thick, with short white spreading pubescence, simple below, short branched above, rather equably but not densely leafy; cauline petioles pubescent, slender, 6–10 cm. long, slightly dilated at the base; cauline leaves to ca. 1 dm. across, 5-fid to 1 cm. or less from the base, pubescent chiefly along the veins, the segments rather broadly cuneate-rhombic, 2–3-lobed to about the middle, then sharply incised into few lanceolate or lance-ovate teeth mostly 3–5 mm. broad, mucronate; inflorescence with several short branches, thus forming a rather diffuse but compact panicle, the axes with short, spreading, yellow, glandular hairs; lower bracts divided, but mostly simple, filiform, 5–7 mm. long; pedicels spreading, 2–4 cm. long, glandular-pubescent; bracteoles filiform, 2–3 mm. long, near or above the middle of the pedicel; flowers few to several on each branch of the inflorescence, not crowded; sepals somewhat strigulose, bright bluish purple, the spur dark wine-red; upper sepal 12 mm. by 5 mm., broad-ovate, apiculate, the spur spreading decurved, 20–22 mm. long, 4–5 mm. wide at base, rapidly narrowed; lateral sepals 12 mm. long, 4.5 mm. wide, rounded-obtuse at apex; lower sepals 12 mm. long, 4 mm. wide, more apiculate; petals pale, the upper laminae strongly oblique, 8–9 mm. long, 4 mm. wide, glabrous, emarginate, the spur 20 mm. long; lower laminae 6 mm. long, divided two-thirds their length into lance-oblong ciliate lobes, claw appendiculate, 5 mm. long; stamens 5–6 mm. long; anthers dull slaty green; carpels 3, strigulose.

Caulis 10–16 dm. altus, 7–8 mm. crassus, pubescens, supra breve ramosus, foliosus; petioli caulium 6–10 cm. longi, base dilatati, pubescentes; folia caulium 6–10 cm. lata, 5-fida, praesertim in venis pubescentia, segmenta foliorum cuneato-rhombea, 2–3-lobata, tum incisa lobulis paucis lanceolatis vel lanceo-ovatis; inflorescentia ramosa, axes aureo-glandulosi; bracteae infimae divisae, aliae integrae, filiformes, 5–7 mm. longae; pedicelli divaricati, 2–4 cm. longi, glanduloso-pubescentes; bracteolae filiformes, 2–3 mm. longae; flores pauci vel plures; sepala strigulosa, caeruleo-purpurea, 12 mm. longa, calcar 20–22 mm. longum, base 4–5 mm. crassum; petala pallida, laminae superiores obliquae, 9 mm. longae, glabrae, emarginatae; laminae inferiores 6 mm. longae cum 2 lobis lanceo-oblongis ciliatisque; unguis 5 mm. longus appendiculatus; stamina 6 mm. longa; antherae subviridia; carpella 3, strigulosa.

TYPE: Southeastern Tibet, Tsanang La, 3200 m., July 15, 1938, *Ludlow*

& Sherriff 5833 (BM), growing in clearings in mixed forest. Characterized by its small flowers in a branched compact, but not dense, inflorescence. Mr. Sherriff's collections, largely made with Mr. Ludlow, have been of great help in the preparation of this paper.

178. **Delphinium siamense** (Craib) Munz, comb. nov. FIG. 15, I.

Delphinium stapeliosum Brühl var. *siamense* Craib, Florae Siamensis Enumeratio **1:** 19. 1925.

Stem slender, 3–5 dm. tall, few branched above, scattered-leafy, with a few spreading white hairs below, strigulose upward, often quite loosely so; lower petioles slender, 1–2.5 dm. long, vaginate, with scattered white hairs, the upper petioles shorter; blades mostly round-pentagonal in outline, cordate at base, 3–7 cm. long, 4–10 cm. wide, divided halfway or farther with sharply acute sinuses and broad cuneate-rhombic segments, sparingly strigose above, glabrous beneath except on the veins, the segments shallowly but sharply trilobed then incised with lobules or few teeth triangular-lanceolate or broader (2–6 mm. wide), acute to acuminate, mucronate; upper leaves reduced; inflorescence of a few slender-stemmed racemes (the central 4–6–8-flowered), these loosely strigose; lowest bract trifid or entire, the upper lance-linear, 10–15 mm. long; pedicels mostly 1–2 cm. long, ascending; bracteoles linear, 5–7 mm. long, at or below the middle of the pedicel; flowers light blue, the sepals strigose, the upper round-ovate, 14 mm. long, 9 mm. wide, obtuse, the spur straight, 3.5 mm. wide at base, 16–18 mm. long, tapered very gradually to a blunt tip; lateral sepals round-obovate, 13–14 mm. long, 12 mm. wide, rounded at apex; lower sepals obovate, 14 mm. long, 8 mm. wide, obtuse; petals pale, the upper laminae somewhat oblique, 11 mm. by 5 mm., glabrous, strongly bidentate at apex, the spur 17–18 mm. long; lower laminae more or less obovate, 6 mm. by 4 mm., bearded, deeply bifid into broad oblong lobes, the claw 6 mm. long; stamens 6–7 mm. long, glabrous, the darkish anthers 1 mm. long; carpels 3, strigose.

TYPE: Siam, Doi Chiengdao, 2100 m., open rocky ground, *Kerr 6612* (K, BM); seen.

OTHER COLLECTIONS: Doi Chiengdao, *Put 337*, Herb. A. F. G. Kerr (BM, K), *4454* (BM, K); Doi Pa Mawn, 1510 m., *H. B. G. Garrett 452* (K).

179. **Delphinium sparsiflorum** Maxim. Bull. Acad. Pétersb. **23:** 307. 1877. FIG. 15, J.

Perennial, the rather coarse stem 10–15 dm. tall, subglabrous, rather equably leafy in lower half, the petioles scarcely dilated at base, slender, to ca. 1 dm. long; leaf blades sparsely strigose, paler beneath, to ca. 1.5 dm. in diameter, ternate, then the 2 lateral parts divided nearly or quite to the base, they and the central one with cuneate base and incisely pinnately lobed, each lobe with few large, mucronate, lanceolate or ovate teeth or lobules; flowers scattered in an open diffuse panicle forming the whole upper part of the plant; lower bracts foliaceous, more or less coarsely incisely lobed, 1–3 cm. long, the upper subulate, entire, 2–4 mm. long; pedicels filiform, glabrous, 2–4 cm. long; bracteoles alternate or paired, ca. 2 mm. long; flowers pale blue, the upper sepal broadly ovate, 9 mm. long, 8 mm. wide, subglabrous except for a very minute puberulence about the obtuse apex; spur conical, ca. 7 mm. long, 3.5 mm. wide at base; lateral sepals 10–11 mm. long, 6–7 mm. wide, glabrous except at the tip; lower sepals 10–11 mm. long, 4–5 mm. wide, also minutely puberulent at apex; laminae of upper petals 8–9 mm. long, pale, suboblong, glabrous; lower laminae pilose, 7 mm. long, the blade bifid, 4 mm. long, the claw ciliate; stamens ca. 4 mm. long, glabrous; anthers dark, 1 mm. long; follicles 3, sparsely pilose, to ca. 12 mm. long, 3 mm. wide, the styles an additional 2 mm.

TYPE: Kansu, China; Terra Tangutorum, *Przewalski*, 1872 (LE), seen. Huth says this region is Tangutica at River Tetung, 2600 m.

ILLUSTRATION. MAXIMOWICZ, Fl. Tangut. *pl. 5.* 1889.

The only collection I have seen in addition to the type is from southwestern Kansu, Tao River Basin, at 3000 m., *Rock 13191* (GH).

180. **Delphinium sungpanense** W. T. Wang, Acta Bot. Sinica **10**: 149. 1962.

Stem about 9 dm. tall, 2 mm. thick, smooth, glabrous below inflorescence, equably leafy; middle cauline leaves with rather long petioles, the blades broadly pentagonal, 6 cm. long, 10 cm. wide, trisect, the middle segment rhombic, long-acuminate, cuneate at base, trifid to middle, the middle lobe narrow-rhombic or lance-rhombic, with 1 lobule on each side below the middle, the lateral lobes triangular-ovate or obliquely ovate; lateral segments broadly rhombic, parted and lobed as in the middle segment; blades subglabrous below, strigulose above; racemes ca. 15 cm. long, lax, about 8-flowered; lower bracts trisect or linear, 4.5–5 cm. long, others linear, shorter; pedicels 1.5–5 cm. long, strigulose, bibracteolate above; bracteoles remote from the flower, linear, 5–7 mm. long, glabrous; sepals purple-blue, oblong-obovate, 8 mm. long, strigulose, short-corniculate, the spur 19–22 mm. long, 2.5 mm. wide at base, decurved into a right angle; upper petal laminae yellowish, entire, glabrous; lower blue, subequal to sepals, ovate, bifid to middle into lance-triangular lobes, ciliate, yellow bearded near middle, claw shorter than limb, appendiculate; stamens glabrous; carpels 3, glabrous.

TYPE: Sungpan, Szechwan, *W. P. Fang 4038* (PE?); not seen.

Said to be near *D. giraldii*, but racemose, the axes and pedicels densely puberulent, and the spur decurved into a right angle.

181. **Delphinium taliense** Franchet, Bull. Soc. Philom. Paris VIII. **5**: 174. 1893. FIG. 15, K.

Stem robust, to 1 m. and more in height, much branched from base, glabrous and glaucous; leaves numerous and finely pubescent, with petioles

8–12 cm. long and somewhat dilated at base, the blades 5–10 cm. wide, deeply divided in the lower leaves into 3 broad segments, these cuneate-obovate, trifid, incised, then shallowly lobed, the ultimate teeth few, broadly ovate, mucronate, 5–15 mm. long, 5–12 mm. broad; the divisions of the upper leaves lanceolate, subentire or few lobed; branches of inflorescence elongate, arched, with an entire linear leaf at the base; bracts linear-setaceous, 8–10 mm. long; pedicels 2–4 cm. long; bracteoles setaceous, minute, placed a little below the flower; sepals puberulent, blue with a whitish band on the back, 15–20 mm. long, obtuse to rounded, spur straight or slightly curved, 22–25 mm. long, 3 mm. wide at the base; upper petals bluish to whitish, the laminae slightly oblique, 9 mm. long, glabrous, deeply emarginate, the spur ca. 21 mm. long; lower laminae sometimes white, deeply bilobed, yellow bearded near base, ciliate, round-obovate, 7 mm. long, the claw 5 mm. long, appendiculate; follicles 3, glabrous; seeds black, pyramidal, truncate, somewhat rugulose, winged on angles.

TYPE: Yunnan, Mt. Pen-gay-tzé, below Tali, *Delavay 9* (P), seen.

OTHER COLLECTIONS. **Yunnan:** *Bodinier & Ducloux 379* (P); *Delavay*, Sept. 22, 1887, at 2000 m. (P).

This species, *Delphinium taliense*, suggests *D. yunnanense* in the long segments of its upper leaves. It has stem leaves like those of *D. exaltatum*, and has been confused with *D. elatum*, which has the spur equal to the sepals, and almost black petals.

182. **Delphinium ternatum** Huth, Bot. Jahrb. **20**: 421. 1895.

FIG. 15, L.

Perennial, 5–10 dm. tall, erect, soft-pubescent, the petioles to 1 dm. long, scarcely dilate at the base, the leaf blades 4–8 cm. broad, glabrescent on both surfaces, ciliate on margins, ternate, the leaflets deeply tripartite, the parts entire or sparsely serrate-incised, subsessile, cuneate, the final lobules lanceolate, somewhat acuminate, to 3 cm. long; inflorescence branched, the racemes lax, glabrous; bracts linear, 5 mm. long; pedicels 1–2 cm. long in fruit, divergent, shorter in flower; bracteoles linear, at about the middle of the pedicel, 2–3 mm. long; flowers blue, the sepals round-ovate, glabrous, the upper 12 mm. by 5 mm., subacute, the spur 15 mm. long; lateral sepals elliptic, rounded-obtuse, 13 mm. by 5 mm.; lower sepals more pointed; upper petals yellowish with bluish tinge, the laminae oblique, 10 mm. long, bidentate, the spur 15 mm. long; the lower laminae bluish, deeply divided, sparsely white-bearded, 6.5 mm. by 4 mm., the claw 5.5 mm.; anthers yellow; follicles 3, hirsute; seeds squamate, the scales contiguous.

TYPE: Huth cited two specimens from Buchara: (1) Darwas, Omar ad fluvii Pänsch ripam sinistram, *Regel*, 1882 (LE) and (2) distr. Hissar, mts. near Hakimi in valley of R. Karatag, *Regel*, 1882 at 1600–2300 m. (LE). Both seen; I would take the Hissar specimen collected by Regel as lectotype since it has more leaves intact than his other collection.

Apparently belonging here is Mt. Kuhitang, eastern Turcomania, July 14, 1931, *S. Nevski 790* (K).

183. **Delphinium trifoliolatum** Finet & Gagnep. Bull. Soc. Bot. France 51: 481. *plate 6A, figs. 1–6.* 1904. FIG. 15, M.

Perennial from a short thick root; stem slender, subflexuous, striate, simple or branched above, 3–7 dm. tall, more or less strigulose throughout, densely so in the inflorescence, leafy throughout, the leaves rather remote; petioles very slender, 3–10 cm. long, somwhat inflated at the base; the blades round-pentagonal in outline, strigose to strigulose on both surfaces, especially along the veins, 4–10 cm. in diameter, trifid to the base, the lateral segments bifid almost to the base, all 5 segments thus formed more or less petiolulate, lance-ovate, narrow-cuneate at base, 1–2 cm. wide, shallowly incised or unequally sharply dentate into acute teeth 2–4 mm. long; upper leaves somewhat reduced and passing into trifoliolate bracts 5–20 mm. long; racemes lax, rather few flowered, the pedicels strigose, 5–30 mm. long, very slender, divergent; bracteoles lance-oblong, 3–8 mm. long, near the summit of the pedicel; flowers pale blue, sepals strigulose, yellowish near the apex; upper sepal ovate, 10 mm. long, 6 mm. wide, subobtuse, the spur 18–20 mm. long, 2.5 mm. wide at base, somewhat curved toward the narrow tip; lateral sepals oblong, 10 mm. by 5 mm., rounded at apex, pubescent along midline; lower sepals 12 mm. by 7 mm., more pointed, more pubescent; laminae of upper petals pale, slightly oblique, 10 mm. long, bidentate at the acute apex, glabrous, the spur 20 mm. long; lower laminae bluish, oblong, 7 mm. long, 3 mm. wide, sparsely bearded, cleft to below the middle into lance-oblong lobes; stamens 5 mm. long, glabrous; anthers dark, 1.5 mm. long; follicles 3, glabrous or nearly so, 5 mm. long, the styles 1–2 mm. more.

TYPE: Hupeh, China, *E. H. Wilson 2496,* published as *3496,* July, 1901, holotype (P) seen; isotypes (E, K, NY) seen.

REFERRED HERE: Hupeh, *A. Henry 7448* (BM, GH, K); *E. H. Wilson,* April, 1900 (US). **Szechwan:** Nan-chuan, 1580 m., *K. F. Li 63169* (E).

184. **Delphinium umbrosum** Hand.-Mazz. Symb. Sinicae 7: 278. *fig. 4, nos. 7–9.* 1931. FIG. 15, N.

Rhizome short, thickish, the roots fascicled, long, thick, woody; stem 6–9 dm. tall, simple, sulcate, short- and retrorse-strigose, equably leafy; leaves pentagonal-reniform in outline, to 12 cm. wide, tripartite almost to base, the lateral parts less profoundly bifid, all parts narrowly obovate-rhombic, rather long-acuminate, incised, dark green, sparsely strigose above, densely so beneath; upper petioles gradually shorter, narrowed into slender sheaths; racemes lax, to 10-flowered, densely retrorse-hairy, with normal leaves below and entire lanceolate to linear bracts above; pedicels 1.5–6 cm. long, suberect or arcuate; bracteoles apical or farther down, linear, 8–10 mm. long, strigulose; sepals violet, broadly ovate, 12–15 mm.

long, rounded, the lateral with median nerve dilated at apex, strigulose; spur more than twice the length of the blade of the sepal, deflexed, 3 mm. wide at the base, obtuse; upper petals almost 3 mm. shorter than the sepals, ca. 3.5 mm. wide, oblique; truncate, minutely and acutely bilobed at tip; lower laminae shorter, hairy from the claw, 6 mm. by 3 mm., rather deeply oblong-lobed, the claw 5 mm. long; stamens 6–7 mm. long, glabrous; anthers brown; carpels 3, sparsely hairy.

TYPE: Northwest Yunnan, hemlock forests on the Nguka-la between Dschungdien (Chungtien) and Djitsung on the Djinsche-djiang, 3750–3800 m., *Handel-Mazzetti ? 7809* (W?), not seen. The illustrations are helpful.

SPECIMENS SEEN. **Yunnan:** *C. W. Wang 69052* (A); *H. T. Tsai 52675* (A); *K. M. Feng 1726* (A); *A. Henry 9668* (MO, NY), *9668 A* (US). **Szechwan:** *T. T. Yü 979* (GH). **Upper Burma:** *Forrest 25052* (US), characterized by its long-acuminate leaf lobes.

185. **Delphinium uralense** Nevski in Komarov, Fl. U.S.S.R. 7: 159. 725. 1937. FIG. 15, O.

Delphinium dyctiocarpum DC. subsp. *uralense* (Nevski) B. Pawl, Fragmenta Floristica & Geobotanica **9:** 429. 1963.
Delphinium dyctiocarpum var. *canescens* Korsh. Tent. Fl. Ross. Or. 18. 1898.

Entire plant grayish-strigulose; stems 5–11 dm. tall, ribbed below, rather equably and closely leafy; petioles to 1 dm. long, vaginate at base; leaf blades round-cordate to -reniform, 3.5–7 cm. long, 5.5–12 cm. wide, palmatisect, the segments commonly ternately divided into terminal lance-linear lobes 2–4 mm. wide and with 2–3 teeth, densely strigose on both surfaces, but paler beneath; raceme sometimes branched below, dense, many flowered, the flowers light blue; bracts lance-subulate, stiff, 5–7 mm. long; bracteoles strigose, linear-subulate, 3.5–6 mm. long, placed above the middle of the pedicel which is strigose, suberect, to 1 cm. long; sepals ovate, obtuse, tomentellous, the upper ovate, 14–15 mm. long, 8 mm. wide, the tip subacuminate, upcurved; spur cylindrical, 12 mm. long, 2–2.5 mm. wide, obtusely acuminate, more or less uncinate at tip; lateral sepals elliptic-obovate, 13–14 mm. by 8–9 mm., obtuse; lower sepals 13 mm. by 6 mm.; petals pale, the upper laminae somewhat oblique, 10 mm. long, 3 mm. wide, entire and glabrous, the spur 13 mm. long; lower laminae very oblique, rather oblong, 5 mm. by 3 mm., bifid to one-fourth its length into rounded-oblong lobes, bearded and long-ciliate, the claw 5 mm. long; stamens 5–6 mm. long; anthers dark, round-oblong, 0.8 mm. long; carpels 3, very densely pubescent.

TYPE: Prov. Orenburg, near Andreevka, *D. Litwinow*, July 7, 1893 (LE); seen.

Delphinium uralense differs from *D. dyctiocarpum* which is much less pubescent and has dark petals.

GROUP IX

Leaves rather coarsely lobed as in Group VIII, but the petals very dark, in most cases almost black. Spurs straight or some decurved.

This group is purely artificial and does not correspond with any taxonomic subdivisions that have been proposed.

Key to Species

1\. Spur about half as long again as the blade of the upper sepal.

  2\. Stem and inflorescence axis glabrous or nearly so.

    3\. Sepals mostly glabrous, 10–25 mm. long.

      4\. Upper sepal blade 21–25 mm. long; spur 26–42 mm. long. Szechwan. .... 222. *D. oxycentrum.*

      4\. Upper sepal blade 10–14 mm. long; spur 12–20 mm. long. Altai. .... 199. *D. dyctiocarpum.*

    3\. Sepals not glabrous, 14–16 mm. long. Szechwan. (Treated in Group VIII). .... 169. *D. mitzugense.*

  2\. Stem and/or inflorescence axis pubescent.

    5\. Inflorescence with spreading glandular hairs; bracteoles 3–5 mm. long. Shansi. .... 212. *D. leptopogon.*

    5\. Inflorescence lacking glandular hairs; bracteoles largely 5–10 mm. long.

      6\. Lamina of upper petal ciliate; carpels glabrous; stem pilose. Eastern Siberia. .... 195. *D. crassicaule.*

      6\. Lamina of upper petal glabrous; carpels hairy.

        7\. Stems more or less retrorse-pubescent; bracteoles lance-linear; sepals glabrous within. Western China. ...... 191. *D. chenii.*

        7\. Stems with long spreading hairs; bracteoles lance-ovate; sepals strigose on both surfaces. Semipalatinsk. .. 228. *D. sauricum.*

1\. Spur mostly not half as long again as the blade of the upper sepal.

  8\. Sepals pubescent within.

    9\. Sepals glabrous on the outer surface.

      10\. Inner surface of sepals with long tangled hairs at base, or at least a few hairs near the tip; sepals 12–15 mm. long. Southern Caucasus, adjacent Turkey. .... 190. *D. buschianum.*

      10\. Inner surface of sepals not long-hairy; sepals 18–30 mm. long.

        11\. Spur 15–25 mm. long; laminae of upper petals glabrous. China. (Treated in Group VI). .... 81. *D. albocoeruleum.*

        11\. Spur 12–15 mm. long; laminae of upper petals bristly. Turkey. .... 205. *D. formosum.*

    9\. Sepals pubescent on the outer surface.

      12\. Inflorescence axis with spreading hairs.

        13\. Upper sepal 12–15 mm. long, spur 10–15 mm. long.

          14\. Sepals white with yellow nerves; lamina of upper petal entire, hairy at tip. Uzbekistan. ..... 219. *D. nevskii.*

          14\. Sepals blue or purple; lamina of upper petal emarginate, often glabrous at tip.

            15\. Bracteoles at the base of the flower; sepals deep blue to purple.

              16\. Stems 1–4 dm. tall; spur 10–12 mm. long; lower petioles vaginate. Turkestan. Pamir. (Treated in Group V). .. 62. *D. dasyanthum.*

16. Stem 6–12 dm. tall; spur 12–15 mm. long; lower petioles scarcely dilated. Himalaya. . . . . 224. *D. pyramidale.*

15. Bracteoles remote from the flowers; sepals dilute blue. Bokhara. . . . . 221. *D. oreophilum.*

13. Upper sepal 15–25 mm. long; spur 15–18 mm. long.

17. Lamina of upper petal entire, 10 mm. long; lamina of lower petal 5 mm. long. Altai. . . . . . . 217. *D. mirabile.*

17. Lamina of upper petal not entire, 13–14 mm. long; lamina of lower petal 7–8 mm. long.

18. The lamina of upper petal bidentate; bracteoles ca. 10 mm. long; seeds winged. Himalaya. (Treated in Group V). . . . . 55. *D. vestitum.*

18. Lamina of upper petal emarginate; bracteoles 4–6 mm. long; seeds squamate. Caucasus. . . . . 229. *D. speciosum.*

12. Inflorescence with appressed hairs.

19. Upper sepal slaty to pale blue, 18–20 mm. long. Tibet, China. (Treated in Group VI). . . . . 81. *D. albocoeruleum.*

19. Upper sepal deep blue to purplish, 12–17 mm. long.

20. Lamina of upper petal rounded at apex; upper sepal 12–15 mm. long; spur 11.5–13 mm. long. Western China. . . . . 210. *D. kuanii.*

20. Lamina of upper petal emarginate at apex; upper sepal 15–17 mm. long; spur 18–20 mm. long. Iran. . . . . 201. *D. elbursense.*

8. Sepals not pubescent on inner surface.

21. Sepals glabrous on outer surface except sometimes ciliate on margin.

22. Pedicels glandular-pubescent; stem 10–15 dm. tall, mostly glabrous. Himalaya. 224. *D. pyramidale.*

22. Pedicels not glandular-pubescent.

23. Upper sepal 10–16 mm. long.

24. Flowers ca. 10 in a lax raceme; upper sepal 13–14 mm. long; spur 17–18 mm. long; laminae of upper petals emarginate. Sinkiang. . . . . 213. *D. longiciliatum.*

24. Flowers many in a dense raceme.

25. Upper sepal 10–11 mm. long, the spur 10–13 mm. long.

26. Leaf blades cordate at base; bracteoles ovate to elliptic, 4–5 mm. long; upper petal glabrous at tip. Sikang. . . . 218. *D. naviculare.*

26. Leaf blades almost straight across the base; bracteoles oblanceolate, 5–8 mm. long; upper petal bristly-hairy at tip. Siberia. . . . . 226. *D. retropilosum.*

25. Upper sepal 13–16 mm. long; spur 13–18 mm. long.

27. Lamina of upper petal subtruncate at apex; leaf blades round-cordate in outline. Central and eastern Siberia. . . . . 200. *D. elatum.*

            27. Lamina of upper petal bidentate at apex; leaf blades broader than long. Caucasus. .... 204. *D. flexuosum.*
    23. Upper sepal 18–30 mm. long.
        28. Bracteoles 2–3 mm. wide; upper sepal 18–20 mm. long.
            29. The bracteoles well below the flowers; inflorescence pyramidal-paniculate; stem with scattered long spreading hairs. Ossetia. ... 188. *D. bracteosum.*
            29. The bracteoles subtending the flowers; inflorescence racemose; stem strigulose below, otherwise glabrous. Dagestania. .... 215. *D. mariae.*
        28. Bracteoles 3–5 mm. wide; upper sepal mostly longer.
            30. Spur 12–15 mm. long; upper sepal 20–30 mm. long; inflorescence paniculate. Turkey. .... 205. *D. formosum.*
            30. Spur 18–20 mm. long; upper sepal 20–22 mm. long; inflorescence racemose. Caucasus.
                31. Lamina of upper petal deeply bidentate; upper sepal 20 mm. long. ... 227. *D. ruprechtii.*
                31. Lamina of upper petal emarginate; upper sepal 20–30 mm. long. .... 216. *D. megalanthum.*
21. Sepals not glabrous on outer surface.
    32. Inflorescence with some glandular hairs (yellow, inflated), these often mixed with various non-glandular hairs.
        33. Sepals variegated, pale blue and white. Transcaucasia. .... 202. *D. elisabethae.*
        33. Sepals not so variegated.
            34. Flowers rather large, the sepals mostly 15–22 mm. long.
                35. Lamina of upper petal sharply bidentate, of lower petal long-ciliate. Dagestan. .. 187. *D. arcuatum.*
                35. Lamina of upper petal entire, of lower petal not ciliate. Siberia. .... 220. *D. ochotense.*
            34. Flowers smaller, the sepals 9–14 mm. long.
                36. Upper petal with 2 narrow terminal pointed lobules; flowers white, tinged with green. Southern Tibet. .... 206. *D. hillcoatiae.*
                36. Flowers violet, blue or purple.
                    37. Inflorescence 1–2–(3)-flowered; upper sepal 12–13 mm. long; spur 14–16 mm. long. Bhutan. .... 193. *D. cooperi.*
                    37. Inflorescence with more numerous flowers.
                        38. Plant 2.5–4 dm. tall; raceme 6–15-flowered; spur 14–15 mm. long. Altai. .... 232. *D. ukokense.*
                        38. Plant mostly taller.
                            39. Flowers 3–10; upper sepal 12–14 mm. long. Upper Burma. .... 189. *D. burmaense.*
                            39. Flowers more numerous; upper sepal 12 mm. long.

- 40. Pubescence of sepals not glandular.
  - 41. Sepals villous with spreading white hairs, pale purplish blue; carpels hairy. Afghanistan. .... 186. *D. afghanicum.*
  - 41. Sepals puberulous, pale blue; carpels glabrous. Transcaucasia. .... 225. *D. pyramidatum.*
- 40. Pubescence of sepals short, glandular; sepals 10–18 mm. long; carpels glabrous. Mongolia, etc. .... 208. *D. inconspicuum.*

32. Inflorescence lacking glandular hairs, the hairs white and slender.
  - 42. Petioles scarcely or not dilated at the base.
    - 43. Stems scarcely taller than the basal leaves; sepals 19–25 mm. long. Caucasus. (Treated in Group V). .... 61. *D. caucasicum.*
    - 43. Stems much taller than the basal leaves.
      - 44. Sepals strigulose.
        - 45. Raceme many flowered, the sepals deep blue, 17–18 mm. long; spur 17 mm. long. Turkestan. .... 234. *D. winklerianum.*
        - 45. Raceme 4–10-flowered, lax; sepals purplish, 10–15 mm. long. Sikang.
          - 46. Bracteoles 5–7 mm. long; spur 2–2.5 mm. thick at base; stamens glabrous. .... 203. *D. elliptico-ovatum.*
          - 46. Bracteoles 8–10 mm. long; spur 4–4.5 mm. thick at base; stamens pilose. .... 210. *D. kuanii.*
      - 44. Sepals villous or hairy.
        - 47. Upper sepal 12–15 mm. long, the spur about as long.
          - 48. Raceme lax; stem 10–12 dm. tall; lamina of upper petal glabrous, entire. Siberia. .... 233. *D. villosum.*
          - 48. Raceme subcapitate; stem 2–6 dm. tall; lamina of upper petal bilobulate, setose. Turkestan. .... 223. *D. poltaratzkii.*
        - 47. Upper sepal 18–25 mm. long; spur 18–20 mm. long.
          - 49. Upper sepal ca. 18 mm. long. Upper Assam to Nepal. .. 230. *D. stapeliosum.*
          - 49. Upper sepal 20–22 mm. long. Caucasus. (Treated in Group VIII). .... 148. *D. dasycarpum.*
  - 42. Petioles, at least the lower, more or less dilated at base.

- 50. Upper petals entire at the apex or nearly so.
  - 51. Inflorescence with some glandular hairs; upper sepal 14–17 mm. long; spur about as long. Central Siberia. . . . . 196. *D. crassifolium.*
  - 51. Inflorescence lacking glandular hairs.
    - 52. Hairs of stem mostly spreading; upper sepal 14–16 mm. long; spur 15–20 mm. long. Manchuria, Korea. . . . . . . 214. *D. maackianum.*
    - 52. Hairs of stem retrorse to appressed.
      - 53. Upper sepal ca. 18 mm. long; spur 16–20 mm. long; flowers more or less yellowish-hairy. Burma. . . . . 211. *D. lacei.*
      - 53. Upper sepal 14–15 mm. long.
        - 54. Spur ca. 22 mm. long. Sikang. . . . . 191. *D. chenii.*
        - 54. Spur ca. 12 mm. long. Nepal. (Treated in Group VI). . . . . 97. *D. incisum.*
- 50. Upper petals emarginate or notched at apex.
  - 55. Hairs closely appressed; sepals light blue, the upper 13–15 mm. long; spur 14 mm. long. Transcaucasia. (Treated in Group VI). . . . . 91. *D. crispulum.*
  - 55. Hairs more or less spreading on stems.
    - 56. Sepals nearly or quite glabrous.
      - 57. Lamina of lower petal divided halfway.
        - 58. Upper petal with hairs at tip; sepal spur 15–18 mm. long. Caucasus. . . . . 204. *D. flexuosum.*
        - 58. Upper petal glabrous at tip; sepal spur 13–14 mm. long. Kolgujev Island, northern Siberia. . . . . 197. *D. cryophilum.*
      - 57. Lamina of lower petal mostly less deeply divided.
        - 59. Lamina of upper petal broadened upward, oblique; bracts and bracteoles lanceloate. Central Siberia. . . . . 198. *D. duhmbergii.*
        - 59. Lamina of upper petal scarcely broadened upward, almost straight; bracts and bracteoles linear. Widely distributed across northern Siberia. . . . . 200. *D. elatum.*
    - 56. Sepals pubescent.
      - 60. Pedicels 5–15 mm. long.
        - 61. Bracteoles lance-linear. Caucasus, Transcaucasia. . . 204. *D. flexuosum.*
        - 61. Bracteoles broadly ovate. Asia Media. . . . . 192. *D. confusum.*
      - 60. Pedicels 10–80 mm. long.

- 62. Flowers few, subumbellate, pale violet. East Turkestan. . . . . 194. *D. corymbosum.*
- 62. Flowers several to many, racemose.
  - 63. Bracteoles near the middle of the pedicel.
    - 64. Upper sepal 18 mm. long; spur 20 mm. long. Khasia, Bhutan. . . . . 230. *D. stapeliosum.*
    - 64. Upper sepal 12–16 mm. long; spur 12–16 mm. long. Northern Siberia. . . . . 200. *D. elatum.*
  - 63. Bracteoles very near the flower.
    - 65. Upper sepal 17–18 mm. long; spur often suberect. Nepal. 207. *D. himalayae.*
    - 65. Upper sepal 11–15 mm. long; spur spreading.
      - 66. Sepals strigulose; leaves more or less reniform in outline; bracteoles slightly below the sepals. Sikang. 231. *D. tianshanicum.*
      - 66. Sepals loosely pubescent; leaves rounded in outline; bracteoles subtending the flower. Turkestan, Tianshan. . . 198. *D. duhmbergii.*

186. **Delphinium afghanicum** Rech. f. Anz. Österr. Akad. Wiss. Math.-Nat. 91: 74. 1954. FIG. 16, A.

Perennial from a woody root, forming clumps, each stem 4–10 dm. tall, simple or few branched near the middle, rather evenly leafy to below the inflorescence, loosely villous below, more densely so above with long spreading white nonglandular hairs, mixed with shorter glandular ones in the inflorescence; lower petioles to about 2 dm. long, villous, vaginate at the base, the upper gradually shorter; leaf blades to 6 cm. long by 4 cm. broad, the veins conspicuous beneath, loosely villous, 5-fid about two-thirds of the way to the base, the segments cuneate-obovate, lobed-incised into 3 principal parts, these with broad rounded coarse mucronate teeth; inflorescence racemose or with 1 to few supplementary racemes below, rather laxly flowered; lowest bracts trifid, others lanceolate to lance-linear, villous, 5–10 mm. long; pedicels divaricate, villous, 1–4 cm. long; bracteoles 2, near the flower, lance-linear, 3–4 mm. long; sepals pale purplish blue, densely villous, the upper sepal ovate, 12 mm. long, 6 mm. wide, subacute, the spur subconic, 7–8 mm. long, 3–4 mm. wide at base; lateral sepals elliptic-oblong, 12 mm. long, 5 mm. wide, rounded at apex, hairy on the whole outer surface; lower sepals elliptic, 13 mm. long, 5.5 mm. wide, subacute; petals dark, the upper lamina almost straight, broad in middle, 8.5 mm. long, slightly bidentate at the glabrous apex, the spur 9.5 mm. long; lower lamina almost straight, ovate, 5 mm. by 4 mm., cleft to near the middle, yellow bearded at base, with scattered white hairs on rest of the surface and margin, claw 5 mm. long; stamens 6 mm. long, moderately dilated below, glabrous; anthers brownish, oblong, 1 mm. long; follicles 3, hairy.

TYPE: Afghanistan, Minjan Pass, at 3800 m., July 26, 1937, *W. Koelz 12719* (US); seen. *Delphinium afghanicum* differs from *D. speciosum* in its longer hairs, entire bracts, and lax inflorescence.

187. **Delphinium arcuatum** Busch in Fl. Cauc. Crit. III. 3: 71. 1902.
FIG. 16, B.

Stem 8–10 dm. tall, densely strigulose, somewhat flexuous, sulcate, rather densely and evenly leafy; cauline petioles to 1 dm. long, not vaginate at base, the blades more or less round-reniform in outline, 5–12 cm. broad, sparsely strigose above, densely so beneath, 5-parted to 1–2 cm. from the base, the segments broadly cuneate, 3-lobed distally and with rather many divergent lance-oblong teeth or lobules 3–7 mm. wide; inflorescence few branched below, the main raceme many flowered, to 3 dm. long, more or less strigose to partly spreading-pubescent; lower bracts leafy, palmatifid, others lanceolate, bluish, 1–2 cm. long, 3–4 mm. wide; pedicels arched, with some glandular hairs, usually 3–4 cm. long, the upper 1–2 cm., very densely covered with short spreading hairs; bracteoles just beneath the flower, ovate-lanceolate or ovate, 6.5–12 mm. long, 2.5–3.5 mm. wide, blunt; sepals violet blue, 16–21 mm. long, 6–12 mm. wide, pubescent, the border white-ciliate; upper sepals ovate, 18–20 mm. long, 7 mm. wide, subacute, the spur spreading decurved, 16 mm. long, 4 mm. wide at base; lateral sepals subovate, 20 mm. by 10 mm., rounded-obtuse; lower sepals 18 mm. by 9 mm., more pointed; petals black, the upper laminae almost straight, 11–12 mm. long, glabrous, bidentate, the spur 12 mm. long; lower laminae strongly oblique, oblong, 5.5 mm. by 3 mm., bearded at base, ciliate, bifid to about the middle into 2 lanceolate divergent lobes, claw 6 mm. long; stamens 6–7 mm. long; anthers dark, over 1 mm. long; carpels 3, sparsely strigose.

TYPE: E. Caucasus, Dagestan, distr. Samur near Kurusch, 2400 m., Aug. 1, 1898, *Th. Alexeenko* (LE); seen.

188. **Delphinium bracteosum** Somm. & Levier, Acta Horti Petrop. 13: 25. 1893.
FIG. 16, C.

Erect, light green, with long scattered spreading hairs, the stem fistulose, somewhat angled, subglabrous above, ca. 3 dm. tall; leaves palmately

5-parted, 5–8 cm. in diameter, sparsely hairy on both sides, the sinuses narrow, acute, the segments broad, the lower divergent, incised, the ultimate divisions few, subobtuse, 6–8 mm. wide, the nerves prominent beneath; upper leaves tripartite; petioles not strongly dilated at the base, those of the midcauline leaves equal to the blade, of the upper shorter to none; inflorescence pyramidal-paniculate to simple and few flowered; pedicels glabrous to hairy, the lower longer than the spurs; bracts elliptic or lanceolate to spatulate, villous, 10–20 mm. long; bracteoles blue, near the base of the flower, ca. 10 mm. long, 2 mm. wide; sepals intensely blue, 18–22 mm. long, 12–15 mm. wide, ciliate, otherwise glabrous to hairy; upper sepal 19–22 mm. long, spur straight, 18–24 mm. long; other sepals 18–22 mm. long, 9–10 mm. wide; petals dark, the upper laminae almost straight, 14 mm. long, subemarginate, glabrous; the lower laminae oblong-ovate, 9.5 mm. by 7 mm., long-ciliate, yellow bearded at base, divided about halfway into 2 unequal oblong lobes, claw 6 mm. long, appendiculate; stamens glabrous, 7–8 mm. long; follicles glandular; seeds transversely lamellate-cristate.

TYPE: Zei in Ossetia, central Caucasus, coll. *Lojka* (LE?); not seen.
ILLUSTRATION. DÉCHY, Kaukasus, **3**: *pl. 8, fig. 1–6.* 1907; according to *Index Londinensis.*

SPECIMEN SEEN. **South Ossetia:** *E. & N. Busch*, Aug. 12, 1935, at 2700 m. (BM).

189. **Delphinium burmaense** Munz, sp. nov. FIG. 16, D.

Delphinium stapeliosum Brühl var. *shanicum* Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 102. 1896. Based on Shan Hills, *Collett* (K); seen.

Perennial from a slender woody rootstock; stem slender, mostly dark, with numerous spreading whitish or yellowish hairs ca. 2 mm. long, simple, 2–12 dm. tall, few leaved; basal leaves with slender villous petioles 5–25 cm. long, very vaginate at base, the blades subreniform, rather densely villous on both surfaces, 3–15 cm. broad, 2–8 cm. long, deeply to shallowly notched at base, 3–5-segmented about halfway to base, the segments broad, oblong-ovate to -obovate, sometimes shallowly lobed, but more usually with rounded-ovate coarse mucronate teeth 2–5 mm. deep, 2–10 mm. wide; upper leaves reduced; inflorescence a few-flowered, somewhat secund raceme, villous, more or less glandular; lower bracts foliose, others oblong-linear to lanceolate, 5–12 mm. long; pedicels ascending to erect, 1–5 cm. long; bracteoles subtending the flower, oblong-linear, 4–10 mm. long; flowers violet, mostly 3–10, villous; upper sepal ovate, 12–14 mm. long, 8–10 mm. wide, obtuse, the spur 15–20 mm. long, 2.5–3.5 mm. wide at base; lateral sepals 10–17 mm. long, 7–10 mm. wide, oblong-obovate, rounded at apex; lower sepals 9–14 mm. long, obtuse; petals dark, the upper laminae slightly oblique, 8–10 mm. long, bidentate at the somewhat bristly apex, the spur 15–18 mm. long; lower laminae oblong, bearded, deeply bifid into lance-oblong lobes, the claw 5–7 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, scarcely 1 mm. long; carpels 3, hairy.

Caulis tenuis, villosus, simplex, 2–12 dm. altus, cum foliis paucis; petioli foliorum basilarium 5–25 cm. longi, vaginati; laminae subreniformes, villosae, 3–15 cm. latae, 2–8 cm. longae, 3–5-partitae, segmentis latis, oblongo-ovatis vel -obovatis; inflorescentia racemosa, secunda; bracteae oblongo-lineares vel lanceolatae, 5–12 mm. longae; pedicelli ascendentes vel erecti, 1–5 cm. longi; bracteolae florem subtendentes, oblongo-lineares, 4–10 mm. longae; flores 3–10, villosi, violacei; sepalum superiore ovatum, 12–14 mm. longum, 8–10 mm. latum, obtusum, calcar 15–20 mm. longum, base 2.5–3.5 mm. crassum; sepala lateralia 10–17 mm. longa, 7–10 mm. lata, oblongo-obovata; sepala inferiora 9–14 mm. longa, obtusa; laminae petalorum superiorum atrae, 8–10 mm. longae, bidentatae, setosae, calcar 15–18 mm. longum; laminae inferiores oblongae, barbatae, bifidae, unguis 5–7 mm. longum; stamina 6–7 mm. longa, glabra; carpella 3, hirsuta.

TYPE: Nam-Tamai Valley, Burma, ca. 3000 m., thickets in a steep gulley, Sept. 6, 1937, *F. Kingdon Ward 13170* (BM).

RANGE. Throughout Burma from 1500–4000 m. alt.

OTHER EXAMPLES. **Burma:** Shen Hills, *Collett 964* (K); Shan States, *Hildebrand* (K); *Melville 43* (BM); Upper Adung Valley, no. of Lung Sa, *Kingdon Ward 10115* (BM); Mindat, *Kingdon Ward 22505* (BM, F); Taunggyi, *Dickason 9052* (A); Nam Tami Valley, *Kingdon Ward 3351* (BM); Burma-Tibet frontier, *Kingdon Ward 9819* (BM, F); Taunggyi crags, *Robertson 15* (K); Sirhoi, *Kingdon Ward 18120* (A, BM). A specimen from Assam (Orka La, *Kingdon Ward 14308*, BM) seems to belong here; it is rather depauperate.

Delphinium burmaense differs from ***D. stapeliosum*** from Nepal in its smaller flowers, presence of glandular hairs in the inflorescence and the spreading, not retrorse, hairs on the stems.

190. **Delphinium buschianum** Grossheim, Trud. Azerb. Otdyel. Zakavk. Fil. Akad. Nauk. U.S.S.R. Sect. Bot. **1**: 51. 1933. FIG. 16, E.

Delphinium linearilobum var. *hirticaule* Grossheim, Fl. Cauc. **2**: 99. 1930, fide Nevski in Fl. U.S.S.R. **7**: 143. 1937.

Stem ca. 7.5 dm. high, somewhat angular below, with some divergent retrorse simple white hairs 0.75 mm. long, foliose; inflorescence rather glabrous; petioles scattered hairy, somewhat vaginate; cauline leaves rounded-cordate to almost round in outline, glabrous on both surfaces or weakly pubescent on veins beneath; laminae divided into 3 lobes 3–6 mm. from base, the middle lobe rhombic-lanceolate, somewhat acuminate, the lateral lobes divided into 2 so that there are 5 resultant segments, laciniate into acute or acuminate lanceolate teeth or lobules 3–6 mm. wide, 3–15 mm. long; inflorescence several branched, rather compact, the axes purplish, glabrous, to ca. 2.5 dm. long; bracts purplish, ca. 1 cm. long, lance-linear, rarely ciliate near the tip; bracteoles linear, glabrous or slightly ciliate, placed just below the flower, 5–7 mm. long; sepals dark blue or violet-blue, glabrous on outer surface, with white felt inside in the lower half of long entangled hairs or at least with a few hairs, sometimes weakly ciliate,

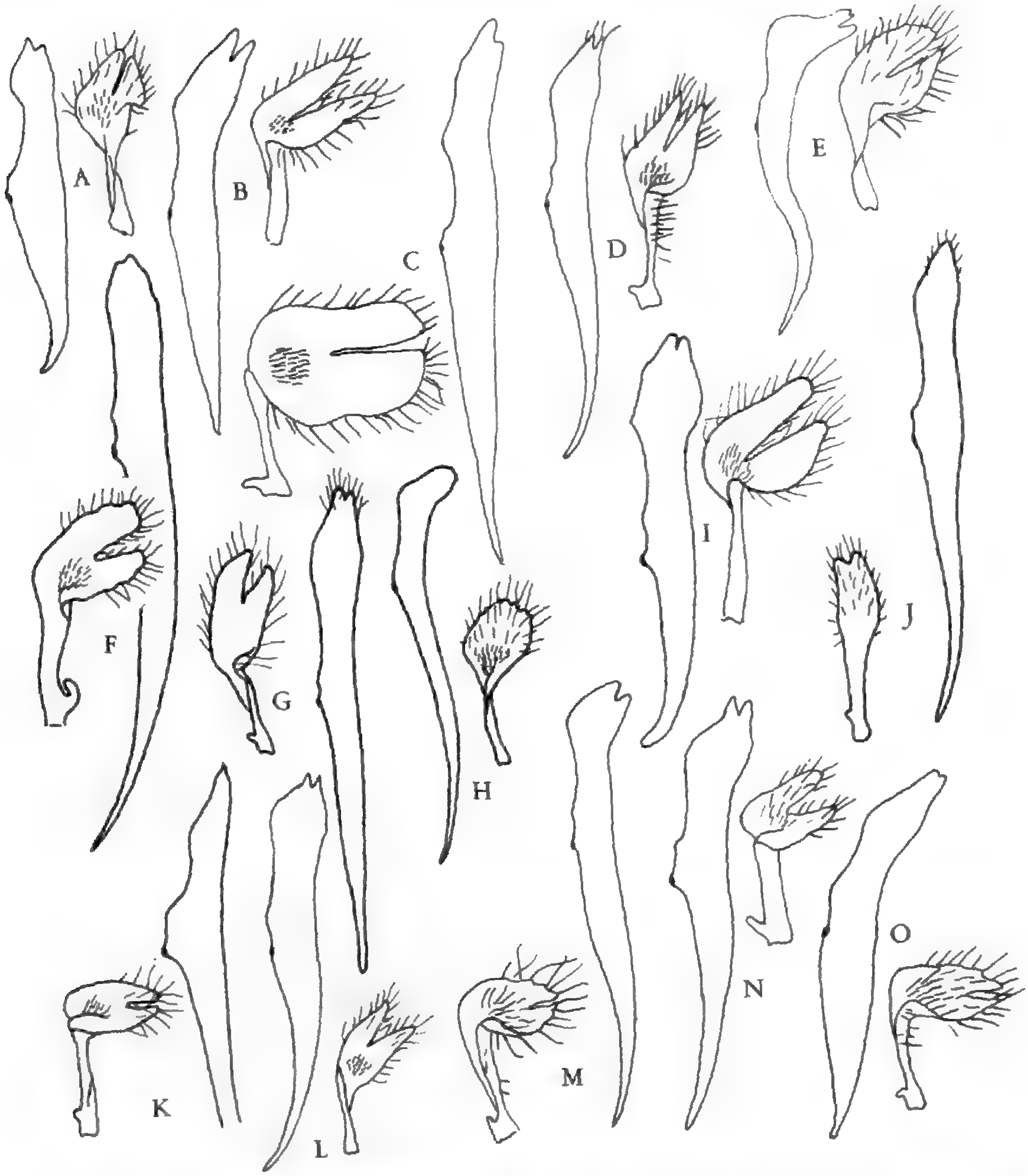

FIGURE 16. **Delphinium,** GROUP IX. Petals drawn, the upper spurred, the lower clawed. A. *D. afghanicum*; upper petal blade 8.5 mm. long, spur 9.5 mm.; lower blade 5 mm. long, claw 5 mm.; drawn from *Koelz 12719* (US). B. *D. arcuatum*; upper blade 11 mm. long, spur 11 mm.; lower blade 5.5 mm. long, claw 5.5 mm.; drawn from *Alexeenko* TYPE (LE). C. *D. bracteosum*; upper lamina 14 mm. long, spur 17 mm.; lower lamina 9.5 mm. long, claw 5 mm.; drawn from *E. & N. Busch* (BM). D. *D. burmaense*; upper lamina 9 mm. long, spur 13 mm.; lower petal lamina 5 mm. long, claw 5.5 mm.; drawn from *Kingdon Ward 13170* (BM). E. *D. buschianum*; upper lamina 9 mm. long, spur 11 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from *Karagin & Safiev* in 1931, TYPE (LE). F. *D. chenii*; upper petal lamina 13 mm. long, spur 22 mm.; lower lamina 6 mm. long, claw 6.5 mm.; drawn from *Yü 12809* (A). G. *D. confusum*; upper lamina 12 mm. long, spur 15 mm.; lower lamina 7 mm. long, claw 5.5 mm.; drawn from *Abolin 8193*, TYPE (LE). H. *D. cooperi*; upper lamina 8 mm. long, spur 16 mm.; lower lamina 4 mm. long, claw 5 mm.; drawn from *Cooper & Bulley 2294*, TYPE (E). I. *D. corymbosum*; upper lamina 11.5 mm. long, spur 10.5 mm.; lower lamina 7 mm. long, claw 7 mm.; drawn from TYPE

ovate, 12–15 mm. long, 7–8 mm. wide, obtuse; spur 10–15 mm. long, often hooked at apex; petals black, the upper laminae somewhat oblique, 9 mm. long, bidentate at the glabrous apex, spur ca. 10 mm. long; lower laminae sparsely bearded, strongly ciliate, very oblique, obovate, 5 mm. by 3 mm., bifid over halfway into lance-oblong divergent lobes, claw 5 mm. long; follicles 3, erect, 10 mm. long, 3 mm. wide, glabrous except along sutures.

TYPE: Southern Caucasus, shores Lake Cevan, *Karjagin & Safiev*, Aug. 15, 1931 (K, LE), seen.

DISTRIBUTION. The species grows on igneous rocks below 2100 m., Soviet and Turkish Armenia, and is represented by *Davis 32562*, in part, (K) from Kars Prov., Turkey.

191. **Delphinium chenii** W. T. Wang, Acta Phytotax. Sinica **6**: 369. 1957. FIG. 16, F.

Delphinium albomarginatum Chen, Bull. Fan Mem. Inst. Biol., Peiping (n.s.) 1: 170. 1948; not Simonova, 1924.

Perennial from a slender rhizome; stem 3–4 dm. tall, simple or short branched above, 3–4 mm. thick, striate, more or less retrorse-pubescent, equably and fairly densely leafy; petioles slender, 3–5 cm. long, scarcely dilated at the base, somewhat retrorse-strigose; blades pentagonal-orbicular in outline, 2–5 cm. in diameter, subglabrous to sparsely pubescent, pallid beneath, parted to near the base into cuneate-obovate segments, these 3-toothed or -lobed, or with a few additional teeth, the ultimate parts lance-ovate, rather short, obtuse to acute; inflorescence racemose or narrow-paniculate, retrorse-pubescent with white and yellow hairs, some rather long; flowers several; bracts largely reduced divided leaves, hairy; pedicels erect, 1–3 cm. long, hairy; bracteoles lance-linear, 5–10 mm. long, pubescent, placed slightly below the flowers; sepals strigose and short-hairy, blue with white margins (especially on the 2 lower pairs); upper sepal broadly ovate, 15 mm. long, 12 mm. wide, somewhat apiculate, the spur 22 mm. long, 4 mm. wide at the base, spreading decurved, narrowed to a subcylindric tip; lateral sepals pubescent on midrib, oblong-ovate, 14 mm. long, 10 mm. wide, rounded at apex; lower sepals rhombic-obovate, 15 mm. long, 9 mm. wide, rounded-obtuse; petals dark, the upper laminae

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sent by *Akegel* (LE). J. *D. crassicaule*; upper lamina 10 mm. long, spur 15 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from Bernhardi Herbarium (MO 1798761). K. *D. crassifolium*; upper lamina 10 mm. long, spur 14 mm.; lower lamina 5 mm. long, claw 6.5 mm.; drawn from *Radde* (GH). L. *D. cryophilum*; upper lamina 10 mm. long, spur 12 mm.; lower lamina 5 mm. long, claw 4 mm.; drawn from *Pohle* in 1902, TYPE (LE). M. *D. duhmbergii*; upper lamina 10 mm. long, spur 16 mm.; lower lamina 4.5 mm. long, claw 5.5 mm.; drawn from *Regel* in 1887 (US). N. *D. dyctiocarpum*; upper lamina 9 mm. long, spur 14 mm.; lower lamina 4.5 mm. long, claw 6 mm.; drawn from *Dress 8603* (BH). O. *D. elatum*; upper lamina 10 mm. long, spur 11 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from *Korshinsky* in 1891, TYPE of *D. korshinskyanum* (LE).

straight, 13 mm. long, 3 mm. wide, glabrous, somewhat erose at the rounded summit, spur 22 mm. long; lower laminae oblique, oblong, 6 mm. long, 4 mm. wide, cleft halfway into ciliate oblong lobes, with patch of yellow hairs at base below the cleft, claw 6.5 mm. long; stamens 6 mm. long, strongly dilated at base, glabrous; anthers dark, 1.2 mm. long; carpels 3, densely yellow-hairy.

TYPE: Southern Sikang, Taucheng, Hsien, Wongtula, 3000 m., *T. T. Yü 12809* (PE), not seen; photo. (E), seen. A sheet at A has the same number, but says "Yunnan" and lacks data.

192. **Delphinium confusum** Popov in Komarov, Fl. U.S.S.R. 7: 136, 723. 1937. FIG. 16, G.

Delphinium duhmbergii Huth, Bot. Jahrb. **20**: 402. 1895, *pro parte*.
Delphinium speciosum Huth, *loc. cit.* 415, *pro parte*.

Stem 3–6.5 dm. tall, densely pilose, the hairs in the lower part 1.5–2 mm. long, the upper part densely soft-pubescent, not glandular; stem rather equably but not densely leafy; petioles to 2 dm. long, dilated at base, long-pilose; leaf blades round-reniform, densely pubescent or more or less pilose on both sides, trifid, the middle segment oblong-obovate, cut into 3 lobes each with 3–4 lance-ovate teeth to 1 cm. long and 8 mm. wide; lateral segments of leaf cut into parts much like those of the middle one; raceme dense, sometimes branched at the base, many flowered; bracts broadly lanceolate or lanceolate, entire or rarely the lower trisect, obtusish, ca. 1 cm. long, densely and short pilose; pedicels 5–15 mm. long, with short spreading hairs; bracteoles broadly ovate, obtuse or subobtuse, 5.5–8 mm. long, 3–5 mm. wide, pubescent; flowers dark violet; sepals ovate or obovate, obtuse, 10–15 mm. long, 5–8 mm. wide, densely pubescent with short hairs without, almost glabrous within; spur spreading horizontally, incurved near the apex, 12–15 mm. long, 2.5–3 mm. wide at base; petals black, the upper laminae almost straight, 12 mm. long, emarginate and bristly at apex, the spur 15 mm. long; lower laminae oblong-obovate, long-ciliate, cleft almost halfway, ca. 7 mm. long, the claw appendiculate, 5.5 mm. long; carpels 3, densely pubescent.

TYPE: Asia Media, m. Akbach-tau, Aug. 12, 1921, *Abolin 8193* (LE); seen. This species keys out near *D. flexuosum* from farther west, but has much broader bracteoles.

193. **Delphinium cooperi** Munz, sp. nov. FIG. 16, H.

From a slender woody rootstock, the stem very slender, 1–4.5 dm. tall, with soft spreading hairs throughout, especially above; leaves few, mostly near the base, 1–2 reduced ones above; petioles spreading-villous, very slender, 2–10 cm. long, somewhat vaginate at base; blades pentagonal-subreniform in outline, mostly 2–5 cm. broad, 3- or 5-fid about 2/3 their length into broad obovate segments with some scattered long hairs on both surfaces and shallowly 2–3-lobed, each lobe with 2–few ovate-mucronate teeth to ca. 5 mm. long and 4 mm. wide; inflorescence open, simple or 1-branched, each with 1–3 flowers; lower bracts compound or trifid, 5–15 mm. long, the upper oblong-elliptic, 5–8 mm. long; pedicels 2–5 cm. long, spreading-villous and with some inflated glandular hairs; bracteoles elliptic, 4–6 mm. long, situated above the middle of the pedicel; flowers purple-violet with yellow hairs; upper sepal obovate, rounded above, 12–13 mm. long, 7–8 mm. wide, the spur decurved, 14–16 mm. long, 3 mm. wide at the base, rather acute; lateral sepals elliptic-ovate, 12–13 mm. by 9–10 mm., obtuse; lower sepals 13 mm. by 8 mm., subacute; petals black, the upper laminae quite oblique, entire, glabrous, 9 mm. long, 3 mm. wide, the spur ca. 13 mm. long; lower laminae oblong-ovate, ca. 4 mm. by 3 mm., bearded and long-ciliate, erose but not bifid, the claw 6 mm. long; stamens 5–6 mm. long, glabrous; anthers dark, 1 mm. long; follicles 3, erect, 13–14 mm. by 2.5 mm., spreading-pubescent, the styles 2.5 mm. long.

Caulis tenuis, 1–4.5 dm. altus, patulo-hirsutus, supra subglandulosus; folia pauca, subbasilaria; petioli villosi, valde tenues, 2–10 cm. longi, base subvaginati; laminae pentagonali-subreniformes, 2–5 cm. latae, 3–5-fid, segmenta 2–3-lobata, supra et infra sparse hirsuta; inflorescentia laxa, integra vel 1-ramosa, in quoque parte cum 1–3 floribus; bracteae inferiores trifidae, 5–15 mm. longae, superiores oblongo-ellipticae, 5–8 mm. longae; pedicelli 2–5 cm. longi, villosi et glandulosi; bracteolae ellipticae, 4–6 mm. longae; flores purpureo-violacei cum pilis aureis; sepala 12–13 mm. longa, 7–10 mm. lata, calcar 14–16 mm. longum, base 3 mm. latum; petala atra, laminae superiores obliquae, glabrae, integrae, 9 mm. longae, calcar 13 mm. longum; laminae inferiores oblongo-ovatae, 4 mm. longae, barbatae, ciliatae, erosae, unguis 6 mm. longus; stamina glabra; follicula 3, erecta, 13–14 mm. longa.

TYPE: Bhutan, Tonjsa, Oct. 3, 1914, *R. E. Cooper*, collector for Bulley *2294* (E) at 2600 m.

OTHER COLLECTIONS. **Bhutan:** Ridang Angduphorang, *Cooper* for Bulley *2024* (E); Chendebi, *Ludlow & Sherriff 3519* (BM, E), *17065* (BM), *19578* (BM).

A collection from Nepal [Lulo Khola, *Polunin, Sykes & Williams 3518*, (BM)] seems near *Delphinium cooperi*, but has the lower petals divided. The proposed species suggests *D. stapeliosum*, but that species lacks glandular hairs.

194. **Delphinium corymbosum** Regel, Acta Horti Petrop. 7: 547. 1880; Gartenflora **1881**: 23, 24. *pl. 1059*. 1881. FIG. 16, I.

? *Delphinium corymbosum* var. *baicalense* Huth, Bot. Jahrb. **20**: 409. 1895. Based on *Karelin & Kiriloff* 1841 (W) as *D. intermedium* var? I have not seen the Vienna specimen, if it is *Karelin & Kiriloff no. 1164*, it is *D. elatum*.

Delphinium umbellatum Regel ex Nevski in Komarov, Fl. U.S.S.R. **7**: 155. 1937, *in synon.*

Stem 3–6 dm. tall, retrorse-pilose, branched above forming a dense corymbose panicle, the stem leafy throughout; lower petioles dilated at the base, 1–1.5 dm. long, upper ones shorter; blades of leaves hairy on both sides, palmately 5-lobed, the lobes broadly cuneate, 3-lobulate at apex, the lobules coarsely crenate-dentate, the teeth callus-tipped; upper cauline leaves short petioled or sessile, palmately 3- or 5-lobed; branchlets of inflorescence with linear entire herbaceous bracts 10–15 mm. long; pedicels 3–7 cm. long; bracteoles linear, 10 mm. long; flowers 4–5 on side branchlets crowded in subumbellate fashion at the apex of the dense terminal raceme; sepals subequal, ovate or lance-ovate, 13–17 mm. long, 6–10 mm. wide, pale violet, greenish on back, hirsute, cucullate at apex; spur 8–10 mm. long, 3–4 mm. wide at base, hirsute, more or less incurved at the obtuse apex; upper petals blackish, the laminae emarginate, ca. 11 mm. long, glabrous, the spur 10.5 mm. long; lower laminae oblong-ovate, 7 mm. long, deeply cleft into oblong lobes, bearded below the lobes, long-ciliate, claw 7 mm. long; follicles 3, densely pubescent.

TYPE: Grown from seeds from alps of east Turkestan, sent by Dr. Akegel, June, 1881, ex horto bot. Petropolitano (LE); seen.

ILLUSTRATION. Gartenflora *pl. 1059.* 1881.

195. **Delphinium crassicaule** Ledeb. Fl. Rossica 1: 62. 1841. FIG. 16, J.

Delphinium caucasicum var. *chinense* Regel, Mem. Acad. Pétersb.. VII. 4: 10. 1861. Based on a collection from Chinese Mongolia, Herb. Fischer; not seen.

Stem to 1 cm. thick in the type, leafy largely below, leafless above, pilose; leaves round in outline, 5- to 7-parted to well above the base, subglabrous to scattered-pilose, especially beneath, the segments cuneate, broad, incised to near the middle into lanceolate, acuminate lobes; raceme rather dense, many flowered; pedicels more or less divaricate, up to more than twice the length of the flower, more or less pilose; bracts lance-linear, long-pilose, entire, to 10 mm. long; bracteoles 2–3, lance-linear, somewhat shorter, located near the base of the flower; sepals blue, subglabrous without, the upper ovate, 12 mm. by 6 mm., acute, the spur slightly decurved, 17 mm. by 3 mm., narrowed rather rapidly to a rather pointed apex; lateral sepals rhombic-obovate, 12 mm. by 5 mm., the narrow apex somewhat recurved; petals dark, the upper laminae acute, ciliate, almost straight, ca. 10 mm. long, the spur ca. 5 mm. long; lower laminae almost straight, 5 mm. long, 2-toothed apically, hairy in distal part, claw 5 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, oblong, 1 mm. long; follicles 3, glabrous.

TYPE: Eastern Siberia, between Wilnick and Olekminsk, *Kruhse* (LE); seen. The type specimen now has no flowers. Three sheets of the Bernhardi Herbarium (MO) seem to be this species; one labeled Ex Museo Berolinensi, June, 1818. Nevski (Fl. U.S.S.R. 7: 154. 1937) cites this species as a synonym of *D. crassifolium*, but the leaf lobes are much sharper.

196. **Delphinium crassifolium** Schrad. ex Spreng. Gesch. Bot. 2: 201. 1818, *nomen*; Ledeb. Fl. Rossica 1: 62. 1841. (A var. *compactum* Malysch was later printed on herbarium labels with a Latin diagnosis). FIG. 16, K.

? *Delphinium crassifolium* var. *tangutica* Maxim. Fl. Tangut. 1: 22. 1839; not known to me.

Perennial from a woody root; stem simple, scapose, slender, with scattered long spreading hairs and shorter glandular ones above, 3–7 dm. tall; petioles 7–15 cm. long, spreading-hairy, vaginate at base; leaf blades rounded angled in outline, 5–15 cm. broad, sparsely hairy on both sides, paler beneath, 5- or 7-parted into broad cuneate trifid segments, these with more or less oblong-ovate teeth or shallow lobes 4–10 mm. broad; racemes strict, 2–15 cm. long, several flowered; bracts lanceolate or narrower, to 10 mm. long; pedicels appressed to the axis, slender, pubescent, 1–5 cm. long; bracteoles lance-linear, 3–6 mm. long, from the middle of the pedicel to near the flower; sepals blue, scattered-pubescent; upper sepal 14–17 mm. long, ovate, obtuse, spur about as long, straight to somewhat curved; lateral sepals oblong, 14–15 mm. long, rounded at apex; lower sepals 16–18 mm. long, obtuse; petals black, the upper laminae almost straight, acute, entire, 10 mm. long, glabrous; lower laminae 5 mm. by 2 mm., cleft about 2 mm., with long white hairs on both sides toward the apex and on the margin, claw 6 mm. long, broad; stamens 6–7 mm. long, the base of the filaments much widened, glabrous; anthers dark, 1 mm. long; follicles 3, glabrous, reticulate; seeds squamate, 1.5 mm. long.

TYPE: Krasnijarsk, Turkestan?, Herb. Ledebour (LE); seen.
ILLUSTRATION. GMELIN, Fl. Sibirica 4: *pl. 79.* 1769.

REPRESENTATIVE SPECIMENS. In alpibus Sajanensibus, *Radde* (GH); var. *compactum* Malyschev, 2300 m., Mts. Sajanenses, Jugum Tunkenense Aug. 14, 1858 (BM, E, K); var. *stubendorffii*, Sibiria orientalis, leg. *Stubendorff* (K, in type cover) I have no record of publication; *crassifolium*, Sibir. media, in herbario Petropolitani (K); Mts. Sajan, *Komarov* in 1902 (P); Issyk-Kul, Songaria, *Krasnow* in 1886 (P).

197. **Delphinium cryophilum** Nevski in Komarov, Fl. U.S.S.R. 7: 146, 724. 1937. FIG. 16, L.

Delphinium elatum var. *intermedium* f. *hirsutum* Pohle in herb.

Perennial, the stem 2–6.5 dm. tall, to almost 10 mm. thick below, retrorsely soft hairy, the hairs 1–2.5 mm. long, rather equably leafy; petioles 5–10 cm. long, strongly dilated at base; laminae with long white hairs on both surfaces, to ca. 1 dm. broad, round-cordate in outline, parted almost to base into rhombic-cuneate parts which are more or less plainly shallowly 3-lobed in their distal portion, then with few deep teeth or lobules (lance-oblong, to almost 1 cm. long, 2–4 mm. wide, acute); central raceme 2–3 dm. long, thick-stemmed, many flowered, with 1 or 2 few flowered, very slender racemes near the base; bracts 1–3 cm. long, narrowly linear to broadly lanceolate; pedicels spreading-hairy, erect, 1–4 cm. long; bracteoles linear-subulate, 4–5 mm. long, near the flower; sepals violet-blue, glabrous except for a few hairs near the apices, the upper sepal ca. 12 mm. by 6 mm., attenuate at tip, the spur spreading, 13–14 mm. long, 3.5–4 mm. wide at base, obtuse; lateral sepals obovate, 12–13 mm. long, 7–8 mm. wide, round-obtuse; lower sepals 11–12 mm. by 4–5 mm., attenuate; petals black, the upper laminae oblique, 10 mm. by 3 mm., short-bidentate, glabrous, the spur 11–12 mm. long; lower laminae yellow-bearded at base, 4–5 mm. long, bifid halfway into lance-oblong ciliate lobes, claw 5 mm. long; stamens 5 mm. long; carpels 3, glabrous.

TYPE: "In decliviis argillosis herbosis insulae Kolgujev, lg. *Pohle*, Aug. 23, 1902 (LE); seen.

198. **Delphinium duhmbergii** Huth, Bull. Herb. Boiss. 1: 330. *pl. 16* (flower). 1893. FIG. 16, M.

Delphinium iliense Huth, Bot. Jahrb. **20:** 402–3. 1895. No type stated. From LE was loaned as type: "Prope lacum Turnkul, flora iliensis, *Krassno* in 1886," originally identified as *D. caucasicum* var. *hirsutum*. *D. iliense* var. *pubiflorum* (cited by Huth) was, Möngötö, *Regel*, 1879, seen (K); *D. iliense* var. *angustatum* (Huth, p. 403), no cited material seen; *D. iliense* var. *macrocentrum* (Huth, p. 403), a *Przewalski*, 1880, specimen from Kansu, China cited, not seen or identified; *D. iliense* var. *hispidum* (Huth, p. 403), no cited material seen.

Delphinium englerianum Huth, Bot. Jahrb. **20:** 418. 1895. First specimen cited was Turkestan, Hissar, "in valle fluminis Jaquob," *Regel*, 1883 (LE, not seen, isotype E, seen). Huth had 3 vars.: var. *incisum* (p. 418), no type cited, opinion expressed it might be *D. incisum* Wall., which it cannot be if related to *D. duhmbergii*; var. *hoffmeisteri* Klotzsch, Reise Wald. 132. 1862; no specimen cited and I do not know the plant; var. *simplex* Huth (p. 418) which I cannot place.

Delphinium turkestanicum Huth, Bot. Jahrb. **20:** 420. 1895. If the first of two specimens cited is taken as type (Aryslyn, 3000 m., *Regel*, 1879 (LE)), it belongs here, but has a few short bristles on upper petal lamina.

Perennial from a woody rhizome, stem slender, 1–8 dm. tall, hirsute below, tending to be glabrous to sparsely hirsute above, mostly leafy at the base or in lower half; lower petioles hairy, 5–20 cm. long, dilated at base, upper much shorter; leaf blades round-pentagonal in outline, subglabrous to hairy above, pilose beneath on veins and margin or on whole surface, 3–6 cm. broad, divided to below middle into cuneate, obovate segments 1–2.5 cm. broad, these shallowly lobed or coarsely toothed, the teeth ovate, mucronate; cauline leaves remote, the uppermost reduced, subsessile; inflorescence racemose or thyrsoid, glabrous to pilose; bracts trifid or mostly lanceolate and entire, 5–12 mm. long, ca. 2 mm. wide; pedicels ascending, 1–3.5 mm. long; bracteoles lanceolate, ciliate, membranous, bluish, 5–7 mm. long, subtending the flower; sepals mostly blue, glabrous to pubescent; the upper sepal ovate, 13–15 mm. long, 8–10 mm. wide, acutish, the spur almost straight, about as long as sepals, 3 mm. wide at base, narrowed to a sharp point; lateral sepals round-ovate, 13–15 mm. long, 10–11 mm. wide, rounded-obtuse; lower sepals 12 mm. by 7 mm., acute; petals almost black, the upper laminae oblique, glabrous or with a few short bristles on the face, bidentate, ca. 10 mm. long, the spur 16–17 mm. long; lower laminae oblique, ovate, 4.5 mm. by 3 mm., cleft ca. 2.5 mm. into somewhat erose lobes with very long cilia and very long hairs at base of lamina, claw 5.5 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, 1.2 mm. long; follicles 3, glabrous to hirsute, to 10 mm. long; seeds triquetrous, winged.

TYPE: Altai Mts., Siberia, *Duhmberg* in 1881 (B), not seen. At Kew are 3 sheets "teste Huth": Turkestania, Dschungarischer Alatau, *Regel* in 1878, and Dschagartai, *Regel* in 1877. These I would use as representative of the species. The third sheet is the Möngötö collection cited above under the discussion of the name *iliense*.

REPRESENTATIVE SPECIMENS. **Asia Media:** *Lipsky 1783* (BM); **Turkestan:** *Regel*, July 18, 1877 (LE); Alatau, *Karelin & Kiriloff 1164* (NY, P); Issinsul, *Regel*, Aug., 1877 (K); Tianschan, *Merzbacher 723* (US); Terskei Alatau, *Artemjev 4266* (BM, E, K); Koksu Valley, *Littledale* (K).

199. **Delphinium dyctiocarpum** DC. Syst. 1: 360. 1817. FIG. 16, N.

Delphinium dictyocarpum Steud. Nom. ed. II. 1: 488. 1840.
Delphinium ciliatum Stev. var. *dictyocarpum* Huth, Bot. Jahrb. 20: 404. 1895.
Delphinium dyctiocarpum var. *glaberrimum* Trautv. Bull. Soc. Nat. Mosc. 33: 81. 1860. I have not seen type. The variety is reduced to synonymy by Nevski in Komarov, Fl. U.S.S.R. 7: 159. 1937.

Perennial from a woody root, the stem 6–15 dm. tall, erect, leafy, robust, glabrous or nearly so, often purplish, mostly simple; lower petioles to ca. 2 dm. long, scarcely dilated at the base, the upper much shorter; leaf blades rounded-pentagonal in outline, the upper ca. 4 cm., the lower ca. 15 cm. broad, subglabrous above except for a few appressed hairs on the veins, strigose or pilose beneath especially on the veins, 3- to 7-parted to within 1 or 2 cm. of the base, the lower part of the segments subcuneate, entire for 1–3 cm. then widening into broad parts that are pinnately incised into lanceolate teeth or lobes to almost 2 cm. long and mostly 2–4 mm. wide, subacuminate; inflorescence a dense raceme or open panicle of racemes, many flowered, nearly or quite glabrous; bracts mostly entire (the lowest trifid), subsetaceous, 5–15 mm. long; pedicels divaricate to suberect, 1–3 cm. long; bracteoles lance-linear to setaceous, 3–7 mm. long, placed well below the flower; sepals violet-blue, glabrous or sometimes minutely strigulose; upper sepal 10–12 mm. long, ovate, acutish, the spur straight, 12–20 mm. long, 2.5–3 mm. wide at base, narrowed to a slender apex; lateral sepals 12 mm. long, 7 mm. wide, elliptic-oblong, with rounded apex; lower sepals 12–14 mm. long, 6 mm. wide, more pointed; petals dark, the upper slightly oblique, the laminae 8–9 mm. long, glabrous, bidentate, the spur 12–24 mm. long; lower laminae strongly oblique, hairy, ovate-oblong, 4.5 mm. long, cleft half its length, the claw broad, 6 mm. long; stamens 5–6 mm. long, glabrous; anthers dark, 1 mm. long; follicles 3, glabrous (ciliate on suture when young), suberect, 10–14 mm. long, 4–5 mm. wide, the styles an additional 3.5 mm.; seeds brown, angled, ca. 2 mm. long, winged on the angles.

TYPE: A cultivated specimen from Siberia (G?); not seen.

EXAMPLES. **Cultivated:** Ithaca, N. Y., *Dress 8603* (BH); Cambridge, Mass. in 1901 (BH); Kew, *Nelmes 804* (BH); ex herbario horti Petropolitani, *Karkoraly* in 1862 (MO, NY). **Wild:** Altai, *Schrenk* (GH, K); Altai occident., *Titov* (NY); Altai borealis, *Burdakova* in 1931 (NY); Songoria, *Schrenk*, ex herb. Trautv. July, 1843 (K).

200. **Delphinium elatum** L. Sp. Pl. **1:** 531. 1753. FIG. 16, O; 17, A, B.

Delphinium palmatifidum DC. Syst. **1:** 358. 1817, and probably vars. *hispidum* and *glabellum* of same reference and based in part on Gmelin, Fl. Sibirica **4:** *pls. 79 and 75*, respectively. This reference and the next three are treated as synonyms of *D. elatum* by Nevski, Fl. U.S.S.R. **7:** 147. 1937.

Delphinium glabellum Turcz. Bull. Soc. Nat. Mosc. **10:** 56. 1837, *nomen*.

Delphinium alpinum Huth, Bot. Jahrb. **20:** 405. 1895, *pro parte*, not same as Waldst. & Kit. Pl. Rar. Hung. **3:** 273. 1812, European. Possibly *D. alpinum* vars. *ajanense* Huth and *productum* Huth, *loc. cit.* 406.

Delphinium discolor Fisch. ex Sweet, Hort. Brit. ed. II. 9. 1830, *nomen*.

Delphinium elatum subsp. *palmatifidum* (DC.) Sergievsk, Animadvers. Syst. Univ. Tomsk **1930:** 3 and vars. *glabellum* (DC.) and *hispidum* (DC.), and *glabrum* Sergievsk.

? *Delphinium elatum* subsp. *subglabrum* Ledeb. Fl. Ross. **1:** 64. 1841.

? *Delphinium elatum* subsp. *intermedium* (Soland.) Fleisch & Lindm. Bull. Acad. Polon. Sci. & Lett. Cl. Math. Nat. **1933:** 96. 1934.

Delphinium intermedium DC. Prodr. **1:** 55. 1824. Based on a European type.

? *Delphinium elatum* var. *longicalcaratum* Huth, Bot. Jahrb. **20:** 398. 1895. Type, "Sibiria pr. fl. Jenisei," *Lessing* (B); not seen.

? *Delphinium atropurpureum* Pall. Reise Statth. Russ. Reich. **1:** 134. 1771. Apparently a name used later for cultivated plants only.

Delphinium korshinskyanum Nevski in Komarov, Fl. U.S.S.R. **7:** 153, 724. 1937. Type, "Inter fl. Zeja & Bureja, near Ivavovskoje," *Korshinsky*, July 11, 1891 (LE); seen.

? *Delphinium elatum* var. *sericeum* W. T. Wang, Acta Bot. Sinica **10:** 81. 1962. Said to be glandular puberulous in the inflorescence, from Sinkiang province, China. I have seen no material and doubt its relationship to the *D. elatum* complex.

Perennial from a woody rhizome, stem 5–20 dm. tall, glabrous to spreading- or retrorse-villous, rather robust, simple below, simple or branched in the inflorescence, leafy, the leaves only gradually reduced upward; basal petioles to 2 dm. long, membranous-dilated at base, glabrous to hairy, the cauline shorter and scarcely dilated below; blades mostly 5–15 cm. broad, more or less rounded-pentagonal in outline, subglabrous to hairy, mostly 5- or 7-parted to within about 1 cm. from the base, the segments broad, cuneate at base, ovate, incised or deeply toothed to lobed with 2–3 coarse terminal teeth 8–20 mm. long, 8–10 mm. wide; inflorescence of subglabrous to hairy racemes solitary at end of each stem, the flowers many, crowded; bracts leaflike and divided or the upper entire, linear, to ca. 1 cm. long; pedicels ascending, mostly 1–3 cm. long; bracteoles linear, 4–6 mm. long, near to flower or above the middle of the pedicel; flowers pale blue to dark blue, the sepals glabrous or ciliate or more or less pubescent without; upper sepal ovate, 12–16 mm. long, subobtuse, the spur about as long or longer, stout, 3–3.5 mm. wide at base, straight or decurved, blunt; lateral sepals mostly 12–16 mm. long, 8–10 mm. wide, rounded at apex; lower about as long, narrower, obtuse; petals almost black or of same color as sepals, the upper laminae suberect, ca. 8 mm. long, bidentate at the glabrous or sparsely bristly apex; lower laminae oblique, long-bristly, 4 mm. by 2 mm., shallowly bilobed, the claw 6 mm. long; stamens 5 mm. long, glabrous, strongly dilated; anthers dark, 1 mm. long; follicles 3, glabrous, 12–15 mm. long, the styles an additional 3 mm.; seeds dark, winged on angles, 2–3 mm. long.

TYPE: Specimen in Hort. Cliff. Herb. (BM) from Silesia; seen.

RANGE. Widely distributed in mountains from central Europe across northern Siberia.

ILLUSTRATIONS. HEGI, Ill. Fl. Mittel-Eur. 3: *pl. 114.* 1909; Bot. Reg. *pl. 1963.* 1837.

COLLECTIONS SEEN. **Siberia orient.:** *Dr. Merk*, Herb. Pallas (BM); Sibiria subalpina, *Jacquin* 1773 (BM); **W. Siberia:** *Mamlev 211* (K, US), *Stabindorff* (F); Lake Baical, *Radde* (K, P); Iter Ircutense, *Kusnezow 885* (MICH), Irkutsk, *Besser* (K); Transbaicalia, *Enander* 7–19–1914 (E); Mongolia, *Ikonnikov-Galitzky 2915* (MO); Soongaria, *Karelin & Kiriloff 1168* (BM, K in part, P); Altai, *Ledebour* (K, P), *Borgand* (GH); Ochotsk Sea, *C. Wright* (GH, K, NY, US); Dahuria, *Turczaninow* in 1828 (UC), *Fischer* in 1842 (P); Jenissei, *Tolmatchew* 174 (GH), *Brenner* in 1876 (US).

A variable species as here recognized. Pawlowski (Fragmenta Flor. & Geobot. **9**: 429. 1963) recognizes subspecies *intermedium* and others, but I do not feel that I understand *D. elatum* well enough to do so. I have seen cultivated material under many names: *D. formosum, D. caucasicum, D. decorum, D. bicolor, D. intermedium* and *D. cuneatum.*

201. **Delphinium elbursense** Rech.f. Anz. Österr. Akad. Wiss. Math.-Nat. **88**: 223. 1951. FIG. 17, C.

Perennial from a rhizome; stem to 6 dm. tall, simple or short branched in the inflorescence, sulcate-striate, with long soft spreading hairs below, deflexed-strigose above, leafy to inflorescence; leaves rather numerous, petioles more or less villous, the lower to 1 dm. long, somewhat dilated at the base, the upper shorter; leaf blades sparsely strigose or with looser hairs on veins, broadly round-cordate, the lower to 12 cm. across, gradually smaller up the stem, 5-parted to within 1 or 2 cm. from the base into cuneate-obovate segments, these incised into lance-oblong teeth or lobes mostly 2–4 mm. wide, obtuse to acute, thickened at apex; inflorescence a rather open raceme 1–3 dm. long, with or without supplementary branches below, densely strigose; bracts trifid or entire and lanceolate, 1–2 cm. long, pubescent; pedicels 1–3 cm. long, ascending; bracteoles 2, lance-linear, near the flower; sepals deep blue, crisp-villous without, with some long loose hairs within; upper sepal ovate, 15–17 mm. long, 10 mm. wide, obtuse, the spur usually slightly curved, 18–20 mm. long, ca. 4 mm. wide at base, narrowed to an acute apex; lateral sepals broadly rhombic-obovate, 20 mm. long, 15 mm. wide, rounded-obtuse; lower sepals elliptic, 18 mm. by 10 mm., acute; petals dark, the upper laminae bidentate, slightly oblique, glabrous, 11 mm. long, the spur 11–12 mm. long; lower laminae somewhat oblique, 5 mm. long, 4 mm. wide, deeply cleft into 2 oblong-lanceolate divaricate, bearded and ciliate lobes, claw 6 mm. long, not appendaged; stamens 6–7 mm. long, glabrous; anthers dark, 1–2 mm. long; follicles 3, pubescent.

TYPE: Iran, prov. Gorgan (Asterabak), Mt. Shahvar near Hadjilang, 2400–2600 m., *K. H. & F. Rechinger 6093a*, July 27, 1948 (W) not seen; isotypes (BH, MO, UC, US) seen.

Possibly too near *D. speciosum*, but perhaps a local entity recognizable by the pubescence.

202. **Delphinium elisabethae** N. Busch, Acta Inst. Bot. Acad. Sci. U.S.S.R. I. fasc. 3: 355. 1937. FIG. 17, D.

Stem perhaps 1 m. tall, retrorse-strigulose and with some spreading hairs, these more numerous and mixed with glandular ones in the inflorescence, stem leafy; cauline petioles 1–6 cm. long, scarcely dilated at base; leaf blades 4–10 cm. broad, green and sparsely strigulose above, paler and more pubescent beneath, deeply 5-fid into rather narrow segments (1–2 cm. wide), these laciniate ca. halfway to midrib into lance-linear lobules and teeth 1–4 mm. wide, 2–15 mm. long; inflorescence densely yellow-glandular, branched at base, side branches with rather compact, few-flowered racemes, central raceme lax, to 2 dm. long; lowest bracts foliose, others lance-linear, pubescent, 5–12 mm. long; pedicels divergent, glandular, 2–5 cm. long; bracteoles ca. 2 mm. long, near the flowers; sepals pale blue, to whitish striped, more or less glandular and pubescent; upper sepal oblong-ovate, 13 mm. long, 5 mm. wide, obtuse, the spur spreading decurved, 10–14 mm. long, 2.5 mm. broad at base; lateral sepals oblong-elliptic, 11 mm. by 5 mm., rounded at apex; lower sepals 14 mm. by 4 mm.; petals black, the upper laminae somewhat oblique, 8 mm. long, glabrous, emarginate, the spur 10 mm. long; lower laminae round-ovate, 5 mm. in diameter, bearded near base, sparsely so on the 2 lobes, claw 5 mm. long; stamens 6–7 mm. long; anthers dark, 1 mm. long; carpels 3, glabrous.

TYPE. Transcaucasia (Ossetia Meridionali) near Sredneje Sba, Aug. 19, 1933, *Eliz. Busch* (LE) seen.

ANOTHER SPECIMEN. **South Ossetia:** *E. & N. Busch*, Aug. 6, 1935 (BM).

203. **Delphinium elliptico-ovatum** W. T. Wang, Acta Bot. Sinica **10**: 83. 1962.

Stem ca. 7 dm. tall, 3 mm. thick at base, sparsely retrorse-hirsute, few branched above, equably leafy; median cauline leaves long petioled, blades as in *D. naviculare*, ca. 5.7 cm. long, 8 cm. wide, 3-parted to 8 mm. from the base, the middle part obovate-rhombic, acuminate, 3-lobed to middle, strigulose on both surfaces; petioles slightly longer than blades, not or scarcely vaginate at base, with the pubescence of the stems; racemes 7–8-flowered, rather lax, the axes loosely retrorse-strigulose; basal bracts trifid, others lanceolate or elliptic-ovate, 8–12 mm. long, 2–2.5 mm. wide; pedicels 1–2.7 cm. long, densely retrorse-strigulose, divergent; bracteoles 1–7 mm. remote from the flower, 5.5–7 mm. long, 2–3 mm. wide, acuminate, strigulose; sepals blue-purple, 10–13 mm. long, strigulose; spur 12–13.5 mm. long, cylindro-subulate, 2–2.5 mm. thick, slightly decurved; petals black, the upper laminae puberulent at apex, the lower round-ovate, bilobed, with triangular lobules, long-ciliate at end, yellow- and white-bearded at base, claw appendiculate, longer than the limb; stamens glabrous; follicles 3, loosely puberulent to glabrous, 9 mm. long, the styles an additional 2.5 mm.; seeds triquetrous, 1.5 mm. long, scaly-laminate.

TYPE: Sinkiang, Wen Chuan, *K. C. Kuan 3858,* Aug. 28, 1957 (PE); not seen. I have seen no material of this species. It is supposed to be near to *D. retropilosum* (Huth) Sambuk, in which the leaves are basally somewhat cuneate, the sepals densely strigulose.

204. **Delphinium flexuosum** Marschall Bieberstein, Fl. Taur. Cauc. **2**: 12. 1808. FIG. 17, E.

Delphinium ciliatum Stev. Ind. Sem. Hort. Dorpat (1811) ex Bieb. Fl. Taur. Cauc. **3**: 370. 1819. A specimen from Narzana (Nartsana) labelled *D. ciliatum* Stev. (K) has been seen.

? *Delphinium flexuosum* vars. *brevipila* Busch and *hirsuta* Busch in Fl. Cauc. Crit. III. **3**: 67. 1902.

Delphinium elatum var. *subciliatum* Ledeb. Fl. Rossica **1**: 64. 1842. A new name for *D. flexuosum* and *D. ciliatum*.

? *Delphinium flexuosum* vars. *dasyanthum* and *lasiocarpum* Rupr. Fl. Cauc. 34, 35. 1869.

Perennial from a woody rhizome with strong fibrous roots; stem flexuous, robust, 4–8 mm. thick, striate, reddish, spreading-hairy to subglabrous, 6–10 dm. tall, leafy, simple or branched above; petioles subglabrous to hairy, dilated at base, the lower to 1 dm. or more long, the upper almost suppressed; leaf blades pentagonal in outline, broader than long, 3–10 dm. broad, glabrous to villous on both surfaces, paler beneath than above, parted to one cm. or so above the base into segments with rather parallel sides near the base, then more or less ovate and trifid or incised into teeth or shallow lobes sublanceolate in shape, acute; inflorescence a dense many-flowered raceme or an open panicle of racemes, glabrous to hairy; lower bracts leafy, trifid, the upper entire, lance-linear, 5–20 mm. long; pedicels

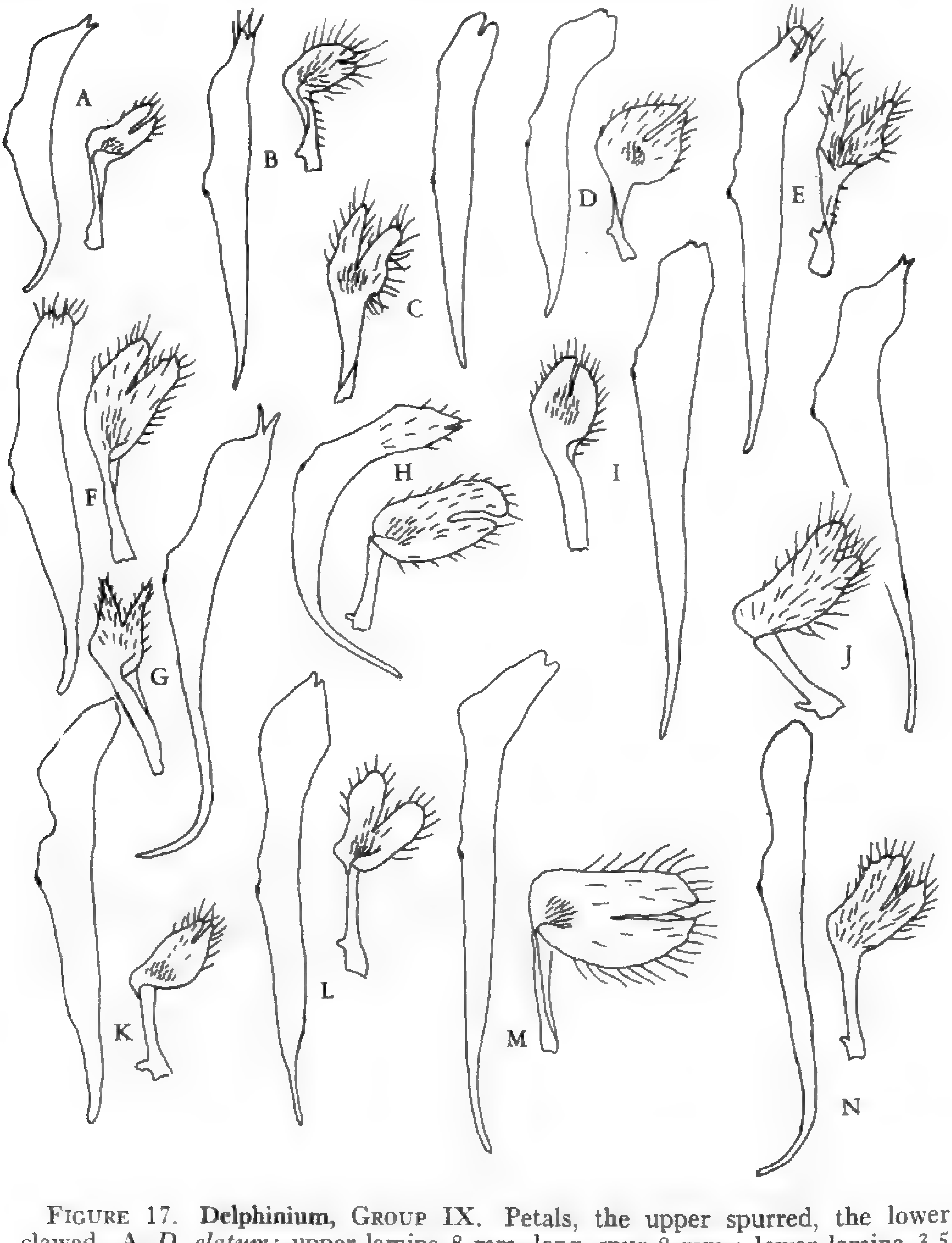

FIGURE 17. **Delphinium,** GROUP IX. Petals, the upper spurred, the lower clawed. A. *D. elatum*; upper lamina 8 mm. long, spur 8 mm.; lower lamina 3.5 mm. long, claw 6 mm.; drawn from *Nilsson* in 1898 (US). B. *D. elatum*; upper lamina 8 mm. long, spur 12 mm.; lower lamina 4 mm. long, claw 6 mm.; drawn from *Korshinsky* on the Amur (US). C. *D. elbursense*; upper lamina 11 mm. long, spur 12 mm.; lower lamina 5 mm. long, claw 6 mm.; drawn from *Rechinger 6093a* (UC). D. *D. elisabethae*; upper lamina 8 mm. long, spur 10 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from *Elizabeth Busch* in 1933, TYPE (LE). E. *D. flexuosum*; upper lamina 9 mm. long, spur 15 mm.; lower lamina 6 mm. long, claw 5 mm.; drawn from *Grossheim & Schiskin 333* (NY). F. *D. formosum*; upper lamina 11 mm. long, spur 12 mm.; lower lamina 6 mm. long, claw 6 mm.; drawn from *Balls 496* (K). G. *D. hillcoatiae*; upper lamina 11 mm. long, spur 17 mm.; lower lamina 4.5 mm. long, claw 5 mm.; drawn from

divaricate, 5–15 mm. long; bracteoles lance-linear, 4–8 mm. long, subtending the flower; sepals blue, glabrous to villous; upper sepal ovate, 13–15 mm. long, 7–8 mm. wide, acute, the spur almost straight, 15–18 mm. long, 3.5–4 mm. wide at base, narrowed to an acute tip; lateral sepals rounded-ovate, 12 mm. by 8 mm., obtuse; lower sepals 13–14 mm. long, 6–7 mm. wide, subacute; petals dark, the upper laminae slightly oblique, 9 mm. long, bidentate, pilose or glabrous, the spur ca. 15 mm. long; lower laminae only slightly oblique, the blade 6 mm. long, long bearded and ciliate, the lance-oblong lobes divaricate, claw 5–6 mm. long; stamens 6–7 mm. long, a few hairs along the margin of the filaments; anthers dark, 1 mm. long; follicles 3, glabrous, divergent, 7–8 mm. long, the styles 2.5 mm. long; seeds triquetrous, 1 mm. long, dark, squamate.

TYPE: No specimen cited, but from LE one was loaned me, from the Caucasus, Mt. Berchtau, *Steven*, ex Herbario Marschall Bieberstein, labelled TYPE; there are photographs at (A, K). Another specimen in the Leningrad loan was "In herbidis montosis circa acidulam Nartsana, 3500′, August 9, 1829," no collector given, labeled *D. flexuosum.*

ILLUSTRATIONS. TREVIRANUS, Delph. & Aquileg. Obs. *pl. 1.* 1817 and Bieberstein, Cent. Pl. Rar. 2, **II**:64. 1843, according to Index Londinensis.

REPRESENTATIVE SPECIMENS. **Transcaucasia:** prov. Tiflis, *Grossheim & Schiskin 333* (BM, K, NY); Mt. Kochta, *Wissjulina* in 1928 (BH); Azerbajdzhan, *Karjagen* in 1935 (BH); Funtel flum., Kchetiuscaja, *Busch* in 1903 (K); in Caucaso iberico lectum, dedit Steven Jan., 1821 (K).

205. **Delphinium formosum** Boiss. & Huet, Diagn. sér. II. **5**: 13. 1856. FIG. 17, F.

Delphinium formosum var. *centiflorum* Huth, Bot. Jahrb. **20**: 411. 1895. Huth cited *Balansa* from "Vallée alpine de Djimil (Lazistan), 2000 m.," this is *1352* (A, K, P) from northeast Turkey.

Perennial, 1–2 m. tall, the stem thick, ridged, pilose below, glabrous above, branched above, equably leafy; leaves subglabrous, 5- or 7-parted to ca. 1 cm. from base, the divisions broadly cuneate-obovate, incisely serrate into teeth or short lobes 3–10 mm. wide; cauline petioles to 1 dm.

Ludlow & Sherriff 2424 (BM). H. *D. himalayae*; upper lamina 10 mm. long, spur 12 mm.; lower lamina 8 mm. long, claw 6 mm.; drawn from *Sharma 117* (E). I. *D. lacei*; upper lamina 8.5 mm. long, spur 19 mm.; lower lamina 4.5 mm. long, claw 5 mm.; drawn from *Lace 6012* (E). J. *D. leptopogon*; upper lamina 9 mm. long, spur 19 mm.; lower lamina 9 mm. long, claw 6 mm.; drawn from *Harry Smith 7109* (A). K. *D. maackianum*; upper lamina 11 mm. long, spur 16 mm.; lower lamina 5 mm. long, claw 5.5 mm.; drawn from *James* in 1886 (GH). L. *D. mariae*; upper lamina 12 mm. long, spur 13 mm.; lower lamina 5 mm. long, claw 6.5 mm.; drawn from *Alexeenko* in 1898, TYPE (LE). M. *D. megalanthum*; upper lamina 13 mm. long, spur 16 mm.; lower lamina 9 mm. long, claw 6.5 mm.; drawn from *Lipsky* in 1892, TYPE (LE). N. *D. mirabile*; upper lamina 10 mm. long, spur 17 mm.; lower lamina 5 mm. long, claw 6.5 mm.; drawn from *Bunge* in 1839 (MO).

long, scarcely dilated at base; upper leaves 3- or 5-parted, reduced, subsessile; inflorescence paniculate, the central raceme densely many flowered, 1–3 dm. long; bracts lanceolate, 1–2 cm. long, entire, or the lowest trifid and larger; pedicels divaricate, 1–5 cm. long, glabrous; bracteoles opposite, ovate to lanceolate, 5–12 mm. long, glabrous, reaching the base of the flower or not; sepals violet-blue, broadly to oblong-ovate, 2–3 cm. long, pubescent to glabrous without and within, the margins ciliate; spur straight or slightly curved, 12–15 mm. long, 4 mm. wide at base, rapidly narrowed; petals black-purple, the upper laminae somewhat oblique, 11 mm. long, somewhat pilose at apex, spur 12 mm. long; lower laminae bifid, yellow bearded, ca. 6 mm. long, ciliate, the claw 6 mm. long; stamens 6–7 mm. long; anthers bluish, 1 mm. long; young follicles glabrous in type collection at Kew, sometimes short-pubescent, divergent in maturity, 12–15 mm. long, 4–5 mm. wide, the styles 3–4 mm. long; seeds brown, almost 2 mm. long, covered with horizontal rows of scales.

TYPE: "Cerca Maadenkhan inter Erzeroum et Baibout," Armenia. *Huet du Pavillon*, 1843 (G) not seen, (BM, K) seen; photo. (BH).

RANGE. Said to grow on coarse limestone scree, rocky slopes, 1500–2790 m., Turkey, Georgia.

ILLUSTRATIONS. Fl. des Serres II. *pl. 1185.* 1857; Rev. Hort. IV. **8:** 528. 1859; Gartenflora **8:** *pl. 253.* 1859.

REPRESENTATIVE COLLECTIONS. **Turkey:** *E. K. Balls 1975, 496*; *Davis 21122, 21211*; *Sintenis 1590*; *du Parquet* in 1886. Cultivated as *D. formosum*, *D. formosum coelestinum*; *D. grandiflorum.*

✓ 206. **Delphinium hillcoatiae** Munz, sp. nov. FIG. 17, G.

Perennial from a woody root, the stem simple or branched from base, often more or less purplish, ridged, with short spreading glandular hairs, quite leafy throughout, 1.5–5 dm. tall, the leaves gradually reduced upward; petioles hairy, 2–8 cm. long, dilated at base; laminae viscid, more or less cupped, not pressing flat, 2–4 cm. long, 4–10 cm. wide, subcuneate at base, parted to within 1 cm. from base into subrhomboid segments, these mostly 3-lobed ca. halfway to the midrib, then each lobe with ca. 3 oblong-ovate teeth 5–6 mm. long and wide, or in upper leaves in turn divided into smaller narrow lobules; raceme terminal, simple, 1–3 dm. long, glandular, spreading-pubescent, 4- to 20-flowered; lower bracts reduced leaves, the upper simple and entire; pedicels divergent, stiff, straight, 1–5 cm. long; bracteoles subtending the flowers, lance-linear, 5–7 mm. long; sepals glandular, white tinged green and with green tips, the spur pale green; upper sepal ovate, 18–19 mm. long, 9–11 mm. wide, apiculate, the spur 20–25 mm. long, 3.5–4 mm. wide at base, spreading decurved; lateral sepals narrowly oblong-obovate, 14–15 mm. by 4–6 mm., apiculate; lower sepals oblong-ovate, 14–15 mm. long, 5–6 mm. wide, apiculate; petals dull velvety black, the upper laminae somewhat oblique, 10–12 mm. long, 3 mm. wide, with 2 narrow lobules 1–1.5 mm. long, the spur 17–20 mm. long; lower laminae subovate, 5 mm. by 2.5–3 mm., somewhat bearded from near base to tip, bifid about 1/3–1/2 its length into lanceolate lobes, the claw 5 mm. long, not appendaged; stamens 6–7 mm. long; anthers dark, 1 mm. long; carpels 3, glabrous.

Perennis de radice lignosa; caulis simplex vel base ramosus, glanduloso-hirsutus, 1.5–5 dm. altus, foliosus; petioli hirsuti, 2–8 cm. longi, base dilatati; laminae foliorum viscidae, 2–4 cm. longae, 4–10 cm. latae, base subcuneatae, profunde partitae; segmenta subrhomboidea, 3-lobata, lobis dentatis; racemus terminalis simplex, 1–3 dm. longus, glanduloso-pubescens, cum 4–20 floribus; bracteae simplices, integrae vel inferiores lobatae; pedicelli divergentes, 1–5 cm. longi; bracteolae lanceo-lineares, 5–7 mm. longae, florem subtendentes; sepala glandulosa, albida, sepalum superiore ovatum, 18–19 mm. longum, 9–11 mm. latum, apiculatum, calcar 20–25 mm. longum; sepala lateralia anguste oblongo-obovata, 14–15 mm. longa; sepala inferiora oblongo-ovata, 14–15 mm. longa; petala subatra; laminae superiores subobliquae, 10–12 mm. longae, acute lobulatae; laminae inferiores subovatae, 5 mm. longae, barbatae, bifidae, unguis 5 mm. longum; carpella 3, glabra.

TYPE: Kap, Chayul Chu, S. Tibet, July 23, 1936, at 11000′, on open dry stony hillside, *Ludlow & Sherriff 2424* (BM).

ADDITIONAL MATERIAL. **Tibet:** Chayul Dzong, slate screes in Nye Chu Valley, 3700 m., Sept. 21, 1935, *Kingdon Ward 12370* (BM).

It is a pleasure to dedicate this species to Miss Dorothy Hillcoat of the Department of Botany, British Museum (Natural History), whose interest in the genus *Delphinium* was most useful to me in my work at that institution.

207. **Delphinium himalayae** Munz, sp. nov. FIG. 17, H.

Delphinium himalayense Chowdhury ex Mukerjee, Bull. Bot. Surv. India **2:** 293–296. 1960, *nomen.*

Perennial, the stem 4–6 dm. tall, simple, slender, more or less retrorse-strigulose throughout, more densely so in the inflorescence; leaves few, largely near the base; petioles 1–2.5 dm. long, dilated at the base; leaf blades to 1 dm. broad, minutely strigulose on both surfaces, but more heavily so beneath, 5-fid to within 1 cm. from the base and the 2 outer segments immediately divided to make 7, these cuneate-obovate, bisect or trisect to ca. the middle, then each part lobulate into few lance-oblong lobules to 1 cm. long and 2–3 mm. wide, mucronate; inflorescence a secund several-flowered raceme 1–1.5 dm. long; lower bracts foliose, others lanceolate to oblong, 1–2 cm. long, conspicuous; pedicels erect, 1–3 cm. long; bracteoles subtending the flower, oblong-linear, 6–10 mm. long; sepals purplish blue, strigose, the upper broadly ovate, 17–18 mm. long, 15–16 mm. wide, obtuse, the spur often suberect, 13–15 mm. long, 4 mm. wide at the base, only gradually narrowed to an obtuse tip; lateral sepals ovate, 14–17 mm. long, 10 mm. wide, subacute; lower sepals asymmetrically ovate, 15 mm. by 12 mm., subacute; petals black, the upper laminae 10–11 mm. long, 4 mm. wide, slightly oblique, bidentate and somewhat bristly at the apex, the spur 13–14 mm. long; lower laminae oblong, 8–10 mm. long, bifid about halfway with 2 linear-oblong lobes and more or less hairy, the claw 6 mm. long, appendiculate; stamens 6–7 mm. long; anthers dark, oblong, 1.5 mm. long; carpels 3, densely pubescent.

Perennis; caulis 4–6 dm. altus, simplex, tenuis, retrorso-strigulosus; folia pauca, vulgo basalia; petioli 1–2.5 dm. longi, base dilatati; laminae foliorum 5–10 cm. latae, strigulosae, 5-fidae; segmenta cuneato-obovata, trisecta, tum lobulata; inflorescentia secunda, racemosa, 10–15 cm. longa; bracteae infimae foliosae, superiores lanceolatae vel oblongae, 1–2 cm. longae, conspicuae; pedicelli erecti, 1–3 cm. longi; bracteolae oblongo-lineares, 6–10 mm. longae, florem subtendentes; sepala purpureo-caerulea, strigosa; sepalum superiore late ovatum, 17–18 mm. longum, 15–16 mm. latum, obtusum, calcar saepe suberectum, 13–16 mm. longum, base 4 mm. latum; sepala lateralia ovata, 14–17 mm. longa, subacuta; sepala inferiora ovata, 15 mm. longa, 12 mm. lata; petala atra, laminae superiores 10–11 mm. longae, parum obliquae, bidentatae, leviter setosae, calcar 13–14 mm. longum; laminae inferiores oblongae, 8–10 mm. longae, bifidae, lobis lineari-oblongis, villosis, unguis 6 mm. longus, exappendiculatus; stamina 6–7 mm. longa, glabra; carpella 3, pubescentia.

TYPE: Nepal, *Ser Oive Wigram 118*, in 1927 (E).

RANGE. The proposed new species, *Delphinium himalayae*, grows in grassy places at ca. 3000 to 4500 m. in Nepal.

EXAMPLES. **Nepal:** Langdeng, *Sharma 117* (BM, E); Pongsing, *Dhwoj 122* (BM, E); below Mugu, *Polunin, Sykes & Williams 5290* (BM); Ghurchi Lekh, *Polunin, Sykes & Williams 5128* (BM); Maharigaon, *Polunin, Sykes & Williams 264* (BM); Chutta, *Polunin, Sykes & Williams 4885* (BM); Balangra Pass, *Polunin, Sykes & Williams 2503* (BM); Langtang Village, *O. Polunin 1489* (BM), *555* (BM); Chilime Kharka road, *Polunin 1413* (BM); Kyangjin Ghyang, *Polunin 1778* (BM).

I have had no contact with Dr. Chowdhury and do not know why he never published *Delphinium himalayense*, the name which appears on some herbarium material in Great Britain. Since I do not know what his species was supposed to include, I do not feel free to use his name, taken up by Mukerjee, but never validly published. My concept of *Delphinium himalayae* is entirely my own, as are the description and citation of herbarium material.

208. **Delphinium inconspicuum** Sergievsk. Animadvers. Syst. Herb. Univ. Tomsk **1930.** (3–4): 6. *fig.* 1930.

Stems many, 2.5–10 dm. tall, leafy throughout, short glandular-pubescent, more so upward; leaves orbicular-cordate or -reniform, 4.5–7 cm. long, 5–14 cm. wide, coarsely toothed, short pilose on both surfaces; raceme simple or few branched below, dense, 3–17 cm. long; lower bracts large, leaflike; bracteoles linear, 0.5 mm. wide; inflorescence pilose and glandular; sepals blue, 8–18 mm. long, 5–9 mm. wide, spur 11–13 mm. long, 2.5 mm. wide at base; petals dark, upper laminae bidentate, glabrous; lower laminae semibifid with unequal oblong lobes, ciliate, the claw hirsute; carpels 3, glabrous; seeds winged.

TYPE: Semipalatinsk in jugo Narymense; not seen. The species apparently occurs also in Mongolia. *Delphinium inconspicuum* seems, from the meager description, to key out near *D. afghanicum* of Afghanistan and *D. pyramidatum* of Transcaucasia, but is far removed from them geographically.

209. **Delphinium kawaguchii** Tamura, Acta Phytotax. & Geobot. Kyoto **15**: 194. *fig. 2.* 1954.

Leaves radical; petioles 16–20 cm. long, pilose, the blades reniform, 7 cm. long, 9 cm. wide, 3–5-fid, the lobes pinnately incised-lobed, pubescent on both surfaces on veins and margins; inflorescence racemose, 3–4 dm. long, 18–23-flowered; lower bracts trifid, upper entire, linear-oblong; pedicels 2–3.5 cm. long; sepals blue, pubescent, the spur cylindric, 18 mm. long, surpassing the sepal blades, 3.5 mm. wide at base, incurved; laminae of upper petals glabrous, 9 mm. long, the spur 16 mm. long; lower laminae 10 mm. long, round-ovate, 2-lobed, the lobes acute, bearded above; carpels 3, densely villous; styles long, glabrous.

TYPE: Tibet near Shigatse, Linbun rivulet, July 29, *Kitamura 103908* (KYO). I have been unable to see material of this species. The original description said that it differs from *D. speciosum* in the inflorescence not being leafy, and from *D. iliense* in its villous carpels, scarcely erect pedicels, and bracteoles not next to the flower.

210. **Delphinium kuanii** W. T. Wang, Acta Bot. Sinica **10**: 84. 1962.

Stem 5 dm. tall, 3 mm. thick at base, longitudinally striate, retrorsely or spreading-hairy, few branched, equally foliose; basal leaves and lower cauline long petioled; blades shaped as in *D. naviculare*, broad-reniform, 5.5 cm. long, 10 cm. wide, 3-parted to ca. 1 cm. above the base, middle part cuneate-obtrapezioid, 3-lobed above, the lobes 1–2-toothed, the teeth deltoid, laxly hirsute on both surfaces, petioles from twice as long as laminae to equal to them, narrowly vaginate, with same indument as the stems; racemes 4–10-flowered, lax, the axes strigulose; lower bracts trifid, others lanceolate, 8–14 mm. long, 2–3 mm. wide, densely strigulose; pedicels 1–3 cm. long, densely retrorse-strigulose, ascending; bracteoles to 15 mm. below the flowers or near them, lance-oblong or lanceolate, 8–10 mm. long, 2–2.5 mm. wide; sepals purplish, elliptic, 12–15 mm. long, densely strigulose without, glabrous to loosely hairy within, spur 11.5–13 mm. long, saccate-cylindric, 4–4.5 mm. thick at base, straight, obtuse; petals black, the upper laminae glabrous, rounded at apex; lower laminae broadly rectangular, with 2 deltoid lobules at the rounded apex, few toothed, yellow bearded at base, claw appendiculate; filaments pilose; carpels 3, densely strigose; style barely 1 mm. long.

TYPE: Sikang, Wen Chuan, Aug. 27, 1957, *K. C. Kuan 4698* (PE), not seen. I have had no material of *Delphinium kuanii*, which the author said was near *D. elliptico-ovatum* but with bracteoles lance-oblong to lanceolate; spur saccate-conic; ovary densely strigulose, and styles shorter.

211. **Delphinium lacei** Munz, sp. nov. FIG. 17, I.

Perennial from thick fleshy roots; stems slender, usually somewhat branched above, often reddish, slender, retrorse-strigulose or -pubescent, scarcely if at all glandular, 4–8 dm. tall, with a few scattered leaves; basal leaves with blades somewhat reniform in outline, 3–6 cm. broad, 5- or 7-fid to ca. 3/4 their length, with a scattering of long hairs on both surfaces, the segments subcuneate, sharply 3-toothed at apex or sometimes 3-lobed, each lobe then sharply toothed, the teeth acute-acuminate, mucronate, lance-ovate; petioles slender, to 1 dm. long, spreading-villous, somewhat dilated at base; upper leaves reduced, the uppermost to ca. 1 cm. long, 3-lobed with broad petioles; inflorescence a few-flowered raceme, with shorter subsidiary branches; bracts mostly lanceolate, 8–15 mm. long, villous; pedicels ascending, 1–3 cm. long, the bracteoles near the middle or above, lanceolate, 5–8 mm. long; flowers bluish, with more or less yellowish hairs throughout; upper sepal ovate, 18 mm. long, 12 mm. wide, obtuse, the spur somewhat decurved, 16–20 mm. long, 2.5–3 mm. wide at base; lateral sepals round-obovate, 15–16 mm. long, 12 mm. wide, rounded-truncate at apex; lower sepals elliptic-obovate, 18 mm. by 10 mm., obtuse; petals black, the upper laminae somewhat oblique, 8 mm. by 3 mm., slightly emarginate at the rounded apex, the spur 15–17 mm. long; lower laminae oblong-ovate, 4.5 mm. by 4 mm., bearded, ciliate, bifid ca. 1.5 mm. into broad lobes, claw broad, 5 mm. long; stamens 6–7 mm. long, glabrous; anthers dark; follicles 3, erect, 12–16 mm. long, 4 mm. wide, pubescent, the styles an additional 3 mm.; seeds black, angled, scarcely winged or squamate, almost 2 mm. long.

Planta perennis, ex radicibus lignosis; caules tenues, supra plerumque ramosi, saepe rubelli, retrorso-pubescentes, vix vel non glandulosi, 4–8 dm. alti, parum foliosi; laminae foliorum basalium subreniformes, 3–6 cm. latae, 5–7-fidae, sparse villosae, segmentibus subcuneatis, apice acute 3-dentatis vel -lobatis; petioli tenues, ad 1 dm. longi, extenso-villosi, subvaginati; folia superiora parva, 3-lobata, late petiolata; inflorescentia racemosa, cum floribus paucis et ramulis brevibus; bracteae lanceolatae, 8–15 mm. longae, villosae; pedicelli ascendentes, 1–3 cm. longi; bracteolae in medio pedicelli, lanceolatae, 5–8 mm. longae; flores subcaerulei, cum pilis aureis; sepalum superiore ovatum, 18 mm. longum, 12 mm. latum, obtusum; calcar curvatum, 16–20 mm. longum, base 2.5–3 mm. latum; sepala lateralia rotundo-obovata, 18 mm. longa, 12 mm. lata; sepala inferiora elliptico-obovata, 18 mm. longa, 10 mm. lata, obtusa; petala atra, laminae superiores 8 mm. longae, parum emarginatae, calcar 15–17 mm. longum; laminae inferiores oblongo-ovatae, 4.5 mm. longae, hirsutae, bifidae, unguis latus, 5 mm. longus; stamina 6–7 mm. longa, glabra; follicula 3, erecta, 12–16 mm. longa, pubescentia; semina atra, angulosa, fere 2 mm. longa.

TYPE: Burma, Ruby Mines district, Bernardmyo, 1750 m., Oct. 25, 1912, *J. H. Lace 6012* (CAL, E 3 sheets, K); seen. I would designate the K sheet as type, those at CAL and E as isotypes.

ANOTHER COLLECTION. **Burma:** Mt. Victoria Ridge, 2700 m., Oct. 26, 1956, *Kingdon Ward 22749* (BM).

212. **Delphinium leptopogon** Hand.-Mazz. Acta Horti Gothob. **13**: 58. 1939. FIG. 17, J.

Perennial, the stem 7–8 dm. tall, branched only above, slender, to 5 mm. thick, glabrous and glaucous below or with some stiff white hairs at base of petioles, evenly but rather remotely leafy; leaf blades roundish in outline, the lower 8–13 cm. wide, green and minutely strigulose on both surfaces, the cauline divided almost to base into 5 divaricate lanceolate, entire to 2–3-toothed segments 5–8 mm. wide, acuminate; petioles not dilated at base, about as long as the blades or the uppermost shorter; inflorescence subcorymbose at the end of each branch, 4–20-flowered, with spreading glandular hairs; bracts leaflike and trifid or entire and lanceolate, 1–2 cm. long; pedicels divaricate to erect, 1–4 cm. long; bracteoles in middle or above, subulate, 3–5 mm. long; sepals violet-blue, densely strigulose; upper sepal ovate, 14 mm. by 8 mm., acute, the spur almost straight, 20–22 mm. long, 4–5 mm. wide at the base, gradually narrowed to a blunt tip; lateral sepals ovate, 17 mm. by 8 mm., acute; lower sepals 15 mm. by 6 mm., subacuminate; petals mostly dark, the upper laminae quite oblique, 9 mm. long, subacuminate, somewhat emarginate, the spur 19 mm. long; lower laminae sometimes yellowish, strongly oblique, oblong, with scattered white hairs, entire to shallowly 2-lobed, ca. 9 mm. by 3 mm., the claw 6 mm. long; stamens 6–7 mm. long, the base only slightly widened, glabrous; anthers dark, linear-oblong, 1.5 mm. long; follicles 3, glabrous to sericeous; seeds winged on angles.

TYPE: Shansi, distr. Chiao-ch'eng, Pa-shui-ko, 1900 m., *Harry Smith 7109*, holotype (UPS), not seen; isotype (A), seen.

I would place in this species also *Rock 13136* (GH, NY) from southwestern Kansu.

213. **Delphinium longiciliatum** W. T. Wang, Acta Bot. Sinica **10**: 84. 1962.

Stem ca. 8 dm. tall, 3 mm. thick at base, loosely spreading- or retrorse-hirsute, simple, equably leafy; middle cauline leaves longish petioled; leaf blade as in *D. naviculare*, broadly pentagonal, 6.5 cm. long, 11 cm. wide, 3-parted, the middle part rhombic, upper trilobed, the middle lobes triangular-ovate, with few coarse teeth, the lateral lobes smaller, obliquely ovate, coarsely 1–2-toothed, loosely strigulose on both surfaces; petioles ca. as long as blades, not vaginate at base, with same pubescence as on the stems; raceme ca. 16 cm. long, 10-flowered, rather lax; pedicels 1–3 cm. long, ascending, glabrous; lower bracts lanceolate, ca. 15 mm. long, 3 mm. wide, others 7–12 mm. long, 1–1.2 mm. wide, acute, long-ciliate; bracteoles to 3–5 mm. below the flower, linear-lanceolate to oblanceolate, 7 mm. long, acute, long-ciliate; sepals purple, the upper ovate, others obovate, 13–14 mm. long, glabrous or slightly ciliate at apex; spur 17–18 mm. long, straight; petals black, the upper laminae emarginate, loosely pilose; lower laminae broadly ovate, with 2 obtuse, triangular lobes, yellow bearded at base, long-ciliate at ends, claw shorter than lamina, appendiculate at base; stamens glabrous; carpels 3, subglabrous.

TYPE: Sinkang, at Ili, Aug. 8, 1957, *K. C. Kuan 3209* (PE?), not seen.

The author of the species suggested that it is near *D. tianshanicum* Wang, but with the sepals, pedicels, and ovaries glabrous.

214. **Delphinium maackianum** Regel, Mém. Acad. Pétersb. VII. **4** (4): 9. 1861. FIG. 17, K.

Delphinium maackianum var. *ussuriense* Regel, *loc. cit.* "bracts and carpels glabrous," apparently based on same material as the species. Var. *lasiocarpum* Regel, based on *Wilford* from the "Coast of Manchuria" (GH, K, P) seen.

Delphinium maackianum var. *cuneatum* Regel ex Huth, Bot. Jahrb. **20**: 400. 1895. Apparently the type collection is "Ad flum. Amur, montes Burgae" (Bureja in Huth), *Radde* (K, P) seen.

Delphinium maackianum Regel var. *palmatum* (Lévl.) Nakai, Jour. Coll. Sci. Imp. Univ. Tokyo **31**: 433. 1911. *D. elatum* var. *palmatum* Lévl., Bull. Acad. Géogr. Bot. **11**: 300. 1902. *D. lycoctonifolium* Lévl., Repert. Sp. Nov. **7**: 100. 1909. All based on *Faurie 26*, from mountains Kan-Ouen-To, Korea (E), isotype (UC); both seen.

Perennial from a woody rhizome, the stem 5–8 dm. tall, glabrous or pubescent below, pubescent above with short spreading hairs, stem simple or branched in the inflorescence, ca. 5–6 mm. thick below, leafy, the petioles glabrous to hairy, dilated at base, the lower to 2 dm. long, the upper much shorter; leaf blades mostly broadly rounded in outline, the lower to 2 dm. wide, not quite as long, subglabrous to strigose on both surfaces, 5- or 7-fid to well above the base into broad cuneate-based ovate segments commonly 2–5 cm. broad and rather shallowly incised or toothed into ovate or lance-ovate lobes or teeth; upper leaves reduced, often only 3-fid; inflorescence loosely paniculate, pubescent, the lower bracts foliaceous, divided, the others ovate or elliptic-ovate, membranous, bluish, glabrous, 5–20 mm. long; pedicels pubescent, ascending, 1–5 cm. long; bracteoles lance-ovate, shorter, inserted well below the flower; sepals dull blue, subglabrous or slightly pubescent, the upper sepal 14–16 mm. long, 8–10 mm. wide, ovate, subacute, the spur straight or curved or even uncinate, 15–20 mm. long, 3.5–4.5 mm. wide at base, narrowed to rather a sharp tip; lateral sepals 12–16 mm. long, 8–10 mm. wide, obtuse; lower sepals 12–14 mm. long, 6–7 mm. wide, subacute; petals dark, the upper laminae slightly oblique, glabrous, subacute, entire or nearly so, 10–11 mm. long, the spur 15–16 mm. long; lower laminae ovate, oblique, 5 mm. long, 3 mm. wide, cleft one half their length, ciliate and sparsely bearded, with a patch of yellow hairs near the base, claw 5.5 mm. long; stamens 6–7 mm. long, glabrous, slightly dilated below; anthers dark, 1.5 mm. long; follicles 2–3, glabrous, divergent, 18–20 mm. long, the styles an additional 3 mm.

TYPE: Manchuria, on the Sungacha River (tributary of the Ussuri River), *Maack*, isotypes (GH, K, P), seen.

DISTRIBUTION. The species occurs in Manchuria and Korea.

EXAMPLES: **Manchuria:** *Komarov 671* (BM, K); *Maximowicz* in 1860 (BM, GH, K, NY, P); *Litvinov 2026* (NY), *3013* (NY); *F. H. Chen 341* (BM, GH, NY, P); *Bohnhof 163* (NY, P). **Korea:** *Chung In-Cho's* collector *9440* (MICH), *10347* (MICH), *9391* (MICH); *Ohwi 2808* (BH); *Bushnell 470* (BM).

215. **Delphinium mariae** Busch in Fl. Cauc. Crit. III. 3: 69. 1903. FIG. 17, L.

Perennial, the stem several dm. tall, strigulose below, otherwise glabrous, angular-sulcate, leafy; cauline leaves slightly strigose on both surfaces, paler beneath, ca. 1 dm. broad, 5-parted almost to the base, the segments narrowly cuneate-obovate, deeply laciniate into lance-linear lobes 1.5–2.5 mm. wide, 5–25 mm. long; petioles scarcely vaginate at base; raceme lax, many flowered, glabrous, to 3.5 dm. long, branched below; bracts linear-lanceolate, 1–2 cm. long; pedicels suberect, 3–4 cm. long; bracteoles subtending the flowers, linear-lanceolate, ca. 10 mm. long, 2 mm. wide; sepals blue-violet, glabrous, slightly ciliate, the upper sepal ovate, 18–20 mm. long, 8 mm. wide, obtuse, the spur spreading decurved, 16–17 mm. long, 3.5 mm. wide at base; lateral sepals elliptic-obovate, 20 mm. by 12 mm., rounded at apex; lower sepals 18 mm. by 7 mm., rounded-truncate at tip; petals black, the upper laminae slightly oblique, 12 mm. long, slightly bidentate at the glabrous apex, the spur 13 mm. long; lower laminae 5 mm. by 4 mm., oblong-obovate, bearded near base, long-ciliate on the round-oblong divergent lobes, the claw appendiculate, 6.5 mm. long; stamens 6–7 mm. long; anthers dark; carpels 3, glabrous.

TYPE: In meadows at 1850 m., between Tsulkan and Gapschina, Dagestan, July 19, 1898, *Alexeenko* (LE), seen.

I have seen no other examples of this species.

216. **Delphinium megalanthum** Nevski in Komarov, Fl. U.S.S.R. 7: 129, 722. 1937. FIG. 17, M.

Delphinium flexuosum var. *paulovii* Akinf. Trav. Soc. Nat. a l'Univ. Imp. Kharkow **XXVII:** 167. 1894. *Delphinium speciosum* var. *paulovii* N. Busch in Fl. Cauc. Crit. III. 3: 64. 1903. Cited as synonyms in the original description of *D. megalanthum*.

Stem 3.5–7.5 dm. tall, ribbed, lightly pilose below, glabrous above, foliose; petioles scarcely dilated at base, ciliate along margin; leaves lightly pilose or glabrous above, more pallid and pilose on veins beneath, ciliate on margins, 5–10 cm. broad, 5-fid, the segments cuneate-obovate, 3-incised to the middle, then coarsely few-lobulate into lanceolate parts 2–5 mm. wide, 2–10 mm. long, acute; racemes erect, branched at base, to 3 dm. long, lax; lowest bracts foliose, others linear-lanceolate, 6–20 mm. long, 1–2.5 mm. wide, glabrous; pedicels strict or slightly spreading, glabrous or almost so, 3–7 cm. long; bracteoles ovate-lanceolate or ovate, 7–9 mm. long, 3–4 mm. wide, obtusely acuminate, glabrous, rarely slightly ciliate, usually violet in color, near or to 0.5 cm. below the flower; sepals blue, the upper 22 mm. long, 10 mm. wide, obtuse, glabrous, the spur 20 mm. long, 4 mm. wide at base, slightly incurved toward the acute tip; lateral sepals 23 mm. by 12–14 mm.; lower ca. 22 mm. long; petals black, the upper laminae slightly oblique, glabrous, emarginate, 13 mm. long, the spur 16 mm. long; lower laminae perpendicular to the claw, oblong, 9 mm. by 4 mm., bearded at base and on the 2 oblong lobes, claw 7 mm. long; stamens 7–8 mm. long; anthers dark, 1.5 mm. long; carpels 3, glabrous.

TYPE: "Caucasus septentrionalis, prope glaciem Bezengi, July 25, 1892, lg. *Lipsky*" (LE); seen. It is near to *D. speciosum* but seems different in its glabrous flowers.

217. **Delphinium mirabile** Sergievsk. Animadvers. Syst. Herb. Univ. Tomsk 1930. 3–4: 5. 1930. FIG. 17, N.

Delphinium laxiflorum var. β *alpinum* Bunge, Fl. Altaica Suppl. 33 [orig. 555]. 1836. Placed here in synonymy by Nevski in Komarov, Fl. U.S.S.R. 7: 131. 1937. I have seen a collection from "Altai" Herbar. Bunge, Fl. orient. altaica, 1839 (MO) which may represent this taxon.

Stem slender, 2.5–4 dm. tall, leafy below, sparsely pilose above, simple or nearly so, angled below; petioles to 1 dm. long, slender, somewhat dilated at base, pilose; leaf blades round-reniform in outline, 3–9 cm. wide, more or less strigulose above, paler and short-hairy beneath, 3-, 5-, or 7-parted almost to base into cuneate-rhombic segments 5–10 mm. wide below, 10–15 mm. wide above, these trilobed to about the middle then sometimes incised into sharp divergent teeth; inflorescence a 5–10-flowered raceme or panicle 7–10 cm. long, strigose and with some short more spreading hairs; bracts entire, mostly linear, 5–15 mm. long, sometimes 2–3-parted, pubescent; pedicels pilose, 1–2 cm. long; bracteoles linear, 3–4 mm. long, placed just below the flower; sepals sordid blue-violet, white pilose on both outer and inner surfaces; upper sepal ca. 18 mm. by 14 mm., apiculate, the spur spreading decurved, 16–17 mm. long, 3.5 mm. wide at base, subcylindric, the apex obtuse; lateral sepals broadly elliptic-obovate, 18 mm. by 10 mm., broadly obtuse; lower sepals 20 mm. by 8 mm., subacute, asymmetrically lance-obovate; petals blackish, the upper laminae almost straight, 10 mm. long, 3 mm. wide, rounded and slightly erose at the summit, spur 17–18 mm. long; lower laminae oblique, oblong, 5 mm. by 3.5 mm., bifid from near the middle into oblong lobes, scattered-hirsute, ciliate, the claw 6.5 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, oblong, 1.3 mm. long; follicles 3, pubescent.

TYPE: "In montibus Altaicis austro-orientalibus ad fl. Taldura," July 18, 1903, *P. Krylov* (TK); not seen.

Drawings and description made from "Altai," Herbar. Bunge (MO).

218. **Delphinium naviculare** W. T. Wang, Acta Bot. Sinica **10**: 82. 1962.

Stem ca. 7 dm. tall, 3.5 mm. thick below, spreading or retrorsely hirsute, glabrescent below the inflorescence, simple, subequally foliose; basal and lower cauline leaves long petioled; leaf blades broadly reniform-pentagonal, 3–4.5 cm. long, 5–5.5 cm. wide, cordate, 3-parted, the middle part rhombic, acute, 3-lobed below the middle, the lateral parts oblique, unequally 2-lobed to the middle, all 5 parts then few toothed, loosely hirsute on both sides; petioles vaginate at base; racemes ca. 3 dm. long, many flowered, rather dense; pedicels 1–3 cm. long, erect-spreading, glabrous; lower bracts 14–17 mm. long, trifid, the lobes lanceolate, acute, the other bracts ovate, 7–10 mm. long, 3.8 mm. wide, abruptly acute; bracteoles near the flowers, ovate to elliptic, 4–5 mm. long, boat-shaped, acuminate, ciliate; sepals purplish, glabrous or ciliate at apex, the upper broadly elliptic, lateral round-obovate, lower elliptic, 9–12 mm. long; spur 12–13.5 mm. long, glabrous, almost straight, conic-subulate; petals black, the upper laminae glabrous, obliquely truncate, entire; lower laminae broad-oblong, with 2 deltoid-ovate lobes to the middle, yellow bearded at base, long-ciliate, the claw exappendiculate; stamens glabrous; carpels 3, glabrous.

TYPE: Sikang, at Chigo-Su, Aug. 11, 1957, *K. C. Kuan 3229* (PE), not seen.

I have not seen this species which Wang says is near *D. ruprechtii* but with smaller flowers and bracteoles. Wang's *Delphinium naviculare* var. *lasiocarpum* (Acta Bot. Sinica **10**: 83. 1962), described as having pedicels and sepals with spreading yellow-glandular hairs, is not known to me and I am uncertain as to its disposition.

219. **Delphinium nevskii** Zakirov, Not. Syst. Herb. Inst. Bot. Acad. Sci. U.S.S.R. **12**: 92. 1950. FIG. 18, A.

Perennial from a woody root, 4–6 dm. tall, the stem white-hairy especially in the inflorescence, 5–7 mm. thick, few branched above, scattered leafy; lower petioles 12–25 cm. long, sulcate, retrorse-pubescent, somewhat vaginate at base, the upper much shortened; lower blades roundish in outline, 6–10 cm. wide, pilose on both surfaces, 3-parted to below the middle, the broad parts 2–3-lobed in distal portion, then with coarse more or less oblong-ovate, mucronulate teeth 4–8 mm. long and almost as broad; central raceme rather dense, hairy, to 2 dm. long, many flowered; bracts lanceolate, white-hairy, 6–8 mm. long, 1–2 mm. wide; pedicels spreading-ascending, 1–2 cm. long, soft-hairy; bracteoles above the middle of the pedicel, subulate-lanceolate, 3–5 mm. long; sepals white with yellow nerves, pilose on both surfaces; upper sepal 15 mm. by 7 mm., acutish, the straight spur 12–15 mm. long, 2.5 mm. wide at base; lateral sepals subelliptic, 13 mm. by 6 mm., obtuse; lower sepals subelliptic, 12 mm. by 6 mm., more pointed; petals blackish, the upper laminae almost straight, 8 mm. long, bidentate, stiff-hairy at apex, the spur ca. 12 mm. long; lower laminae oblong-ovate, oblique, 5 mm. long, bifid about halfway, hairy and white-ciliate, the claw 5 mm. long; stamens 5–6 mm. long, glabrous; anthers pale, 1 mm. long; follicles 3, soft-hairy, 10 mm. long, 3 mm. wide, the styles an additional 3 mm.

TYPE: Uzbekisten, system of River Zeravschan, Mt. Chazrat-Sulton, limestone, 3300–3800 m., Aug. 27, 1942, *K. Zakirov* (LE); seen.

The species is said to be near *D. oreophilum*, differing in smaller white flowers and equal pubescence on both surfaces of the leaves.

220. **Delphinium ochotense** Nevski in Komarov, Fl. U.S.S.R. **7**: 146, 724. 1937. FIG. 18, B.

Delphinium elatum var. *subglabrum* Regel & Tiling, Nouv. Mém. Soc. Nat. Mosc. **11**: 39. 1859, not var. *subglabrum* Ledeb. 1841. Based on same type as *D. ochotense.*

Stem 2–5 dm. tall, with soft short pubescence, slightly glandular above, densely leafy; leaves round-cordate to -reniform, to 15 cm. broad, slightly pubescent, palmatisect, the segments commonly biternately divided into terminal obtuse or subobtuse, broadly elliptic to lanceolate teeth 5–20 mm. long, 4–10 mm. wide; raceme many flowered, the axis and pedicels densely soft-pubescent; bracts linear, 8–20 mm. long, the lowest lanceolate or trifid, to 4 cm. long; pedicels erect, 1–3 cm. long; bracteoles subtending the flower, linear, 4–6 mm. long; sepals blue, ovate to ovate-lanceolate, obtuse, 1.3–2.2 cm. long, 5–9 mm. wide, with some spreading hairs; spur spreading, almost straight or somewhat incurved near the apex, 1.2–1.7 cm. long; petals black, the upper laminae somewhat oblique, 10 mm. long, glabrous, entire, the spur 16–17 mm. long; lower laminae bearded at base, ovate, 4 mm. long, with triangular lobes 1.5 mm. long, claw 6 mm. long.

TYPE: Extreme eastern Siberia, near Ajan, legit *Tiling* (LE); seen.

Delphinium ochotense differs from *D. elatum* in having some glandular hairs in the inflorescence and lower petals with broader laminae.

221. **Delphinium oreophilum** Huth, Bot. Jahrb. **20**: 412. 1895. FIG. 18, C.

Stem thick, erect, subglabrous, 5–6 dm. tall; leaves well distributed on the stem; petioles 2–4 dm. long, dilated at the base; the blades roundish, 8–12 cm. in diameter, divided almost to base into 3 or 5 parts, subglabrous above, quite pubescent beneath especially on the veins, the parts broad, then lobed about halfway to base into broad portions which are in turn divided at tips into lanceolate lobules or teeth 5–15 mm. long; inflorescence somewhat branched at base, the racemes very dense, the central one rather many flowered; bracts, except the lowest, entire, hirsute, 5 mm. long; pedicels hirsute, 1.5–6 cm. long; bracteoles linear, remote from flowers, ca. 2 mm. long; sepals dilute blue, white-hirsute without and within, the upper 12–13 mm. long, 7 mm. wide, the spur straightish or somewhat curved, 12–13 mm. long, 3.5 mm. wide at base, blunt; lateral sepals elliptic-oblong, 16 mm. by 7 mm., rounded at apex; lower sepals 13 mm. by 8 mm.; petals black-violet, the upper laminae short-bristly on face, oblique, 11 mm. long, bidentate at the glabrous tip, spur 11 mm. long; lower laminae yellow bearded on face, white-ciliate at tip, oblong-ovate, oblique, 5 mm. long, bifid to below the middle, claw 6 mm. long; stamens 7–8 mm. long, glabrous; anthers dark, oblong, 1.5 mm. long; carpels 3, densely hirsute; seeds squamate, the scales coalesced in transverse rows.

LECTOTYPE: Buchara oriental; inter Talbas and Sagridascht, 3000–3300 m., *A. Regel*, 1882 (LE); seen.

In 1940 Afanasiev published as a new species *Delphinium rotundifolium* (Not. Syst. Herb. Inst. Bot. Acad. Sci. USSR. **8**: 108) based on *Afanasiev 227* from Turkestan, which he said was near *D. oreophilum*. So far as I can judge from the description this is the case. I have seen no material and therefore am tentatively reducing it to synonymy under *D. oreophilum*.

222. **Delphinium oxycentrum** W. T. Wang, Acta Bot. Sinica **10**: 73. 1962.

Stems 4.5–7 dm. tall, 3.5–4.5 mm. in diameter, glabrous, simple or with one branch above, the branch racemiferous; basal leaves ca. 2, long petioled; leaf blades broadly round-reniform, 4–6 cm. long, 7–11 cm. wide, open-cordate at base, 3-parted to beyond the middle, the parts imbricate, the middle part 3-lobed into ovate incised-lobulate or coarsely toothed lobes, the lateral parts unequally trifid, then lobed and toothed much like the middle one, loosely strigulose on both surfaces or subglabrous above; petioles 2–2.5 dm. long, loosely hirtellous, inconspicuously vaginate at base; cauline leaves 1–2, like the basal but smaller, short petioled or subsessile; racemes terminal, the main one 9–12-flowered, rather dense; lower bracts 3-parted, others spatulate- to linear-oblong, 9–12 mm. long, subglabrous or loosely hairy; pedicels 2–6.5 cm. long, stout, glabrous; bracteoles apical, lance-linear, glabrous or loosely hairy; flowers erect or nearly so; sepals subglabrous or loosely ciliate, the upper 21–25 mm. long, 17–22 mm. wide, the subulate spur 26–42 mm. long, sharply acute; lateral sepals rounded or round-ovate, 14–17 mm. long, 11–14 mm. wide; lower 15–18 mm. long, 6–10 mm. wide; petals blackish brown, glabrous, the

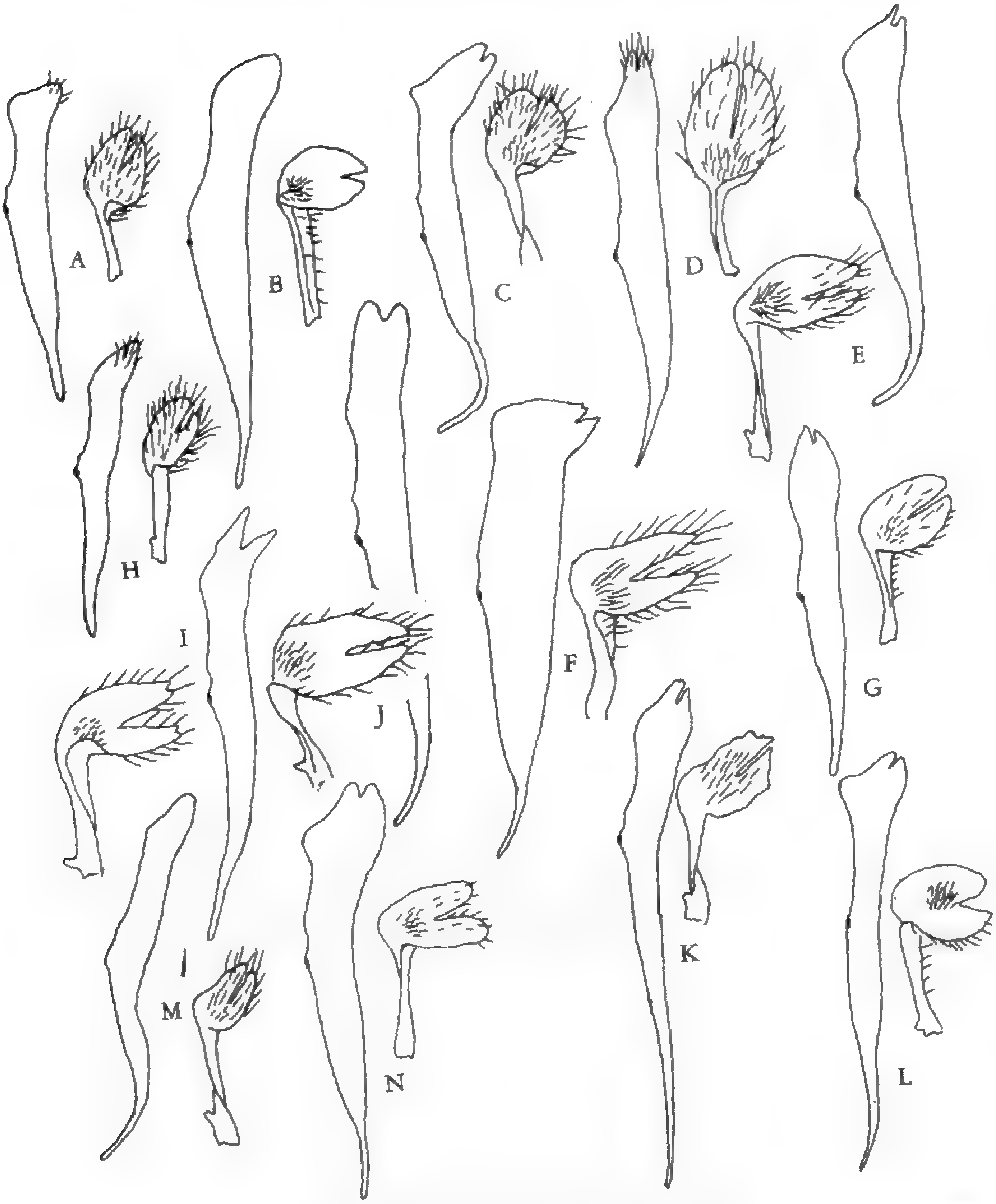

FIGURE 18. **Delphinium,** GROUP IX. Petals, the upper spurred, the lower clawed. A. *D. nevskyi*; upper lamina 8 mm. long, spur 11 mm.; lower lamina 4.5 mm. long, claw 5 mm.; drawn from *Zakirov* in 1942, TYPE (LE). B. *D. ochotense*; upper lamina 10 mm. long, spur 17 mm.; lower lamina 4 mm. long, claw 6 mm.; drawn from *Tiling* near Ajan, TYPE (LE). C. *D. oreophilum*; upper lamina 10 mm. long, spur 11 mm.; lower lamina 5 mm. long, claw 6 mm.; drawn from *Regel* in 1882, TYPE (LE). D. *D. poltaratzkii*; upper lamina 12 mm. long, spur 13 mm.; lower lamina 7 mm. long, claw 6 mm.; drawn from *Ludlow 762* (BM). E. *D. pyramidale*; upper lamina 9 mm. long, spur 14 mm.; lower lamina 6.5 mm. long, claw 7 mm.; drawn from *Stewart 21882* (NY). F. *D. pyramidale*; upper lamina 12 mm. long, spur 15 mm.; lower lamina 7.5 mm. long, claw 6 mm.; drawn from *Ludlow & Sherriff 1534* (E). G. *D. pyramidatum*; upper lamina 9 mm. long, spur 12.5 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from *Alboff 194* (NY). H. *D. retropilosum*; upper lamina 8 mm. long, spur 9 mm.;

upper laminae 2-lobulate; lower laminae ovate, bilobed one-third their length, the lobes triangular, claw 3 to 5 times as long; stamens 10–12 mm. long; carpels 3, glabrous.

TYPE: Szechwan, Kung-ka-ling, 1000 m., Sept. 1, 1937, *Yü 13129* (PE), not seen, photo. (E), seen.

223. **Delphinium poltaratzkii** Rupr. in Osten-Sacken & Rupr. Sert. Tian-shan. 37. 1869. (Mém. Acad. Pétersb. VII. **14**: 4. 1869).

FIG. 18, D.

Perennial, the stem 2.5–5.5 dm. tall, robust, spreading-villous, not glandular, more or less leafy; lower leaves with blades 5–7 cm. long, 6–12 cm. wide, subglabrous above, more or less villous beneath especially on veins, 3- or 5-fid halfway to base or deeper, into broad-rhombic segments shallowly lobed or toothed, the teeth ovate, 3–6 mm. long and wide, mostly acute, mucronate; lower petioles 1–2 dm. long, scarcely dilated at base; upper leaves gradually reduced; inflorescence branched, the terminal raceme 4–10-flowered, the lateral 1–4-flowered, or the inflorescence simple, subcapitate; bracts colored, 2–3 cm. long, the lower trifid, the upper entire, 1–2 cm. long; pedicels 1.5–4 cm. long; bracteoles colored, appressed to sepals, linear-oblong, to 10 mm. long; sepals purplish mauve to saturated blue, the upper sepal ovate, 15–20 mm. long, 10 mm. wide, obtuse, the spur 8–12 mm. long, 5 mm. wide at base; lateral sepals broadly obovate, 14–20 mm. long, 11 mm. wide; lower sepals 12–16 mm. by 9 mm.; petals almost black, the upper laminae almost straight, 12 mm. long, bidentate, the spur 12 mm. long; lower laminae broadly elliptic, 7 mm. long, bearded, bifid two-thirds its length into broad lobes, the claw 6 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, 1.2 mm. long; carpels 3, somewhat pubescent.

TYPE: Turkestan, Tian-shan Mts., below Schamsi, *Poltaratzki* (LE); seen.

The species apparently grows in open grassland at about 2500 m. It is represented by *Ludlow 762* (BM, E) from Koksu-Kensu Junction, Tian Shan.

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lower lamina 4 mm. long, claw 6 mm.; drawn from *Tarchevskaya & Vandysheva* (NY). I. *D. ruprechtii*; upper lamina 12 mm. long, spur 14 mm.; lower lamina 7 mm. long, claw 6 mm.; drawn from *Alexeenko* in 1898, TYPE (LE). J. *D. speciosum*; upper lamina 14 mm. long, spur 20 mm.; lower lamina 8 mm. long, claw 6 mm.; drawn from *Kamennik* in 1933 (NY). K. *D. stapeliosum*; upper lamina 10 mm. long, spur 20 mm.; lower lamina 6 mm. long, claw 6 mm.; drawn from *Clarke 44861* (US). L. *D. tianshanicum*; upper lamina 9 mm. long, spur 14 mm.; lower lamina 5 mm. long, claw 6 mm.; drawn from *Li & Chu* 7003 (E). M. *D. villosum*; upper lamina 9 mm. long, spur 12 mm.; lower lamina 3.5 mm. long, claw 6 mm.; drawn from *Gillett* in 1939 (BH). N. *D. winklerianum*; upper lamina 10 mm. long, spur 14 mm.; lower lamina 5 mm. long, claw 6 mm. drawn from *Winkler 7230*, TYPE (LE).

224. **Delphinium pyramidale** Royle, Illustr. Bot. Himal. 56. 1834.
FIG. 18, E, F.

Delphinium speciosum Bieb. var. *pyramidale* (Royle) Mukerjee, Bull. Bot. Surv. India 2: 293. 1961.

Delphinium ranunculifolium Wall. Cat. n. 4716. 1830, *nomen*; Hook. f. & Thoms. Fl. Ind. 51. 1855, based on *Wallich 4716*, Bhudrinak RB, seen (K).

Delphinium elatum L. var. *ranunculifolium* (Wall.) Hook. f. & Thoms. in Hook. f., Fl. Brit. Ind. **1**: 26. 1872.

Delphinium speciosum Bieb. subsp. *ranunculifolium* (Wall.) Brühl & King, Ann. Bot. Gard. Calc. **5**: 105. 1896.

Delphinium speciosum var. *ranunculifolium* (Wall.) Huth, Bot. Jahrb. **20**: 416. 1895.

Delphinium speciosum var. *bruehlianum* Huth, Bot. Jahrb. **20**: 416. 1895, new name for *D. elatum* var. *ranunculifolium* in Hook. f. Fl. Brit. Ind. **1**: 26. 1872.

? *Delphinium speciosum* subsp. *ranunculifolium* vars. *brachycentra*, *eriantha*, *katatricha*, *lasiantha*, *marriensis*, *oinophylla*, *pulverulenta* and *thyrsantha* Brühl in Brühl and King, Ann. Bot. Gard. Calc. **5**: 106–7. 1896. These are uncertain taxa to me. Illustrative herbarium material has not been available to me on loan.

Delphinium pulchellum Chowdhury ex Mukerjee, Bull. Bot. Surv. India **2**: 293. 1961; *nomen*. I have seen material from Edinburgh annotated "pulchellum" by Chowdhury.

? *D. hoffmeisteri* Klotzsch, Bot. Ergeb. Waldem. Reise 132. 1862. It has been referred to *D. elatum*, but since it came from the Himalaya, it seems south of the range of that species. No material seen.

Perennial from a rhizome, stem 6–12 dm. tall, 4–8 mm. thick, glabrous to spreading-villous, usually leafy throughout, branched only in the inflorescence; lower petioles to 4 dm. long, scarcely dilated at base, glabrous to villous, the upper short; blades rounded-pentagonal in outline, 6–15 cm. wide, glabrous above and beneath, to subtomentose or villous, especially beneath and along the veins, 3- or 5-partite 2/3 to 4/5 the way to the base into broad cuneate segments, these cleft and incised-serrate, the ultimate lobes ovate to lanceolate, mostly 2–7 mm. wide, mucronate; upper leaves passing into foliose parted bracts, these lanceolate to lance-ovate, to ca. 15 mm. long; inflorescence racemose or a group of racemes, many flowered, variously pubescent; pedicels ascending, to ca. 5 cm. long; bracteoles lanceolate, 3–8 mm. long, subtending the blue or purple flowers; sepals pubescent without and within; upper sepal 15 mm. by 7 mm., ovate, obtuse, spur straight or decurved, 12–15 mm. long, 3.5 mm. wide at base, gradually narrowed to a blunt apex; lateral sepals rhombic-ovate, 17 mm. by 10 mm., subtruncate at apex; lower sepals 16 mm. by 8 mm., obtuse, narrow-obovate; petals bluish black, the upper laminae slightly oblique, 10 mm. long, bidentate at apex, the spur 14 mm. long; lower laminae elliptic-oblong, 6.5 mm. by 3.5 mm., cleft to the middle into lance-oblong lobes long-ciliate, hairy outside and with patch of long hairs at inner base of lamina, claw 7 mm. long; stamens 7–8 mm. long, with strongly dilated glabrous filaments; anthers dark, 1 mm. long; follicles mostly 3, glabrous or pubescent, more or less divergent, 12–15 mm. long, 3–4 mm. wide, the styles an additional 3 mm. long; seeds blackish, obpyramidal, 1.5 mm. long, densely clothed with laminate scales.

TYPE: Peer Punjal (Pir Panjal), *Royle.* Through the very great kindness of Mr. E. F. Greenwood, Keeper of Botany, City of Liverpool Museums, I have had photographs of the type of *Delphinium pyramidale.* This name has to replace the name *D. ranunculifolium* which was for many years a *nomen nudum.*

RANGE. Apparently from West Pakistan to Nepal at elevations of about 2000 to 3500 m.

ILLUSTRATION. BRÜHL & KING, Ann. Bot. Gard. Calc. **5**: *pl. 127.* 1896; COVENTRY, Wild Fl. Kashmir **2**: *pl. 6.* 1927.

EXAMPLES SEEN. **Swat:** *R. R. Stewart 29167* (MICH). **Kumaon:** *Strachey & Winterbottom 2* (GH, K). **Kashmir:** *Duthie* Aug. 25, 1892 (BM, E); *C. B. Clarke 29506* (BM, K); *R. R. & I. D. Stewart 18357* (GH, NY); *Stewart 18316* (UC, US), *8079* (NY), *5268* (PHIL), *28781* (E); *Duthie 19114* (K); *Koelz 9313* (NA, NY); *Jacquemont 908* (P). **Nepal:** *Sharma E98* (BM); *Dhwoj 234* (E); *F. M. Bailey* in 1936 (E). **W. Tibet:** *Falconer 62* (GH, K, P); *Polunin, Sykes & Williams 5120* (BM); *Polunin 2629* (BM).

225. **Delphinium pyramidatum** Alboff, Descr. Nouv. Esp. Pl. (1891) II. (Trav. Soc. Hort. Odessa 1891); Busch in Fl. Cauc. Crit. III. **3**: 71. 1902. FIG. 18, G.

Delphinium elatum L. var. *pyramidatum* (Alboff) Huth, Bot. Jahrb. **20**: 399. 1895.

Delphinium flexuosum var. *glandulosum* O. Kapeller ex Grossh. Fl. Cauc. **2**: 100. 1930, according to Nevski in Fl. U.S.S.R. **7**: 142. 1937.

Stem 1–1.5 m. tall, robust, leafy; leaves 5- or 7-parted, the parts deeply incised into narrow-lanceolate acuminate lobes; inflorescence pyramidate-paniculate to ca. 4 dm. long, glandular-pubescent and strigulose, much branched and with very numerous crowded flowers; bracts narrow-linear, to 2 cm. or more long; pedicels 3–5 cm. long, ascending, pubescent; bracteoles linear, 10–12 mm. long, placed just above the middle of the pedicels; calyx pale blue, more or less puberulous; upper sepal ovate, obtuse, 12 mm. long, 8 mm. wide, the spur decurved, 10 mm. long, 3 mm. wide at base; lateral sepals asymmetric, oblong, 17 mm. by 7 mm., rounded at the broad apex; lower sepals lance-ovate, 14 mm. by 4 mm., pointed; petals blackish brown, the upper laminae erect, glabrous, bidentate at apex, 9 mm. long, the spur 12.5 mm. long; lower laminae oblique, 5 mm. long, cleft to middle, more or less bearded, the claw pubescent, 6 mm. long; stamens 6.5 mm. long, glabrous; anthers dark, oblong, 1 mm. long; follicles 3, glabrous; seeds winged at angles.

TYPE: West subalpine Transcaucasia, Abkhasia, 1300–1400 m., Aug., 1893, *Alboff 195*, isotype (P); seen.

ADDITIONAL COLLECTIONS. *Alboff 194* (NY), *196* (P), *182* (K).

226. **Delphinium retropilosum** (Huth) Sambuk, Soc. Bot. Russ. **14**: 428. 1929. FIG. 18, H.

Delphinium duhmbergii Huth var. *retropilosum* Huth, Bot. Jahrb. **20**: 402. 1895.

Delphinium pterospermum Turcz., *nomen*, according to Nevski in Fl. U.S.S.R. **7**: 152. 1937.

Stem 6–8 dm. tall, 6 mm. thick, striate, densely clothed on lower half with white retrorse-spreading hairs 2–3 mm. long, subglabrous above, few branched in inflorescence, rather closely leafy; lower leaves gone by anthesis, main cauline petioles hairy, 5–8 cm. long, dilated at base; blades roundish-elliptic in outline, almost straight across the base, 4–5 cm. long, 6–8 cm. wide, green and glabrous above, conspicuously veined and paler and hairy beneath, palmately 5-fid to 1 or 1.5 cm. above the base into cuneate obovate segments laciniate into 3 main lobes, these toothed or incised into lanceolate lobules 2–3 mm. wide and up to 10 mm. or more long; inflorescence a long, many flowered raceme with short branches below, subglabrous; lower bracts more or less foliose, palmately divided, 15–20 mm. long, with some long bristly hairs; upper bracts lacking; pedicels erect, 1–2 cm. long, angled; bracteoles oblanceolate, 5–8 mm. long; strongly ciliate, placed near the base of the flower; sepals blue, mostly glabrous except for a few marginal hairs; upper sepal ovate, 10 mm. long, 5–6 mm. wide, the spur straight, 1 cm. long, 2.5 mm. wide at base; lateral sepals more or less elliptic, 8 mm. long, 4 mm. wide, rounded at apex, with a few marginal hairs; lower sepals 9 mm. by 5 mm., obtuse; petals dark, the upper laminae slightly oblique, entire, 8 mm. long, with a few bristly hairs, the spur 9 mm. long; lower laminae oblong, 4 mm. by 2 mm., unequally lobed, with long yellow hairs on the surface and long white cilia, claw 6 mm. long; stamens 5 mm. long, glabrous, moderately dilated; anthers dark, 1 mm. long; follicles 3, somewhat pubescent.

TYPE: Indicated only as coming from Siberia.

ILLUSTRATION. Fl. U.S.S.R. 7: *pl. 10*. 1937, drawing of leaf.

I would place two herbarium specimens that I have seen (both from NY, since I was unable to borrow any from LE) in this species: North Altai, *Tarchevskaya & Vandysheva*, July 10, 1932, and Tomsk, without collector, in 1913.

227. **Delphinium ruprechtii** Nevski in Komarov, Fl. U.S.S.R. 7: 138, 723. 1937. FIG. 18, I.

Delphinium flexuosum var. *bracteolatum* N. Busch in Fl. Cauc. Crit. III. 3: 67. 1903, *pro parte*, according to Nevski.

Stem to 1 m. tall, ribbed, lightly pilose or almost glabrous, ridged, leafy; petioles not dilated at base, pilose, to ca. 1 dm. long; leaves like those of *D. flexuosum*, scarcely pubescent above, to 12 cm. wide, pilose on nerves beneath, palmatifid almost to base, the middle segment oblong-rhombic, divided into 3 lobes, each with 3 to 5 lanceolate teeth, lateral segments like the middle one, the ultimate teeth 5–15 mm. long, 3–6 mm. wide; raceme dense, usually branched, the axis glabrous, many flowered, to 3 dm. long; bracts lanceolate, more or less ciliate on margin, 10–15 mm. long, 2–4 mm. wide, somewhat bluish; pedicels glabrous, divergent, 1–4 cm. long; bracteoles elliptic or elliptic-ovate, 5.5–8 mm. long, 4–4.7 mm. wide, subobtuse, violet tinged, glabrous; sepals glabrous without, ciliolate within, the margin densely ciliate, blue, the upper oblong-ovate, subacute, 20 mm. by 10 mm.; spur 18–20 mm. long, 3.5 mm. wide at base; lateral sepals elliptic, 20 mm. by 10 mm., obtuse; lower sepals somewhat narrower; petals black, the upper laminae almost straight, 12 mm. long, deeply bidentate, glabrous, the spur 14 mm. long; lower laminae 7 mm. long, oblong-ovate, short bearded at base, bifid to middle into oblong, ciliate lobes, claw appendiculate, 6 mm. long; stamens 7–8 mm. long, glabrous; carpels 3, glabrous.

TYPE: "Dagestania, inter pagos Czirch & Rhycza," leg. *Alexeenko,* July 23, 1898 (LE); seen.

Differs from *Delphinium flexuosum* and *D. bracteosum* in its elliptic or elliptic-ovate glabrous bracteoles.

228. **Delphinium sauricum** Schischk. Animadvers. Syst. Herb. Univ. Tomsk **1936**(8): 1. 1937.

Stems solitary, erect, 3–5 dm. tall, from a thick rhizome, with longish spreading hairs; leaves petioled, these 6–14 cm. long, densely hirsute; blades round-reniform, deeply cordate at base, 4–6 cm. long, 2.5–4 cm. wide, deeply divided or coarsely toothed, with long appressed hairs on both surfaces; inflorescence racemiform, 1–2.5 dm. long, 6–10-flowered; lower bracts 2–3-lobed to middle, shorter than or subequal to the pedicels, upper bracts entire, lance-ovate, violet; bracteoles 2, lance-ovate, to 10 mm. long, 3–4 mm. wide; sepals blue-violet, more or less appressed hairy on both surfaces and mixed with a few lageniform hairs, broadly ovate, 14–15 mm. long, 10–11 mm. wide, the lower narrower, 15 mm. by 8 mm.; spur 20–23 mm. long; petals black-fuscous, the upper laminae 10 mm. long, 4–5 mm. wide, the lower deeply bifid, ciliate, yellow bearded on surface near the base; carpels 3, strigose.

TYPE: Montes Saur. In jugo Mus-tau toward head of Ulkun-Obo River, in alpine meadows, July 26, 1914, *W. Saposhnikov* (TK); I was unable to borrow material.

229. **Delphinium speciosum** Bieb. Fl. Taur. Cauc. **2**: 12. 1808.
FIG. 18, J.

Delphinium speciosum var. *typicum biebersteinii* and *speciosum* var. *gymnopus* and var. *trichocarpum* Rupr. Fl. Cauc. 35. 1869, *fide* Nevski in Fl. U.S.S.R. **7**: 128. 1937.

Delphinium ironorum N. Busch, Bull. Acad. Sci. U.S.S.R. **1931**: 450. 1931.

Based on a collection by *E. & N. Busch*, Aug. 24, 1930, at 2750 m., from Dzhomakh, Mount? or Mountain Pass? Bakh-fandar (LE); seen.

Delphinium bracteosum var. *macranthum* Som. & Levier, and var. *albidum* Som. & Levier, Acta Horti Petrop. **13:** *25.* 1893; according to Nevski.

? *Delphinium caucasicum* var. *bracteosum* Schrenk & Trautv. Bull. Soc. Mosc. 80. 1860.

? *Delphinium speciosum* var. *bracteosum* Huth, Bot. Jahrb. **20:** 416. 1895.

? *Delphinium boissieri* Boiss. & Buhse, Nouv. Mém. Soc. Nat. Mosc. **12:** 8. 1860. *Delphinium speciosum* var. *boissieri* Buhse, Reise Turcm. u. Pers. p. 8. "Beim Dorfe Livan auf der Thalsohle," no. 539, June 18, 1947. Collector? Not seen.

Perennial from a woody root, the stem 3–8 dm. tall, simple or branched above, villous, striate, rather equably leafy throughout; leaves 3–12 cm. wide, rounded-pentagonal in outline, more or less villous on both surfaces, the hairs especially long on the veins of the upper surface, more generally distributed beneath, blades mostly 5-parted to near the base into broad cuneate segments, these incised-serrate into lanceolate lobes 2–10 mm. wide, long pointed; petioles somewhat dilated at base, villous, 3–15 cm. long; flowers racemose on axis or branches, the inflorescence densely villous, several to many flowered; lower bracts 3-parted to the base, the upper entire, lanceolate, villous, 7–15 mm. long; pedicels almost erect, 1–3 cm. long; bracteoles lanceolate, villous, 4–6 mm. long, placed just beneath the flower; sepals violet, villous without and somewhat within, upper sepal ovate, 18–25 mm. long, 8 mm. wide, rather sharply pointed, the spur 17–18 mm. long, 3 mm. wide at base, tapered rather rapidly to the narrow, somewhat decurved apex; lateral sepals 18–25 mm. by 10 mm.; lower sepals 20 mm. by 9 mm.; petals black, the upper laminae straight, 14 mm. long, deeply emarginate, glabrous, the spur 20 mm. long; lower laminae 8 mm. long, 4 mm. wide, oblong, turned to one side, with a patch of long yellow hairs near the base, white-ciliate, cleft ca. 3 mm., the claw broad, 6 mm. long; stamens glabrous, 6 mm. long; anthers dark, oblong, 1.2 mm. long; carpels 3, somewhat villous, becoming 15 mm. long; seeds dark, transversely lamellate-squamate, ca. 2 mm. long.

TYPE: Mt. Kaischaur, Caucasus, Herb. M. a. Bieberst., plant in photograph (K) has 1 leaf and is in fruit. Another specimen labeled *Delphinium speciosum*, M. Comm. Stephan, ex Herb. Bieberstein, typus (photo. K).

ILLUSTRATIONS. DELESSERT, Icon. Select. 1: *pl. 62.* 1820; Bot. Reg. **18:** *pl. 1503.* 1832.

DISTRIBUTION. The species seems to range from the Caucasus to Turkestan.

EXAMPLES. Hisiar, in valle fl. Jaquob, *A. Regel*, Iter Turkestanicum (E, K); **Caucasus:** *Bunge* in 1856 (P); South Ossetia, *E. & K. Busch* in 1935 (BM); Patcha Pass, Seraischeniar, *Komarov* in 1892 (K); Circassia, source of the Lascha, *Alboff* in 1894 (P).

230. **Delphinium stapeliosum** Brühl ex Huth, Bot. Jahrb. **20**: 419. 1895 and in Brühl & King, Ann. Bot. Gard. Calc. **5**: 102. 1896. FIG. 18, K.

Delphinium stapeliosum var. *khasianum* Brühl in Brühl & King, Ann. Bot. Gard. Calc. 5: 102. 1896.

Stem erect, slender, 4–15 dm. tall, branched above, retrorse-pubescent, scattered leafy, the upper leaves reduced; lower petioles to 2.5 dm. long, slightly dilated at base, pubescent, the upper shorter; leaf blade to 15 cm. across, palmately 5-fid to 1 cm. or more from base, deep green and sparsely pubescent above, paler and more pubescent beneath especially on the veins, the segments broadly cuneate, entire in lower part, trifid above and then incised-dentate with large lance-ovate or broader teeth, acute; racemes lax, rather few flowered or the terminal raceme with more; bracts lanceolate to lance-linear, to ca. 10 mm. long; pedicels ascending, gray-pubescent, 1–8 cm. long; bracteoles lance-linear, 7–10 mm. long, alternate, near the middle of the pedicel; sepals blue to violet or reddish, hairy without, the upper sepal ovate, 18 mm. by 10 mm., obtuse, the spur slightly curved, 20 mm. long, 4 mm. wide at base, the apex fairly slender; lateral sepals rhombic-ovate, 18 mm. by 15 mm., rounded-truncate at apex; lower sepals somewhat narrower, 17 mm. by 10 mm., obtuse; petals blue-black, the upper laminae almost straight, 10 mm. long, glabrous, bidentate at apex, the spur 2 cm. long; lower laminae oblong, 6 mm. by 3 mm., deeply cleft, bearded but not ciliate, the claw 6 mm. long; stamens 5–6 mm. long, glabrous; anthers dark, linear, 1.3 mm. long; follicles 3, pubescent, divergent, slender, 12–18 mm. long, the styles an additional 3.5 mm.; seeds obpyramidal, winged along the edges, puckered on the sides.

LECTOTYPE: No specimens are cited in Brühl & King, but in Huth there is cited "Assam: Khasia Hills ad 2000 m. alt.," *Hooker and Thomson.* I would select the K specimen as the lectotype and cite also BM, E, GH, NY.

DISTRIBUTION. Eastern Nepal and Khasia, Assam, at elevations of about 1200 to 3000 m.

REPRESENTATIVE SPECIMENS. **E. Nepal:** *Stainton 1162* (BM); *Stainton, Sykes & Williams 7867* (BM), *8587* (BM). **Khasia:** *Clarke 16354* (BM, K), *16117* (BM), *16381* (E), *6168* (K), *38970* (US), *40301* (US), *44861* (US); *Hooker & Thomson* (BM, E, GH, K, NY); *Griffiths 461* (BM, K), *827* (K); *Chaud 7192* (E, MICH), *31250* (MICH), *Koelz 25579* (MICH), *31250* (E, MICH).

231. **Delphinium tianshanicum** W. T. Wang, Acta Bot. Sinica **10**: 85. 1962. FIG. 18, L.

Stems 5–11 dm. tall, terete, 2–5 mm. thick at base, sparsely retrorse-hirsute, few branched above, mostly simple, equably foliose; lower leaves long petioled (to 5 times as long as the blades); blades as in *D. naviculare*, broadly reniform or pentagonal-reniform, 3–9 cm. long, 5–14 cm. wide, cordate, 3-parted to 1 or 2 cm. from the base, the middle part rhombic, acute, 3-lobed above the middle, the lobes somewhat ovate, coarsely 4–5-

toothed, the lateral parts smaller, 2–3-toothed, densely strigulose on both surfaces; racemes 7–14-flowered, rather dense; lower bracts trifid, the others lance-linear, 8–14 mm. long, 1–1.5 mm. wide, strigulose; pedicels 2–6 cm. long, densely retrorse-strigulose, suberect; bracteoles 1.5–6 mm. below the flower, linear to lance-linear, 5–9 mm. long, strigulose; sepals blue-purple, ovate or obovate, 11–15 mm. long, densely strigulose; spur 11–14 mm. long, cylindric-subulate, 3 mm. thick at base, straight or slightly decurved; petals black, the upper laminae glabrous, emarginate, 9 mm. long; lower laminae subobovate, 5 mm. long, 2-lobed to near the middle, claw 6 mm. long, short-appendiculate; stamens glabrous; anthers over 1 mm. long; follicles 9–11 mm. long, densely strigulose, the styles 2 mm. long; seeds obconic, triquetrous 1.5 mm. long, scaly-lamellate.

TYPE: Sinkiang, *T. N. Liou 3620*, Aug. 24, 1931 (PE); not seen. Other specimens cited in the original description are also from Sinkiang, Hoshuo, 2300 m., *Li & Chu 7003* (E), seen, and Sha, 1700 m., *Kuan 2290* (E), seen.

232. **Delphinium ukokense** Sergievsk. Animadvers. Syst. Herb. Univ. Tomsk **1954**: 9. 1955.

Erect perennial, 2.5–4 dm. tall, 2–4 mm. thick below, leafy almost to the inflorescence, short-pubescent throughout, with gland-tipped hairs mixed in; leaves 3.5–6 cm. long, 4–6 cm. wide, round-reniform or rounded, 3- or 5-parted to 4/5 or 5/6 their length, the lobes rhombic, coarsely toothed above, short-pubescent on both surfaces; raceme 10–12 cm. long, lax, 6–15-flowered; lower bracts leafy; pedicels 5–10 mm. long; bracteoles linear; sepals blue, pilose; spur slightly curved at tip, 14–15 mm. long; petals brown, the upper laminae glabrous, the lower yellow-pubescent down to middle, ciliate; carpels 3, glabrous.

TYPE: Altai, Ukok, *Saposhnikov* in Herb. Krylov (TK); not available to me.

The author compared his species, *Delphinium ukokense*, with *D. mirabile*, but said the stems of the former were glandular-pubescent their whole length, the petioles shorter than or equal to the laminae; the flowers smaller; spur 14–15, not 16–20 mm. long; and the carpels glabrous.

233. **Delphinium villosum** Stev. ex DC. Syst. 1: 546. 1817; Prodr. 1: 55. 1824. FIG. 18, M.

Delphinium villosum var. *anomalum* Huth, Bot. Jahrb. **20:** 412. 1895. Huth cited "in deserto Tentek," *Schrenk* 1840 (LE); not seen.

Delphinium villosum var. *winkleri* Huth, *loc. cit.* Huth cited Alexander Mts., Dschilamysch, 1600–2000 m., *Fetissow*, 1880 (LE); not seen.

Delphinium rha Schipcz. ex Nevski in Komarov, Fl. U.S.S.R. **7:** 152. 1937, *in synon.*

Stem 10–12 dm. tall, leafy, simple, glabrous below; petioles scarcely dilated at base, to 15 cm. long, the upper reduced; blades glabrous or slightly pubescent on veins above, subvillous beneath, the lower truncate-cordate at base, the upper cuneate, all broader than long, the lower to 15 cm. broad, 3- or 5-parted to 1 cm. or more from the base, the parts cuneate-obovate, shallowly incised or coarsely toothed, with acute or acuminate teeth or lobes; raceme simple or few branched, many flowered, rather lax, 2–4 dm. long, minutely strigulose and with some retrorse-spreading soft pubescence; bracts mostly linear-subulate, villous, to ca. 1 cm. long; pedicels erect-divergent, 1–7 cm. long; bracteoles like the bracts, placed slightly below the flowers; sepals deep blue, sparsely villous; upper sepal 12–15 mm. long, 6–8 mm. wide, acute, the spur straight, about as long, rather slender; lateral sepals oblong-obovate, 12–14 mm. long, 6–8 mm. wide, villous along midrib, rounded at apex; lower sepals more pointed and more hairy; petals dark, the upper laminae almost straight, glabrous, 9 mm. long, entire, the spur 12 mm. long; lower laminae oblong-ovate, 3.5 mm. by 2.5 mm., long-bearded, cleft, the claw 6 mm. long; stamens 6–7 mm. long, the filaments ciliate; anthers dark, 1 mm. long; follicles 3, glabrous except on the ciliate sutures, oblong, 12–15 mm. long, 4–5 mm. wide, the styles an additional 3 mm.; seeds brown, 2.5 mm. long, slightly winged along the 3 angles.

TYPE: Hort. Dorpat, *Steven* in 1817 (G?) not seen; photograph (BH), seen.

EXAMPLES OF THE SPECIES. Cultivated at Ottawa from Tabor Bot. Gard.; **Germany:** *Gillett*, July 7, 1939 (BH); **Chinese Turkestan:** Mts. Bogdo-ola & Urumtschi, *Merzbacher 1304* (GH).

234. **Delphinium winklerianum** Huth, Bot. Jahrb. 20: 419. 1896.

FIG. 18, N.

Perennial, 6–8 dm. tall, with scattered stiff white hairs, rather equably leafy; midcauline leaves with petioles 2–8 cm. long, villous, scarcely vaginate, the blades ca. 1 dm. across, broadly cordate at base, 3-parted to ca. 1.5 cm. from base into broad-cuneate obovate segments ca. 4 cm. by 3–3.5 cm., scattered stiff-hairy on both surfaces, each segment with ca. 3 coarse ovate teeth to 1.5 cm. long and broad, mucronate, the uppermost leaves reduced; inflorescence with 2–3 basal branches, the central raceme to ca. 3 dm. long, laxly many flowered, somewhat strigulose, the pedicels suberect, 3–10 cm. long; lower bracts foliose, upper lance-linear, 1–1.5 cm. long; bracteoles subtending the flower, lanceolate, 8–10 mm. long, 2–2.5 mm. wide; flowers deep blue, sepals strigulose without, glabrous within, the upper sepal ovate, 17 mm. by 10 mm., obtuse, the spur spreading decurved, 17 mm. long, 3.5 mm. wide at base, blunt; lateral sepals broadly elliptic-obovate, 18 mm. long, 14 mm. wide, rounded at apex; lower sepals elliptic-ovate, 16 mm. by 8 mm., subacute; petals black, the upper laminae almost straight, 10 mm. long, rounded and bidentate at the glabrous tip, the spur 13 mm. long; lower laminae strongly oblique, oblong-obovate, 5 mm. by 3.5 mm., somewhat bearded, bifid about halfway into rounded-oblong lobes, the claw 6 mm. long; stamens 7–8 mm. long, the anthers dark, rounded, ca. 1 mm. long; carpels 3, hairy.

TYPE: June 4, 1881, Kasch, Turkestan, sem. m. Dr. A. Regel, *C. Winkler 7230* (LE); seen.

[*To be continued*]

VOLUME 49 NUMBER 2

JOURNAL
OF THE
ARNOLD ARBORETUM
HARVARD UNIVERSITY

APRIL, 1968

PUBLISHED BY
THE ARNOLD ARBORETUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS

THE JOURNAL OF THE ARNOLD ARBORETUM

Published quarterly by the Arnold Arboretum of Harvard University.

Subscription price $10.00 per year.

Volumes I–XX, reprinted, and back issues of volumes XXI–XLV are available from the KRAUS REPRINT CORPORATION, 16 EAST 46TH STREET, NEW YORK, N.Y. 10017.

Subscriptions and remittances should be addressed to MISS DULCIE A. POWELL, ARNOLD ARBORETUM, 22 DIVINITY AVENUE, CAMBRIDGE, MASSACHUSETTS 02138.

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Volume 49, No. 1, including pages 1–166, was issued January 15, 1967.

Second-class postage paid at Boston, Massachusetts

JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. 49 APRIL 1968 NUMBER 2

FLOWERS, FRUITS, AND PHYLOGENY OF ALANGIACEAE

RICHARD H. EYDE

PUBLICATIONS ON THE ALANGIACEAE include an excellent monograph (Bloembergen, 1939) and a series of carefully documented anatomical studies (Govindarajalu & Swamy, 1956; Govindarajalu, 1961; 1962 a, b, c), but details of the flower and fruit have never been adequately scrutinized for evolutionary trends or for evidence of extra-familial affinities. This article will emphasize three neglected features that are known to have taxonomic value in many groups of plants: the floral vascular system, the secretory canals, and the stone or endocarp portion of the fruit wall. Species groups within the Alangiaceae differ greatly with respect to these structural features, and some of the differences can be interpreted to show directions of evolutionary change.

Although many older botanical works recognized two genera of Alangiaceae, *Alangium* Lam. and *Marlea* Roxb., Bloembergen's (1939) opinion that *Marlea* deserves only sectional status is now followed in most treatments. Bloembergen's monograph lists 18 species of *Alangium*, all woody, distributed in eastern Asia, Africa, Australia, and islands of the Pacific and Indian Oceans. Japanese botanists accept an additional species, *A. premnifolium* Ohwi (1938, p. 30, 1965, p. 652), considered doubtful by Bloembergen (p. 172, 173). Three species have been described since Bloembergen's monograph appeared. Two of these, *A. chungii* Li (1943, p. 448) and *A. tonkinense* Gagnepain (1950, p. 22), are based on single collections, and their circumscriptions differ so little from those of better known species [1] that an anatomical study need not be concerned with them. The third, *A. grisolleoides* Capuron (1962) is sufficiently distinct to merit a special commentary later in this paper.

Bloembergen distributed the species in four sections, using the number of stamens and characters of style, stigma, and embryo as basis for distinction. Govindarajalu's anatomical observations strongly support the soundness of this distribution. Although I believe the order in which

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[1] *Alangium tonkinense* differs from *A. salviifolium* mainly in that its leaves are cuspidate and its filaments not dilated. I have examined the type of *A. chungii* (*Chung 82038*, A) and I think it belongs to *A. kurzii* Craib. The only fertile material labeled *A. premnifolium* that I have seen, a flowering specimen from Okinawa (*Kanashiro 692*, A), also belongs to *A. kurzii*.

Bloembergen listed the sections obscures their evolutionary relationships, I follow his delimitation of taxa throughout this paper. I also adhere to his nomenclature and orthography, with two minor exceptions: (1) section ANGOLUM Baill., which includes the type species, is herein called section ALANGIUM in accordance with Article 22 of the current *International Code of Botanical Nomenclature* (1966), and (2) the specific epithet *salviifolium* is spelled according to Recommendation 73G of the *Code*.

MATERIAL

Cooperating botanists and foresters (see Acknowledgments) supplied the following collections in liquid preservative.

Section CONOSTIGMA Bloemb.	
A. havilandii Bloemb.	SAR *S.22767*; Sarawak
A. ridleyi King	(1) cult., Bogor, *VIII. H. 14* (2) cult., Bogor, *IX. A. 20.*
A. javanicum (Bl.) Wangerin	(1) *P.P. Sam, s.n.* (SAN *36750*). (2) cult., Bogor, *VIII. F. 25.*
Section ALANGIUM	
A. salviifolium (L.f.) Wangerin	(1) *Govindarajalu 6840A*; Madras, India (2) cult., Bogor, Indonesia, *III. G. 41.* (3) cult., Bogor, *XVII. C. 136.*
A. longiflorum Merr.	(1) *B. Hernaez 635*; Makiling Natl. Park, Philippines (2) without voucher; Makiling Natl. Park
Section MARLEA Baill.	
A. platanifolium (S. & Z.) Harms	(1) cult., Bot. Gard. Tohoku Univ. (2) *K. Sohma, s.n.*, Shiraishi Pass, Iwate Pref., Japan
A. chinense (Lour.) Harms	(1) cult., Tjibodas, Indonesia (2) without voucher; Makiling Natl. Park
A. rotundifolium (Hassk.) Bloemb.	cult., Tjibodas

To verify the identifications, I consulted Bloembergen's descriptions and compared the material with herbarium specimens that Bloembergen annotated or cited. Some of the collections are from individual trees that Bloembergen mentioned and that still survive in Indonesian gardens. The infraspecific identity of the specimens seems unimportant to this investigation; so I have not tried to make subspecific or varietal distinctions.

Unable to obtain pickled material of *A. villosum* (Bl.) Wangerin, the only species in Bloembergen's section RHYTIDANDRA, I removed a few dried flowers from sheets in the U.S. National Herbarium. (Because of Dr. A. C. Smith's field activities, the Herbarium is well supplied with the Fijian variant of *A. villosum.*) My remarks on mature fruits of *Alangium* are drawn mostly from the examination of dried specimens in the U.S. National Herbarium, and in the Gray Herbarium and the Herbarium of the Arnold Arboretum of Harvard University.

Sectioning and staining procedures were routine (Eyde, 1963, 1966), but clearing of flowers required some experimentation. Good results were obtained through Fuchs' (1963) "Method No. 1," with the concentration of NaOH reduced to 5 percent to prevent maceration of tissues. Another successful procedure included the following steps: overnight immersion of the flowers in 5 percent NaOH at 60°C, immersion for several hours in warm "CLP" (Bersier & Bocquet, 1960), transfer through an ethanol series to toluene. In most cases, it was necessary to cut the flowers into thick freehand sections before clearing.

OBSERVATIONS

General. Bloembergen (1939) followed Wangerin (1910) and several earlier authorities in using the relative number of stamens and petals to subdivide *Alangium.* Stamens of Bloembergen's sections MARLEA, RHYTIDANDRA, and CONOSTIGMA — collectively corresponding to subgenus MARLEA of Wangerin's treatment — were said to equal the petals in number. Neither Bloembergen nor Wangerin added that the number of stamens may be one more or one less than the number of petals. I have recorded the following counts for corolla (C) and androecium (A). *A. havilandii*: C4, A4; C5, A5; C6, A5. *A. ridleyi*: C5, A5; C6, A6. *A. javanicum*: C6, A6; C7, A7; C8, A8. *A. grisolleoides*: C4, A3; C5, A5. *A. platanifolium*: C6, A7; C7, A7. *A. chinense*: C7, A7; C8, A8; C8, A9. *A. rotundifolium*: C7, A7; C8, A8. *A. villosum*: C5, A5; C5, A6; C6, A5; C6, A6. For section ALANGIUM ("subgenus Eualangium") Wangerin gave the number as two to four times the number of petals; Bloembergen's description says two to six times the number of petals. My observations, which follow, indicate that Wangerin was more nearly correct. *A. salviifolium*: C5, A12; C5, A17; C6, A15; C6, A26; C7, A26; C7, A28; C8, A30. *A. longiflorum*: C4, A14; C4, A16. With limited material, I have not tried to estimate the frequency with which any of these numbers occur. Not uncommonly, flowers are found in which one petal is "double"; i.e., it is seen as an abnormally broad single appendage when sectioned near its base but as two normal appendages in distal sections. This condition is not restricted to any particular group of species. I also found one flower of *A. grisolleoides* (C4, A3) in which a stamen with six anther sacs and two vascular bundles is clearly a double structure.

Regardless of their number, the stamens are arranged in a single whorl around a prominent pulvinate disc. Dehiscence of the linear anthers is latrorse to somewhat introrse. As Bloembergen emphasized, variations in the form of the filaments and in the length of their trichomes are important for separating the species. A distinctive character of section CONOSTIGMA is the papillose epidermis of the anther.

The microspore mother cells in a developing anther are surrounded by four cell layers: an inner tapetum, an outer epidermis, and two undifferentiated intermediate layers. The subepidermal layer never develops the "fibrous" thickenings of a typical endothecium. Another unusual feature, already reported by Gopinath (1945), is the arrangement of microspore mother cells in a single file in each anther lobe; this is caused by the conversion of primary sporogenous cells into microsporocytes without intervening divisions. Following meiosis, all surrounding layers degenerate except for the thin-walled epidermis, which usually ruptures before the corolla opens. In most species the septa between anther-halves also degenerate before the pollen is released, but anthers of *A. longiflorum* retain four locules at anthesis.

The trichomes and crystal inclusions of *Alangium* flowers are described in detail by Govindarajalu (1962 b, c). My observations agree with his except that I have found druses to be plentiful in floral tissues of section CONOSTIGMA, where he found none. Included in my material is one species, *A. havilandii*, that Govindarajalu did not examine: the floral trichomes are

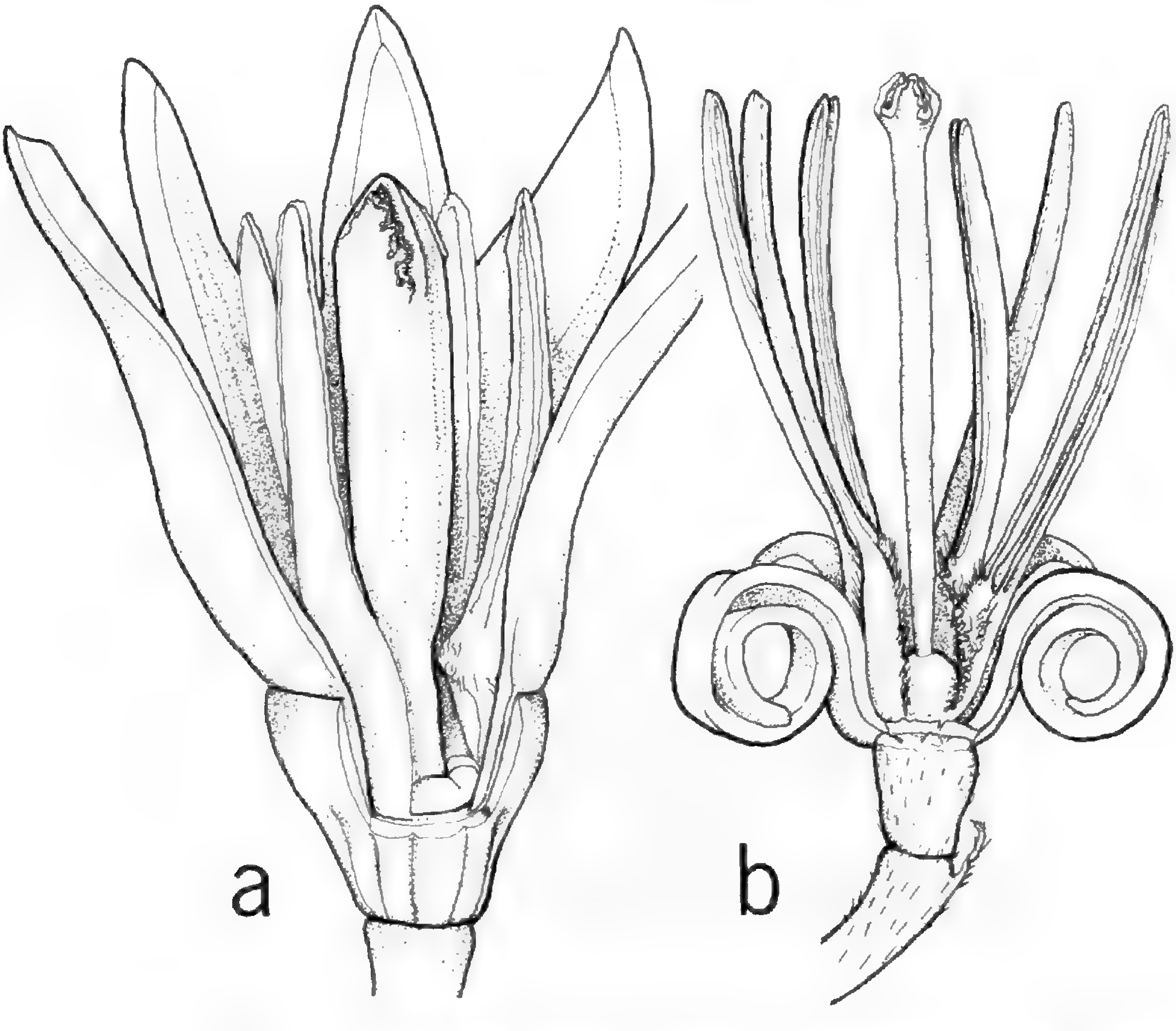

FIG. 1. a, flower of *Alangium ridleyi* (section CONOSTIGMA), cult., Bogor, *IX.A. 20*, × 3.5. b, flower of *A. chinense* (section MARLEA), cult., Tjibodas, *s.n.*, × 4.3. Part of each flower has been cut away to show disc.

of the type that he called "stellate-peltate," as could have been predicted from his observations on the other members of section CONOSTIGMA.

Sectional differences in the form of the stigmatic area were stressed by Bloembergen. He named section CONOSTIGMA for the "conical" termination of the style, but the four stigmatic rays (FIG. 1, a; FIG. 2, a) give it a pyramidal appearance to my eye. In section MARLEA (FIG. 1, b) the stigma is capitate and lacks the rays, but is distinctly four-lobed. Section ALANGIUM has a capitate stigma that is not four-lobed — here I contradict Bloembergen — but irregularly folded and convoluted (FIG. 2, b). *Alangium villosum* (sect. RHYTIDANDRA) is distinguished by two styles, each stigmatic along its ventral surface and slightly bifid at its apex. These are basally united for about half their length (Bloembergen, 1939, *Fig. 7, b, k*) in a stylar column. Microtome sections through the stylar column of *A. villosum* reveal a symmetrically four-lobed stylar canal. When cut about halfway between base and apex, the style in section CONOSTIGMA has a similar cross section, but in section MARLEA the four-lobed appearance is less symmetrical, and in section ALANGIUM the stylar canal is very irregular, often three-lobed. Followed downward through serial sections, the stylar canal of any species loses its lobed appearance, becoming oval or elliptical in outline at its base (Clarke, 1850, *Figs. 4–7*). It is always hollow at anthesis and filled with a mucilaginous exudate.

The ovary, completely inferior throughout the genus, is one-locular in sections CONOSTIGMA, ALANGIUM, and RHYTIDANDRA. In some species of section MARLEA two-locular ovaries are common, but the locules are usually unequal, and one of them may be empty (FIG. 5, b). Except for such cases, the ovules are solitary in each locule, pendent and anatropous with the micropyle directed laterally (FIG. 2, c; 5, a).

Vascular system. The most conspicuous sectional differences are in the number of carpel bundles and in the extent of fusion of calyx bundles to bundles supplying petals and stamens. The vascular systems of sections CONOSTIGMA and ALANGIUM differ somewhat (FIG. 4), but the differences that separate these two groups from sections MARLEA and RHYTIDANDRA are much greater.

Pedicels in all species of *Alangium* contain a rather compact cylinder of vascular tissue, difficult to resolve into individual strands. At the base of the flower this cylinder expands into a circle of 10 or more major bundles (usually twice the number of petals). In *A. javanicum* and *A. ridleyi* two additional series of bundles diverge radially from the first within the short distance of a few 15μ microtome sections and still below the base of the ovarian cavity. The inner series, containing up to 30 fine strands, comprises the gynoecial vasculature. The middle series supplies stamens and petals, and the outer series supplies the calyx (FIGS. 2, c, d; 3, a). In *A. havilandii* the two outer series and the middle series are united for a distance; their divergence takes place about halfway up the ovary wall. And in section ALANGIUM (FIG. 3, b-d), these two series remain united almost to the insertion of petals and stamens.

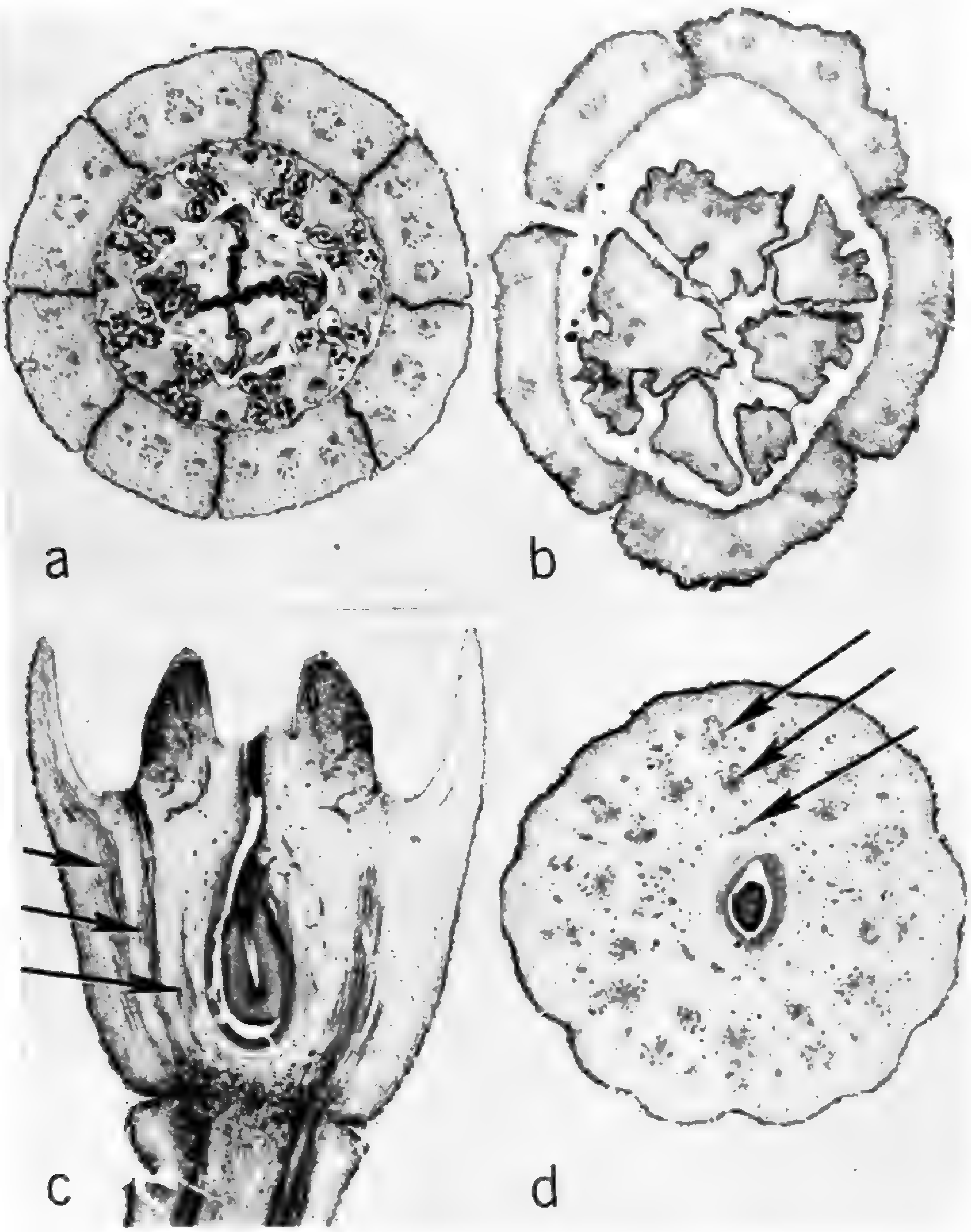

FIG. 2. Flowers of *Alangium.* a, *A. javanicum, P. P. Sam, s.n.*; cross section near apex showing 4 stigmatic rays; × 16. b. *A. longiflorum, B. Hernaez 635,* US; cross section near apex, showing asymmetrical convolutions of stigma; × 20. c, *A. javanicum, P. P. Sam, s.n.*, longitudinal section of ovary, showing attachment of ovule; arrows indicate 3 series of vascular bundles; × 13. d. *A. javanicum, P. P. Sam, s.n.*, cross section through inferior ovary showing vascular bundles in 3 series (arrows); × 17.

In section CONOSTIGMA there are some heavy tangential and radial strands near the level of insertion of petals and stamens. These interconnect the bundles of the outer and the intermediate series. A special vascular feature in *Alangium javanicum* and *A. ridleyi* is the occurrence of extra longitudinal bundles between the principal strands of the outer series, bundles that terminate blindly at their basal end, not connecting with any other bundles. At their apical end these join with main bundles of the outer series and with the bundles of the intermediate series in supplying branches to the disc.

The dorsal supply in section CONOSTIGMA is peculiar in that a discrete

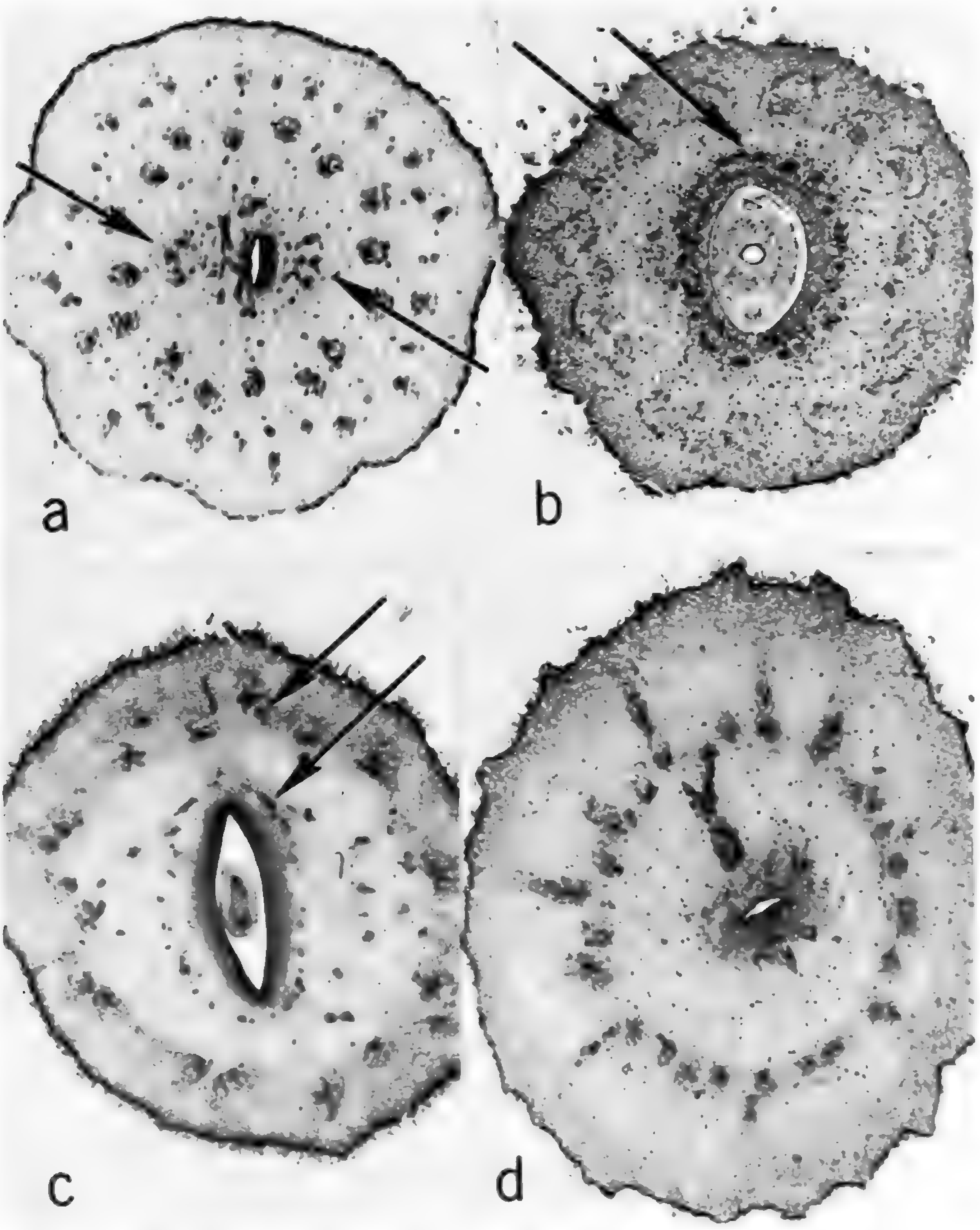

FIG. 3. Gynoecia of *Alangium* in cross section. a. *A. javanicum* (same flower as in FIG. 2, d), placental region; all bundles of inner series except those in the 2 dorsal complexes (arrows) converge on the placenta; × 17. b. *A. salviifolium*, cult., Bogor, *XVII.C.136*, US; there are only 2 series of vascular bundles (arrows); × 18. c, *A. longiflorum*, *B. Hernaez 635*, US; arrows indicate 2 series of bundles; × 17. d. *A. salviifolium*, *Govindarajalu 6840.A*, US; section comparable to that in FIG. 3, a, showing transverse path of one dorsal complex toward base of style (see also FIG. 6, b); × 19.

carpellary midvein is absent from the ovary wall. The position where a single dorsal bundle would be expected is occupied by a group of three or more fine, anastomosing strands, and on the other side of the ovary from this group is a second cluster of fine bundles (FIGS. 2, d; 3, a). Although these two groups of bundles can be considered a part of the inner series, they tend to lie a little to the outside of other members of the series. Followed distally, the members of each dorsal group merge, forming a pair of well defined stylar bundles (FIG. 4, a). The two stylar bundles bifurcate a short distance above the base of the style, and profuse ramification of the resulting four branches supplies the stigma.

Section ALANGIUM has a similarly complex dorsal supply, but the component strands separate from the outer series at a higher level, passing transversely across the upper part of the ovary to enter the style (FIG. 4, b). Also, the stylar bundles bifurcate closer to the stigmatic region than they do in section CONOSTIGMA.

Ovules receive a similar vascular supply in both of these sections. The entire inner series except the dorsals converges at the placenta (FIG. 3, a), uniting in an ovular bundle that passes down one side of the ovule and up the other.

Floral vasculature of section MARLEA and section RHYTIDANDRA differs from that in the foregoing sections primarily in the fewer gynoecial bundles. The inner series in section MARLEA usually contains, in addition to the two dorsals, only two pairs of gynoecial bundles, one pair at each

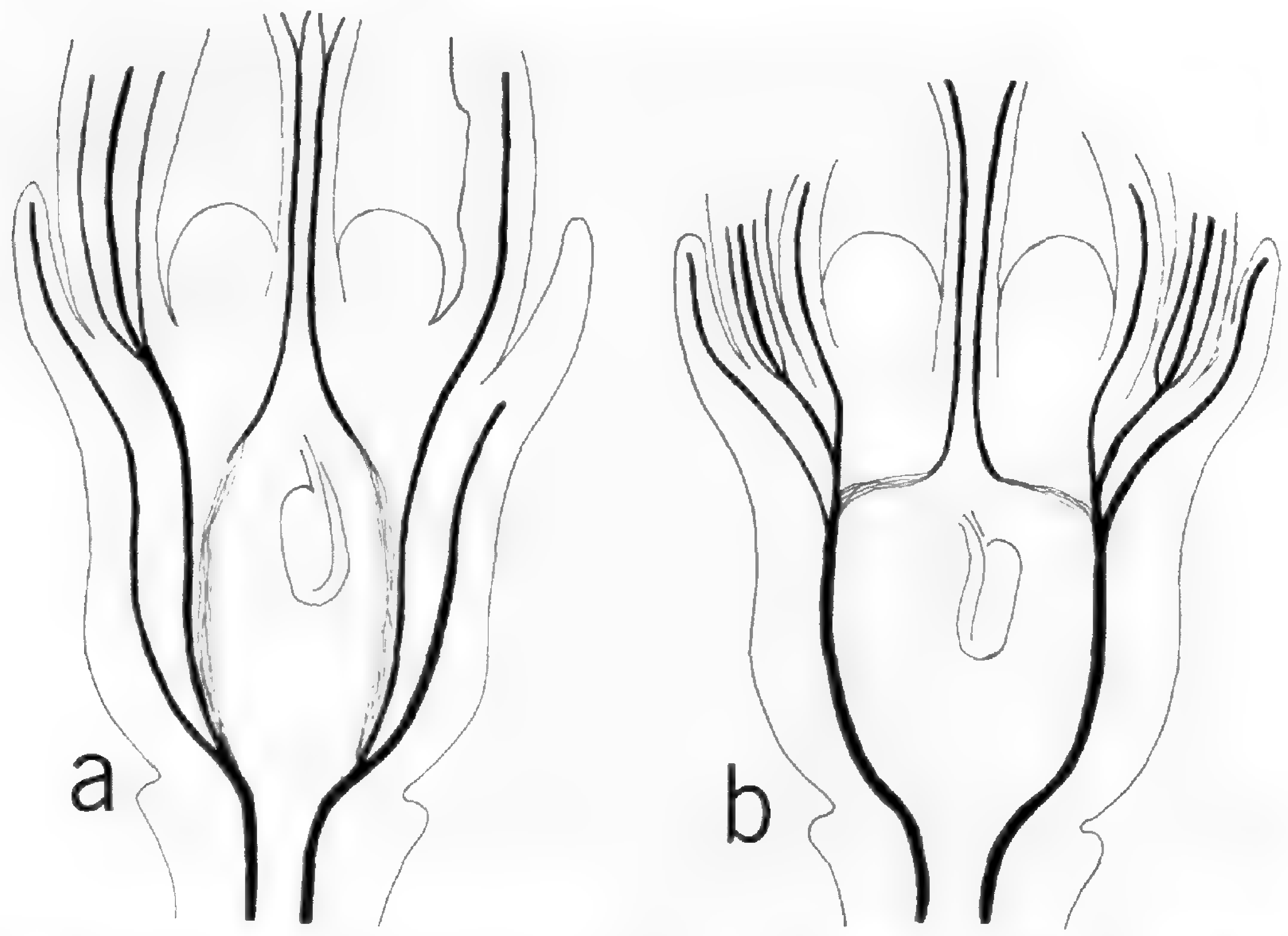

FIG. 4. Dorsal vasculature in section CONOSTIGMA (a, based on *Alangium ridleyi*) and section ALANGIUM (b, based on *A. longiflorum*). Diagrams represent longitudinal sections cut so as to include both dorsal carpel bundles. For part of their length the dorsals are made up of fine anastomosing strands.

side of the ovarian septum (FIG. 2, b). The paired structure is less evident in some cross sections than others because the two strands of each pair branch and anastomose somewhat; cross sections through the upper part of the ovary are best for showing distinct pairs (Eyde, 1968, *Fig. 13*). I refer to these pairs as ventral bundles, since that term has been used for similarly situated pairs in *Cornus* (Wilkinson, 1944) and *Nyssa* (Eyde, 1963); however, as I have stated in earlier papers, the homology of these bundles to the centrally or marginally located ventrals of other families is uncertain. Paired bundles supplying the ovule or ovules diverge from both sets of ventrals and pass transversely through the summit of the ovary. An unusual feature, never observed in *Cornus* or *Nyssa*, is the occurrence of additional transverse (or oblique) bundles lower in the ovarian septum (FIGS. 5, a; 8, r). These branch at intervals from the ventrals and end blindly in the septum, perhaps indicating the former location of ovules eliminated in the course of evolution. The ventrals in some flowers end abruptly where the ovular strands diverge; in other flowers they end in the base of the style.

A single outer series of prominent bundles supplies the calyx, corolla, and androecium in section MARLEA, as in section ALANGIUM, but in section MARLEA the dorsal bundles (FIG. 5, a, b) are free for most of their length. Furthermore, the dorsal supply in section MARLEA usually consists of single bundles,[2] unlike the dorsal complexes of sections CONOSTIGMA and ALANGIUM. The two dorsals pass through the style and divide into four strands a little below the stigma.

Dorsal bundles of section RHYTIDANDRA are also discrete, but they are united with the outer bundles to a greater degree than in section MARLEA (also, because there is only one locule, the ventral bundles lie more to one side of the ovary). One of the dorsals diverges a little below the insertion of stamens and petals; the other, always the midvein of the "lost" carpel, is independent for about half the length of the ovary (indicated diagrammatically in FIG. 9). Both dorsals pass into the stylar column as discrete bundles, but they divide below the separation of the two styles; thus the free portions of the styles each receive two bundles.

Petals of *Alangium* species contain three to seven parallel vascular strands that merge basally in the region of insertion. The most common number is five. Where petals are thick (section CONOSTIGMA), additional small strands are often located internal to the others. These are "inverted" bundles, oriented with their xylem toward that of the principal petal bundles. Stamens of *Alangium* species commonly contain only one bundle, but two slender lateral strands flank the principal bundle in *A. ridleyi.*

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[2] Both of my collections of *A. platanifolium* (sect. MARLEA) have fairly discrete dorsal bundles rising through the ovary wall and continuing into the style. But in Horne's (1914, p. 266, 267) material of this species, several small strands form the basal part of the dorsals. This anomaly confused Horne's interpretation of the gynoecial vasculature. He stated that "the so-called dorsal ribs are merely collections of small ovular strands," even though he correctly portrayed their passage into the style (see his *Text-fig. 6, G, H*). Horne worked with very young flowers, which may have contributed to the misinterpretation.

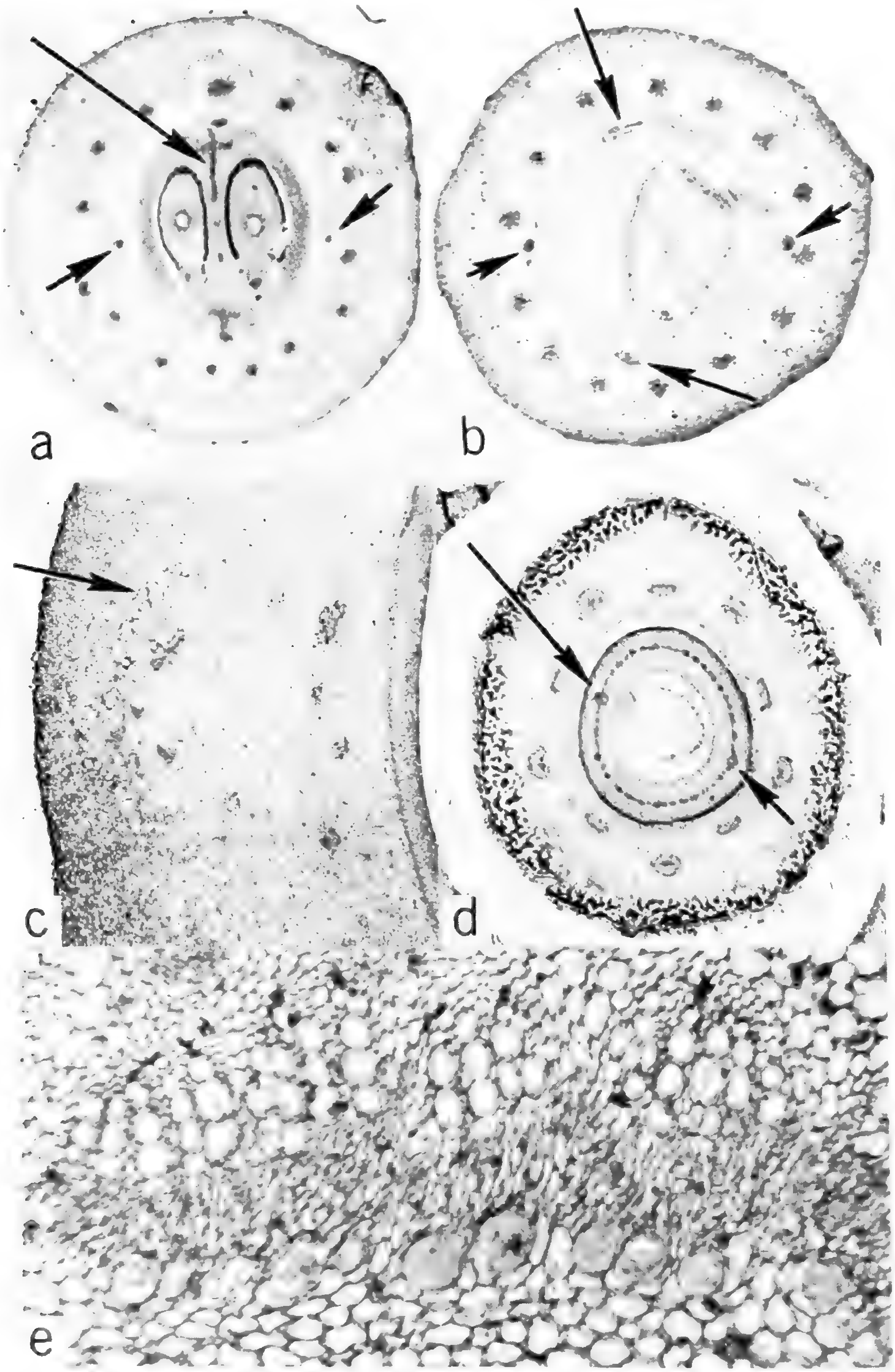

FIG. 5. a. *Alangium chinense*, Makiling Natl. Park; cross section through gynoecium showing subequal carpels, transverse bundle (long arrow) which ends blindly in septum; shorter arrows indicate dorsal bundles; × 23. b. *A. platanifolium*, cult., Tohoku; cross section through gynoecium showing 1 empty, 1 fer-

The filaments of *A. rotundifolium* and *A. chinense* also have some thin "extra" bundles.

The nectariferous disc is thoroughly vascularized in all species of *Alangium*, receiving transverse strands from the bundles that supply calyx, corolla, and androecium. Although the fine vascular ramification within the disc is usually composed of phloem only, as is the case in most dicotyledons (Frei, 1955), I have observed xylem in preparations of *A. chinense* and *A. rotundifolium*; its presence may relate to stage of development. Floral vascular bundles, especially those of the hypanthium and gynoecium, tend to be amphicribral in all species.

Secretory structures. Sertorius (1893, p. 561) recorded the occurrence of "sehr grosse Sekretzellen" in fruits of *Alangium*, and Faure (1924, *Fig. XV, 1, 7*) figured "poches sécretrices," erroneously providing them with a secretory epithelium of small cells. Schnarf's (1922, *Figs. 1, 3*) drawings of sectioned flowers portray the secretory structures accurately and indicate their proximity to a vascular bundle. None of these authors realized, however, that the structures are articulated laticifers.

The laticifers begin as longitudinal files of elongating parenchyma cells, which enlarge to a diameter several times that of adjacent parenchyma cells and eventually become vessels by the disintegration or rupture of transverse walls. They are usually arranged in an arc around the phloem of floral vascular bundles, and where phloem completely surrounds the xylem of a bundle, a ring of laticifers may surround the phloem. The laticifers do not actually differentiate within the phloem: there are usually three or more parenchyma cells between a laticifer and the nearest sieve tube. In this respect the laticifers of *Alangium* differ from the very similar structures of *Argemone mexicana* (Papaveraceae) figured by Kapoor and Sharma (1963). Laticifers can accompany vascular bundles in any part of the *Alangium* flower with the possible exception of the ovule and the style, but they terminate at the base of the flower or extend only a short distance into the pedicel.

The content of the laticifers stains darkly and usually includes the pellets (Kügelchen) that Schnarf (1922) observed. Laticifers of a maturing ovary often seem to be partially empty when examined in cross section, and the pickled material does not "bleed" when cut, as it should if the contents are under pressure (Esau, 1965, p. 323).

One would not expect laticifers to be abundant in flowers of *Alangium* and to be absent from other parts of the plant. Having at my disposal some pickled leaves of *A. chinense*, I prepared simple freehand sections

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tile locule; arrows indicate dorsal and ventral bundles; × 27. c, *A. longiflorum*, *B. Hernaez 635*, US; cross section of fruit wall showing thin endocarp (right) and empty laticifers (arrow); × 11. d, *Metteniusa nucifera*, *Steyermark, Wurdack & Prance 95863*, NY; cross section of floral tube and gynoecium; arrows indicate dorsal (short) and ventral (long) bundles; × 18. e, *A. chinense*. Makiling Natl. Park; cross section of petiole showing medullary vascular tissue and accompanying laticifers (bottom); × 150.

FIG. 6. a. *Alangium javanicum*, *P. P. Sam, s.n.*, inferior part of flower; laticifers in longitudinal section; × 75. b. *A. javanicum*, cult., Bogor, *VIII.F.25*; fruit;

of a petiole and found laticifers in abundance around the major vascular bundles (FIG. 5, e). It is probable that other anatomists have overlooked the secretory structures in leaves because they were working with dried material. Govindarajalu had living material of *A. salviifolium*, but I have observed that laticifers are inconspicuous or absent in flowers of this species; perhaps they are equally difficult to detect in other parts of the plant.

Latex vessels are plentiful in fruits of section ALANGIUM, although they are hard to find in the flowers. In section MARLEA and in section RHYTIDANDRA, however, laticifers are conspicuous at all stages of flower and fruit. Their arrangement in cross sections creates an attractive "scalloped" effect (FIG. 5, a), which Clarke (1850) showed in his *Fig. 8* and *9*, even though he did not understand the reason for it. Laticifers of sections MARLEA and RHYTIDANDRA expand with the growth of the fruit so that they appear as tangentially elongate cavities in cross sections through the mature fruit wall. Section CONOSTIGMA is peculiar in that the floral laticifers seem to disappear as the fruits develop. My longitudinally sectioned flowers of *A. javanicum* show many latex vessels of large diameter (FIG. 6, a), some of them branching and perhaps anastomosing with neighboring vessels. Fruits of this species, although they contain densely-staining tanniniferous cells in great numbers (FIG. 6, b), have no laticifers. Some of the tannin cells are aligned in such a way as to suggest that they have been derived from laticifers through a secondary development of cross walls; i.e., through the reversion of coenocytic laticifers to a cellular condition. I offer this inference cautiously because my flowers and fruits are from different sources. Moreover, I do not know that anyone has ever documented a reappearance of the cellular condition in laticifers.

Endocarp. Fruits of most species contain a thick, woody stone, but the innermost tissue of fruits belonging to section ALANGIUM is thin, leathery, and easily opened with an ordinary razor blade. It is difficult to separate the intact endocarp from outer tissues of such fruits, and when this has been done (by boiling in 5 percent NaOH) the endocarp collapses readily (FIG. 7, f). The endocarp of *A. longiflorum* is so little lignified that satisfactory sections can be prepared by the paraffin method (FIG. 5, c).

The stones of section CONOSTIGMA (FIG. 7, a–e; see also Harms, 1906, *Fig. 16*) are more massive than those of other sections; they are further distinguished by the many fine longitudinal ridges on their surfaces. The ridges may be very faint or fairly conspicuous, straight or undulating. They undoubtedly arise in association with the many fine vascular bundles of the gynoecial series. This can be verified by examining the apex of the

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tangential section showing vascular bundles and adjacent tissue. Absence of laticifers may be caused by reversion from coenocytic to cellular condition (see text); × 54. c, *Mastixia* cf. *pentandra, Kostermans & Soegeng 920*, US; cross section through wall of young fruit showing two secretory canals with epithelial cells; × 210.

stone, where the bundles converge and pass into the endocarp. No matter how carefully the stone is cleaned, remnants of vascular tissue adhere to the apical end.

Serial sections show that the fleshy outer tissue of the fruit wall in section

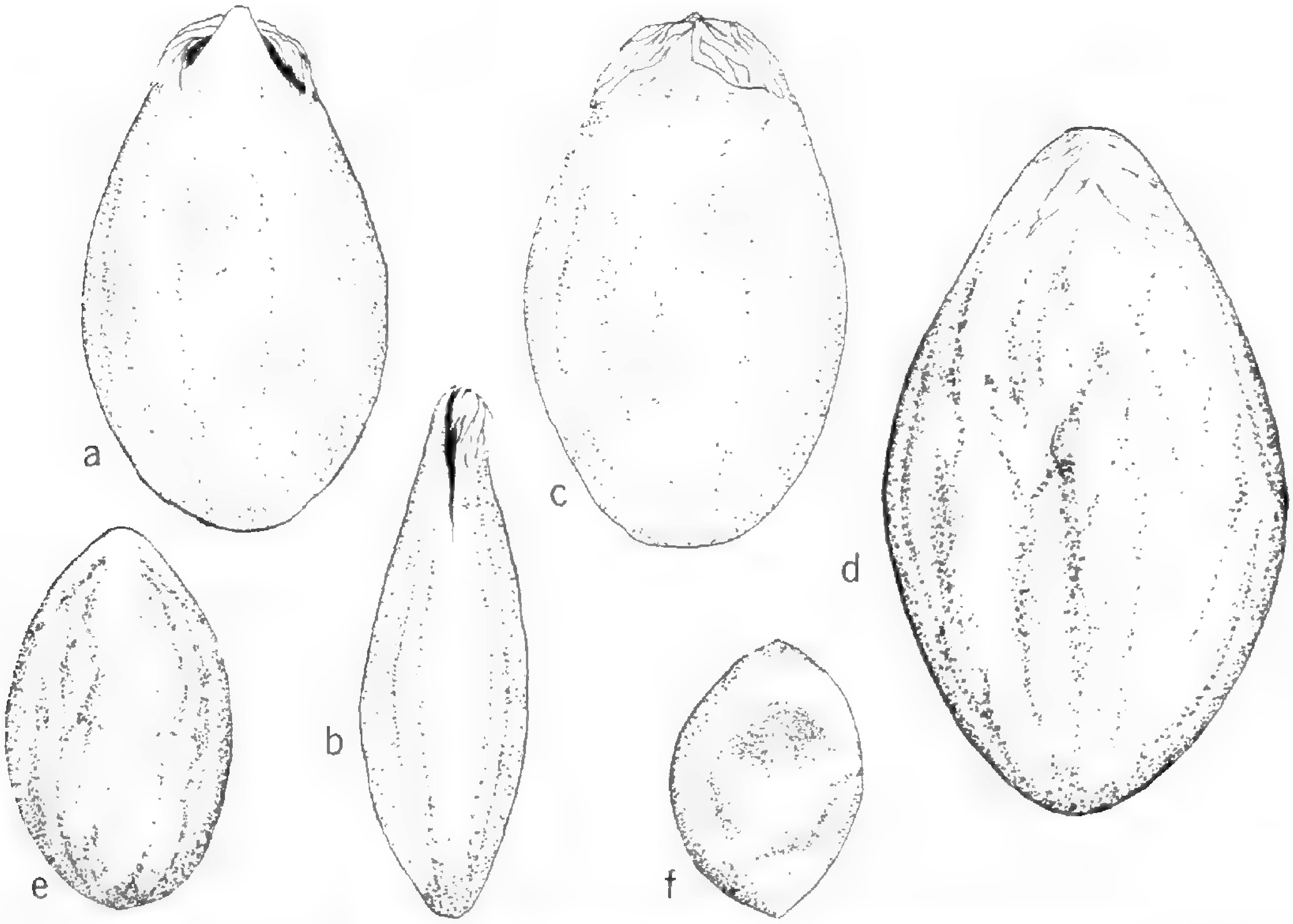

FIG. 7. Stones of section CONOSTIGMA (a–e) and section ALANGIUM (f). a–c, *Alangium javanicum*, cult., Bogor, *VIII.F.25*, US; 3 views of 1 stone. d, *A. ridleyi*, cult., Bogor, *VIII.H.14*, US. e, *A. grisolleoides*, *Service Forestier 20056-SF*, P. f, *A. salviifolium*, *Mrs. D. J. Collins 1521*, US. All, × 2.

CONOSTIGMA has a broad zone of radially elongate cells immediately peripheral to the stone. In all of my specimens this zone contains large irregular cavities, apparently resulting from tearing of the cells as the fruit wall expands.

Fruits of section MARLEA are often two-carpellate, and stones from different species can be arranged in a sequence to show the gradual loss of one of the carpels. *A. kurzii* (FIG. 8, a–c) commonly has two nearly equal locules in its fruit; therefore, a plane through the septum of the endocarp divides it into roughly identical halves. In *A. chinense* (FIG. 8, p, q), one half is smaller than the other, but both locules can be fertile notwithstanding. Gynoecial asymmetry is more pronounced in *A. platanifolium* (FIG. 8, n, o), *A. alpinum* (FIG. 8, g–i), and *A. rotundifolium* (FIG. 8, m). In stones of these species one of the carpels is reduced to a shield-like prominence, often with a tightly closed abortive locule. *A. griffithii* (FIG. 8, s–u) completes the series; its stones bear no trace of a second carpel. In *A. barbatum* (FIG. 8, d–f, j–l) different collections show marked differences in the degree of reduction of the second carpel.

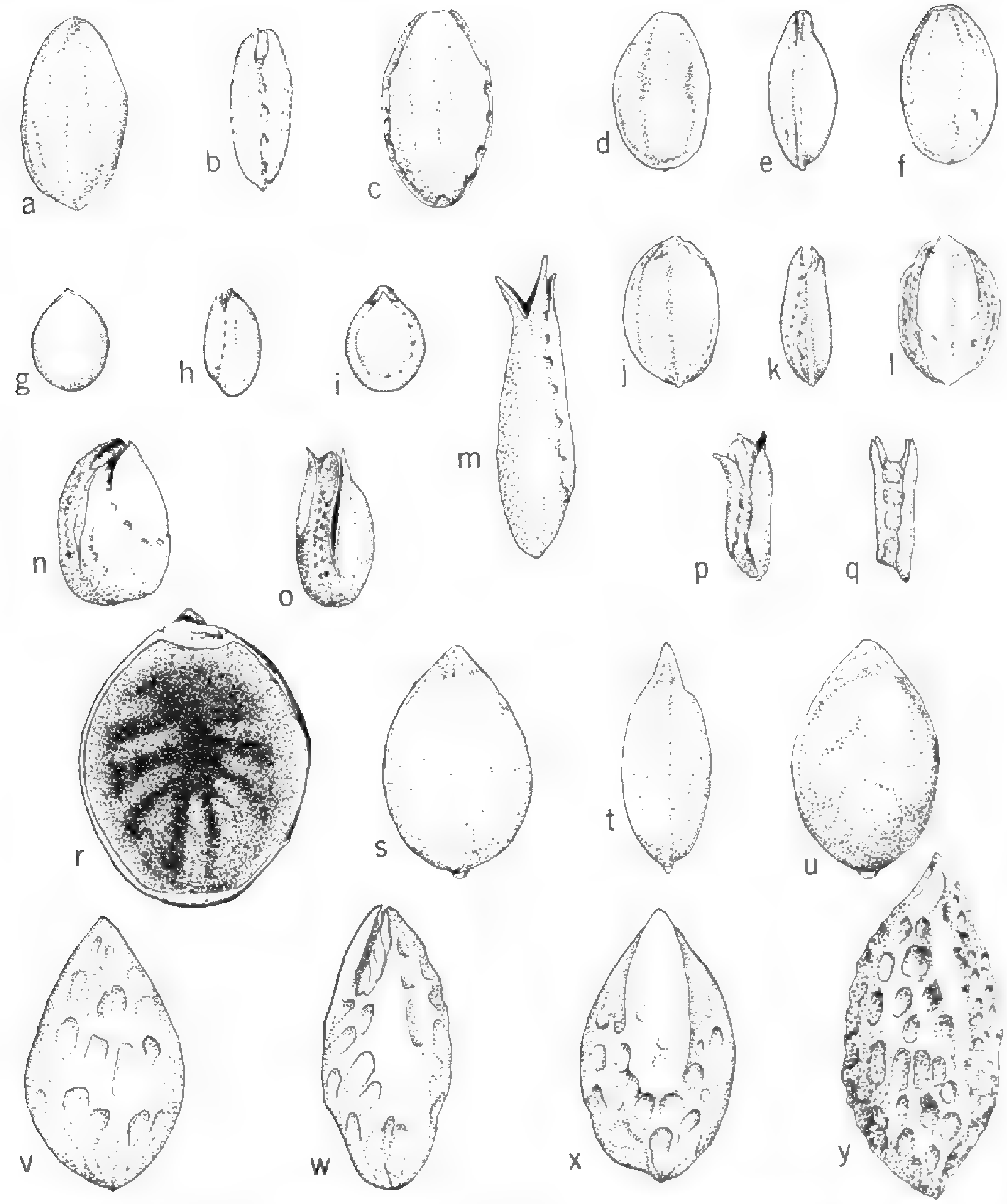

Fig. 8. Stones of section MARLEA (a–u) and section RHYTIDANDRA (v–y). a–c, *Alangium kurzii, J. & M. S. Clemens 3740,* US; 3 stones shown in different views. d–f, *A. barbatum, C. S. Fan & Y. Y. Li 315,* A; 3 views of 1 stone; note subequal 2-carpellate structure. g–i, *A. alpinum, G. Forrest 27290,* US; 3 views of 1 stone. j–l, *A. barbatum, J. & M. S. Clemens 4200,* US; 3 views of one stone; 1 carpel much smaller than other (cf. d–f). m, *A. rotundifolium, Koorders 25821B.* A. n, *A. platanifolium, E. H. Wilson 142,* US; ventral vascular bundles adhere to lateral surface. o, *A. platanifolium, E. H. Wilson 3272,* US; repeated boiling and drying caused longitudinal opening into fertile locule, probably indicating method of germination. p–q, *A. chinense, C. Y. Chiao, s.n. (Herb. Univ. Nanking 14620),* US; 2 stones in side view; softer apical tissue of q has been removed by repeated boiling and abrasion. r, *A. platanifolium,* same specimen as o with part of stone split away by forcible enlargement of opening, rotated to show concave ventral wall of locule; ridges appear where vascular bundles pass into septum. s–u, *A. griffithii, Kepong Field No. 79003,* US. v–y, *A. villosum* subsp. *vitiense.* v–x, *A. C. Smith 7409,* US; 3 views of 1 stone showing large pits in surface, abortive second carpel. y, *A. C. Smith 5249,* US; orientation is intermediate between that of w and that of x; note absence of second carpel. All × 2 except r, × 4.

From its shape and lack of sculpturing the stone of *A. griffithii* might at first glance be confused with stones belonging to section CONOSTIGMA. Stones of the other species of section MARLEA are unmistakable. They are slightly ridged longitudinally and deeply pitted in the region between the two carpels. When one of the carpels is much smaller than the other, the pitting is confined to the side with the rudimentary carpel. Most of the pits occur where vascular bundles pass into the septum from the ventral carpellary bundles. Breaking open the fertile locule longitudinally to show the septum in face view exposes a radial pattern formed by these bundles (FIG. 8, r).

Stones of section RHYTIDANDRA (FIG. 8, v–y) also have a rudimentary second carpel in most cases, but they are easily distinguished from stones of section MARLEA by their larger size, more inflated appearance, and more profuse pitting. Pits are larger than those of section MARLEA, and they

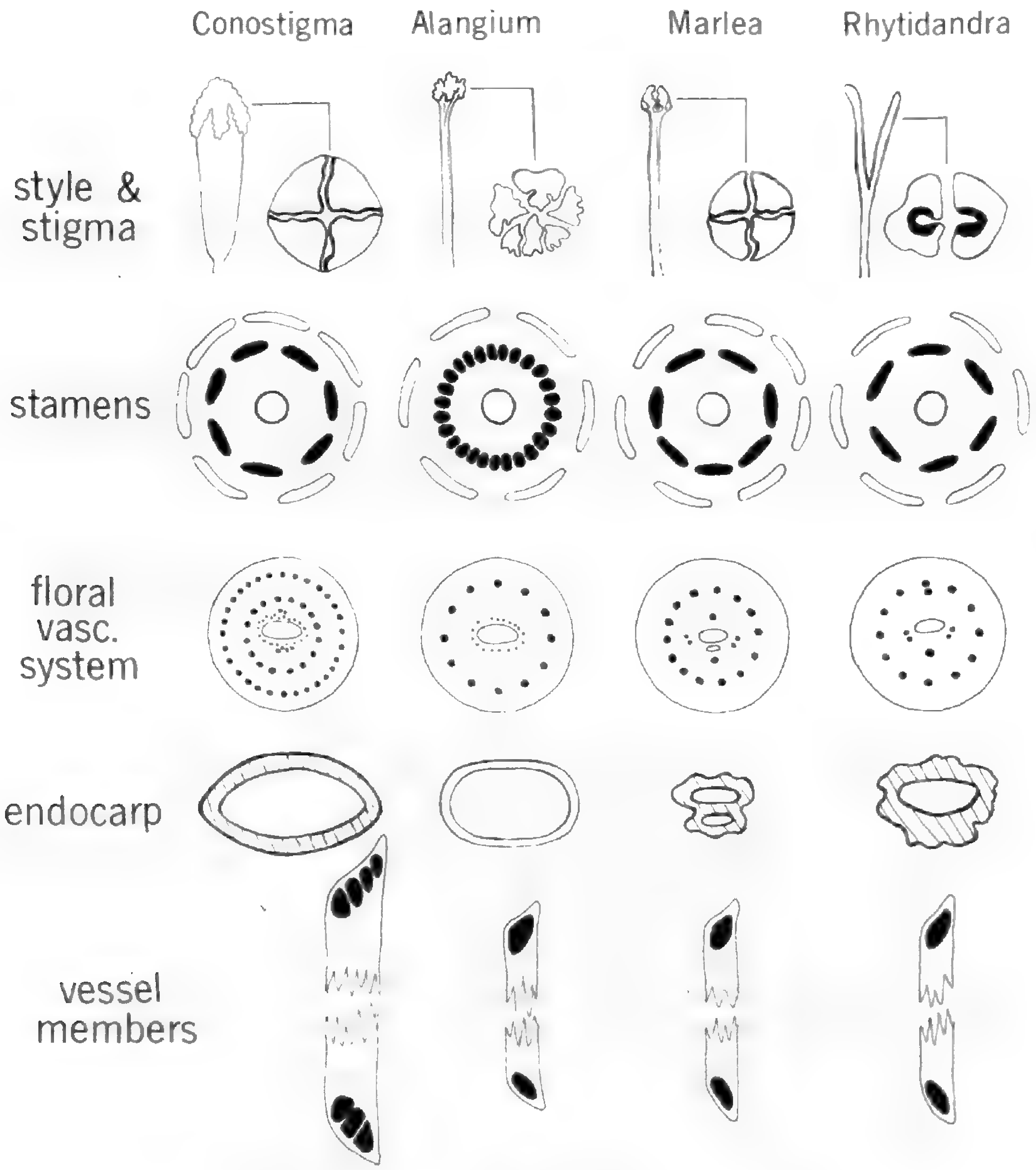

FIG. 9. Some sectional differences in *Alangium*.

cover almost the entire surface of the stone. Most of them are not associated with vascular bundles, and I have no ontogenetic explanation for their presence.

Histologically, the stones of all *Alangium* species are very much alike. Macerations show the component sclereids to be more or less equidimensional and irregularly lobed like the pieces of a jig-saw puzzle. To judge from the position of the cracks (FIG. 7, a, b; FIG. 8, m, o) that appear in repeatedly boiled and dried specimens, all of the stones open in the same manner at germination.

DISCUSSION, CONCLUSIONS

Evolutionary trends within the Alangiaceae. FIGURE 9 summarizes five structural features to which I attach evolutionary importance. The first four rows of the diagram represent sectional differences[3] described in this article. The bottom row, based on observations of other workers (Metcalfe & Chalk, 1950; Govindarajalu, 1961), shows two distinctive features in the secondary xylem of section CONOSTIGMA: the vessel members have scalariform perforation plates, and they are about twice as large as the vessel members in other sections.

Pollen provides still another set of characters. The information in TABLE 1, taken from Erdtman (1952) and Cookson (1957, *A. javanicum* only), reveals sectional differences in the number of pores, in the presence and distinctness of colpi (furrows), and in surface markings.

TABLE 1. **Sectional differences in the pollen characters of Alangium.**[a]

CONOSTIGMA	ALANGIUM	MARLEA	RHYTIDANDRA
(2 –) 3 (–4)-colporate or colpoidorate; small-meshed surface pattern	3–5-porate; warts on surface	3(–4)-colporate or colpoidorate; surface granular, reticulate, or striate	4(–5)-colpoidorate; warts on surface

[a] Adapted from descriptions by Erdtman (1952) and Cookson (1957).

FIGURE 10 is an evolutionary diagram that will account for the sectional differences. I visualize members of the ancestral group as having pluricarpellate gynoecia, isomerous androecia, separate bundles to all floral appendages, vessels with scalariform perforations, 3-colporate pollen grains, and multiple styles. Arrows indicate the direction of structural changes, and the size of the lobes roughly indicates the relative number of species in each section.

I assume a direct derivation of section ALANGIUM from section CONOSTIGMA in order to account for the strong similarities between the two and

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[3] Cytological studies should be undertaken to determine whether each section has its own chromosome number. I know of only two counts for Alangiaceae: $n = 8$ in *A. lamarckii* (= *A. salviifolium*; Gopinath, 1945) and $2n = 22$ in "*A. begonifolium*" (one or another species of section MARLEA; Wanscher, 1933).

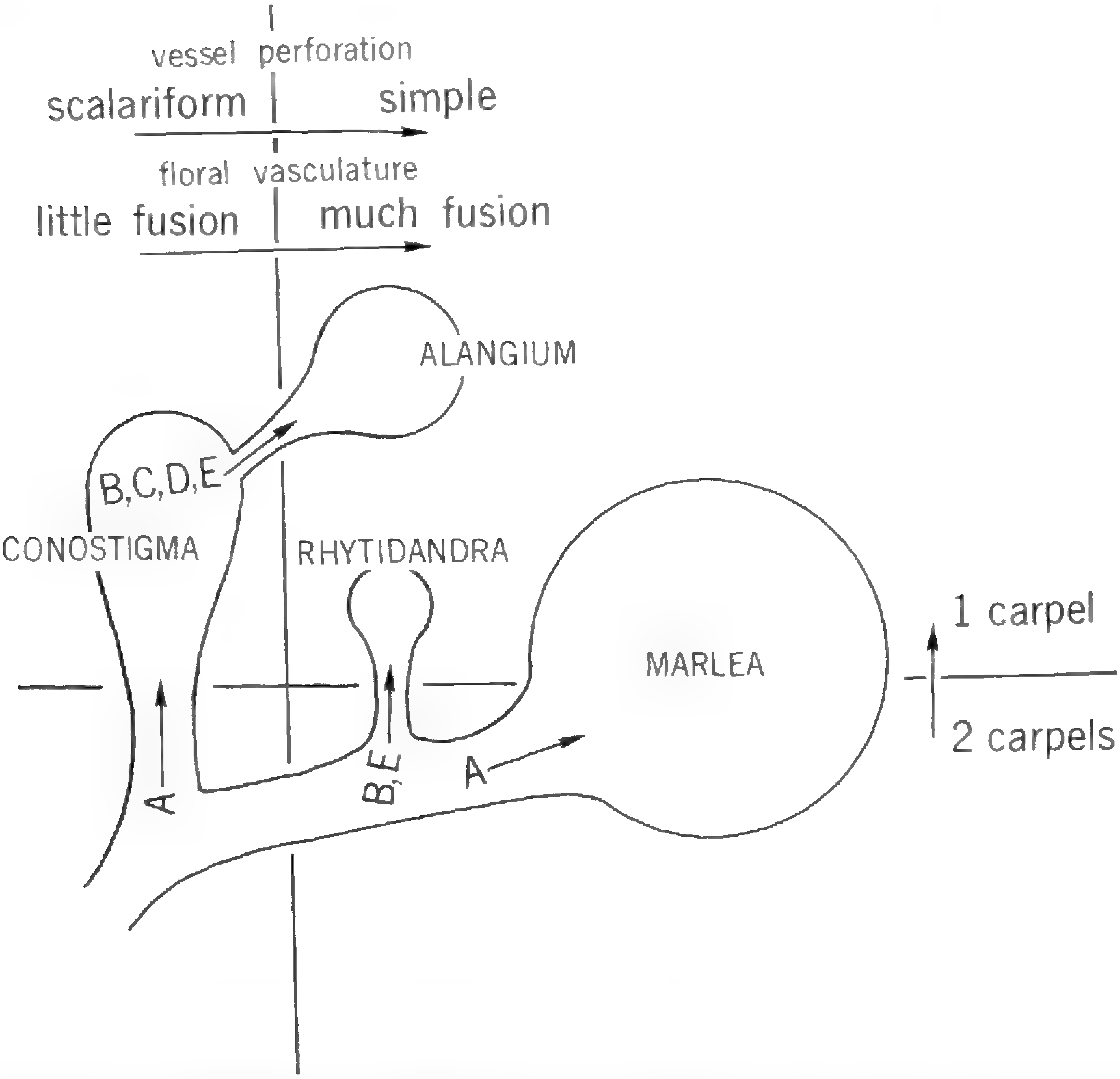

FIG. 10. Evolutionary relationships in *Alangium*. Area of each lobe roughly indicates the relative number of species in the corresponding subgeneric section. Arrows indicate directions of structural change: A, union of styles; B, fusion of dorsal carpel bundles with peripheral bundles (see FIG. 4); C, loss of woody endocarp; D, increase in number of stamens; E, increase in number of pores in pollen. Plants of the hypothetical ancestral group are thought to have had multiple carpels and styles; vessels with scalariform perforation plates; independent bundles to sepals, petals, stamens; isomerous androecium; 3-colporate pollen.

for the concentration of primitive characters in section CONOSTIGMA. Sections RHYTIDANDRA and MARLEA also have many characters in common; I explain this by assuming a close common ancestry. A direct derivation of either one from the other would be unconvincing, because section RHYTIDANDRA retains the more primitive stylar characters while some species of section MARLEA retain the more primitive two-locular condition.

This kind of diagram is necessarily speculative, but I have tried to adhere to the most conservative and widely followed concepts of evolutionary morphology. The derivation of simple perforations from scalariform perforations is universally accepted by wood anatomists, and the gradual union of floral structures (in this case, styles and vascular bundles) is another trend generally recognized as irreversible (Stebbins, 1967, p. 135). That the two-carpellate gynoecium preceded the one-carpellate (pseudomonomerous) gynoecium is unlikely to be challenged because all degrees of reduction can still be seen in section MARLEA: it would be difficult to interpret this evolutionary series in the opposite direction without assigning some selective value to the abortive carpels in intermediate forms. My view of evolutionary changes in the pollen is based on the fact that grains of the 3-colporate type occur very early in the fossil record of angiosperms and are retained in many of the less specialized groups of dicotyledons. From this I infer that 3-colporate pollen grains of *Alangium* are more primitive than pollen with four or five pores and with colpi poorly developed (the colpoidorate condition) or absent.

Erdtman (1954, p. 79) has hinted that *Alangium* might be made into two genera on the basis of pollen characters. From his earlier remarks (1952, p. 40), I gather that he would separate the species with porate grains from those with colporate grains, thus requiring the recognition of section ALANGIUM as one genus and the three remaining sections as another (a reinstatement of *Marlea* Roxb.).[4] However, this is not the only arrangement that could be made if only pollen characters were considered: section ALANGIUM, lacking colpi, could be allied with section RHYTIDANDRA, in which colpi are poorly developed, for these two sections share the warty surface pattern. However, to adopt either of these arrangements would be to ignore all of the other characters discussed in this paper. It seems, therefore, that the same changes — development of a warty exine, increase in the number of pores — have occurred in separate evolutionary lines within the Alangiaceae. If it were necessary to divide *Alangium* into two genera — and I do not see that anything would be gained by doing so — a consideration of all characters would require that section CONOSTIGMA and section ALANGIUM be put in one genus, section MARLEA and section RHYTIDANDRA in the other.

The association of many stamens with advanced characters in section ALANGIUM will seem unusual to some floral morphologists, for we tend to look for oligomerization of all whorls, including the androecium (Takhtajan, 1959, p. 76; 1964, p. 69). Indeed, the traditional view that evolution favors a change from polystemony to oligostemony was codified a half century ago as Bessey's (1915) 24th dictum. Recently, however, Stebbins (1967, p. 121–123) listed several taxa for which considerations of comparative morphology indicate the opposite trend. The most compelling evidence for adding Alangiaceae to this list is in the vascular supply to the stamens. If flowers with many stamens were primitive, each stamen would have a corresponding vascular strand in the extracarpellary portion of the ovary wall, as is the case in section CONOSTIGMA. But section ALANGIUM has far fewer bundles in the inferior part of the flower than section CONO-

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[4] Yeramian (1967), in a publication that reached me after my manuscript had gone to the editor, explicitly separates the pollen of *Alangium* into two main types, "zonocolporate" and "panporate," corresponding to "subgenus Marlea" and "subgenus Alangium," respectively. Apparently, Mrs. Yeramian did not consult Bloembergen's monograph before writing her paper.

STIGMA, and the extracarpellary strands are arranged in a single series, each bundle supplying several stamens. Also, the stamens of all *Alangium* species are in a single whorl. This is a clue that *Alangium* is a special case, since taxa in which gradual oligomerization of the androecium has occurred often retain transitional stages in the loss of whorls.

Systematic position of A. grisolleoides. By a happy coincidence, Monsieur R. Capuron was working at the herbarium of the Muséum National d'Histoire Naturelle, Paris, when I visited there in 1964, and he kindly gave me a few flowers and fruits from his collections of *A. grisolleoides*. This Madagascan rarity, discovered only a few years ago,[5] is clearly a member of section CONOSTIGMA, as Capuron (1962) surmised. Although its floral trichomes do not occur in the stellate-peltate pattern, it has the Conostigma type of endocarp (FIG. 7, e) and the characteristic papillose epidermis on anthers and style. It is the only dioecious species of *Alangium*.[6] I did not get good serial sections from the flowers (all staminate) that Monsieur Capuron gave me, but the preparations were adequate to show a tiny empty locule in the rudimentary ovary. It is noteworthy that this species, with its reduced number of floral appendages, has evolved in the same group that gave rise to the polystemonous section ALANGIUM.

Place of Alangiaceae in the general system. Some of our most influential systematic works place Alangiaceae near Cornaceae (Němejc, 1956; Hutchinson, 1959, 1967; Melchior, 1964; Takhtajan, 1966; Soó, 1967). This concept has a long history (Harms, 1897, and Horne, 1914, review the early opinions), and it has been the prevailing one among those who have worked with the two families. I began my own investigation of Alangiaceae with the belief that *Alangium* is related to *Cornus*, as suggested by embryological studies (Chopra & Kaur, 1965), and to *Nyssa*, as suggested by similarities in the general appearance of the plants[7] and their pollen grains (Erdtman, 1952). I expected to find an even closer resemblance between *Alangium* and *Mastixia*, the only cornaceous genus with secretory canals. In fact, however, the secretory structures of *Mastixia* are true resin canals with secretory epithelia (FIG. 6, c), not at all like the laticifers of *Alangium*. Furthermore, I have come to realize, con-

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[5] The discovery extended the range for section CONOSTIGMA well beyond the area mapped by Bloembergen (1939, *Fig. 8*). The known range for section ALANGIUM (Bloembergen's *Fig. 2*) has also been extended by the addition of *A. salviifolium* to the flora of tropical East Africa (Verdcourt, 1958).

[6] Bloembergen (1939, p. 195) mentions specimens of *A. griffithii* and *A. salviifolium* with sterile anthers; these may indicate a tendency toward dioecism in section MARLEA and section ALANGIUM.

[7] Species of *Alangium* can be confused with *Nyssa* in the herbarium. Thus, "*Alangium*" *shweliense* W.W. Sm. is a synonym of *Nyssa sinensis* Oliv. and "*Nyssa*" *hollrungii* Schum. is *Alangium javanicum* (Bloembergen, 1939). Nevertheless, *Alangium* does not resemble *Nyssa* — in floral characters or almost any other characters — as much as *Nyssa* resembles *Cornus*. Consequently, systems that place Alangiaceae and Nyssaceae in Myrtales while placing Cornaceae in Umbelliflorae are manifestly in error.

trary to an earlier assumption (Eyde, 1968), that the gynoecial vasculature of *Alangium* is not exactly like that of *Cornus*. The difference is that *Alangium* has extra (ovular?) bundles ending blindly in the septum. Were such bundles present in the ancestors of *Cornus*, or do they indicate an entirely different origin for the vasculature of *Alangium*? Atypical arrangement of gynoecial vascular bundles must be studied further in other plant families before a confident choice can be made between these two alternatives. It might also be informative to examine the vasculature of a three-locular *Alangium* flower like the one Clarke (1850) figured (I have never seen one). In any case, there now seem to be good reasons for doubting the close affinity of Alangiaceae to Cornaceae and Nyssaceae, and the opposing views therefore deserve careful consideration.

Several modern works link Alangiaceae with Rhizophoraceae and Combretaceae in the Myrtales (Roederer, 1930; Pulle, 1952; Novák, 1954; Vinogradov, 1959). Therefore, I sectioned some flowers of Combretaceae (*Combretum*, *Terminalia*) as a part of this investigation, but I found no structural resemblance to *Alangium*. Flowers of Combretaceae have gamopetalous corollas, biseriate androecia, and unilocular gynoecia with two or more ovules — all points of difference from *Alangium* — and there are corresponding differences in the floral vascular system. Another dissimilarity is that the ovules of Combretaceae have two integuments: there is no trace of a second integument in *Alangium*.[8] Still another is that the characteristic rudimentary stipules of the Myrtales (Weberling, 1960) are lacking in *Alangium*. Furthermore, the pollen of *Alangium* and Combretaceae are "± different" (Erdtman, 1952, p. 40) and the xylem characters are distinctly different (Janssonius, 1918, p. 707). Finally, the known alkaloids of Rhizophoraceae are quite unlike those of Alangiaceae (Hegnauer, personal communication). In short, all lines of evidence weigh heavily against the alliance of these three families.

Hallier (1905; 1912, p. 221) once considered Olacaceae the closest family to Alangiaceae, although he later (1918, p. 117) modified this opinion. H. K. Airy Shaw, in his revision of Willis' (1966) *Dictionary*, cautiously offers a similar idea. Under Alangiaceae, Shaw says "Relationships obscure; perhaps some connection with Olacaceae and Ehretiaceae." The suggestion of an affinity with Olacaceae is worthy of further investigation, because many olacaceous genera have non-articulated laticifers (Metcalfe & Chalk, 1967). However, the ventral carpellary vascular system differs from that of *Alangium* in that the bundles rise through the center of the flower (Agarwal, 1963 a, b). The floral structure of *Ehretia* (Johri & Vasil, 1956) is even less like that of *Alangium*.

Shaw adds *Metteniusa* to the Alangiaceae, a change that I do not accept. *Metteniusa* is a genus of uncertain systematic position (Icacinaceae and Olacaceae have been suggested) with epipetalous stamens and a superior

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[8] Mauritzon's (1939, p. 114) comments on *Alangium* are especially pertinent. Observations of other embryologists are reviewed by Johri (1963, p. 424) and Chopra & Kaur (1965). Hutchinson (1967, p. 41), in attributing two integuments to *Alangium*, repeats an error from his 1959 work, despite Takhtajan's (1959, p. 239) effort to correct him.

ovary. A sectioned gynoecium (FIG. 5, d), followed serially from base to style, displays the vascular system and the ventral suture of a single carpel, more like a *Prunus* gynoecium than the complex pluricarpellate or pseudomonomerous gynoecium of *Alangium*.

Recent discovery of the alkaloids emetine, cephaeline, and psychotrine in *Alangium salviifolium* indicates to Hegnauer (1965, p. 245; 1966, p. 219) that the Alangiaceae may be related to the Rubiaceae, the only other family in which these substances are known to occur. Alkaloids are not perfect taxonomic indicators, to be sure, but the suggestion is supported by *Alangium*-like characters in certain rubiaceous flowers. There are rubiaceous taxa (*Oxyanthus natalensis*, *Gardenia resinifera*, *Mussaenda* sp.) in which all or part of the ovular supply passes through the septum. *Guettarda speciosa*, like certain species of *Alangium*, has a great many gynoecial bundles around its locules. Furthermore, a vascularized disc is of common occurrence in the Rubiaceae. (Details of floral vasculature are taken from Rao, Ramarethinam, & Iyer, 1964.) Most Rubiaceae are sympetalous, with epipetalous stamens, but in *Synaptantha* free stamens accompany a corolla that is divided almost to its base. Among the many poorly known genera of this large family may be others that are even more like *Alangium* than those I have mentioned.

In conclusion, therefore, I urge other workers to look into the Rubiaceae for the closest allies of Alangiaceae. It is conceivable, as Hegnauer (1965) suggested, that *Alangium* is related both to the Rubiaceae and to the Cornales (sensu Takhtajan, 1966), forming a link between the two groups; however, I do not share that opinion at present.

SUMMARY

Principal observations and conclusions resulting from an anatomical study of flowers and fruits of *Alangium* (the only genus of Alangiaceae) can be summarized as follows:

1. The secretory structures of *Alangium* are non-articulated laticifers.
2. Marked differences in the number of gynoecial vascular bundles separate Bloembergen's section CONOSTIGMA and section ALANGIUM from section MARLEA and section RHYTIDANDRA. In addition, section CONOSTIGMA differs from section ALANGIUM and section MARLEA from section RHYTIDANDRA in the degree to which gynoecial bundles are united with other bundles of the flower.
3. Characters of the endocarp further substantiate Bloembergen's concept of four subgeneric sections. Surface features of the woody stone can be used to separate three of the sections, and the fourth (section ALANGIUM) is distinguished by its poorly lignified endocarp.
4. In section ALANGIUM stamens are much more numerous than petals, but their number is variable and not an exact multiple of the petal number as earlier treatments would lead one to believe. Polystemony is probably an advanced condition in *Alangium*, because it is associated with a reduced gynoecium, an advanced floral vascular system, and advanced characters of the pollen and wood.

5. The prevailing opinion that the Alangiaceae belong to the Cornales is not well supported by anatomical characters of the flower. However, all indications weigh heavily against a close affinity to Combretaceae or Rhizophoraceae, and present evidence is insufficient to prove a relationship with Olacaceae. Similarity in alkaloid content and in certain details of floral structure suggest that the closest allies of Alangiaceae may be found in the Rubiaceae.

ACKNOWLEDGMENTS

For Indonesian specimens of *Alangium,* I thank Professor C.G.G.J. van Steenis, Leiden, Dr. A. Kostermans and Dr. W. Soegeng Reksodihardjo, Bogor; for Philippine specimens, Mr. M. Q. Lagrimas and Mr. M. Monsalud, University of the Philippines, and Professor W. L. Stern, University of Maryland. Professor E. Govindarajalu, Madras, and the late Professor P. Maheshwari sent the Indian material. Other collections of *Alangium* came from Dr. W. Meijer, Sandakan, Malaysia, Mr. L. S. V. Murthy, Kuching, Sarawak, and Dr. K. Sohma, Sendai, Japan. Dr. David Bierhorst, Cornell University, and Dr. P. B. Tomlinson, Fairchild Gardens, supplied flowers of *Terminalia* and *Combretum* for comparison with *Alangium,* and Dr. John J. Wurdack, Smithsonian Institution, gave me the specimens of *Metteniusa nucifera.* Credit is due Mrs. Xavier F. Smith for microtechnical assistance, Miss Anne Donovan for the drawings, and Victor Krantz for the photographs. My colleague Harold Robinson patiently listened to my ideas on phylogeny as they were forming and suggested several improvements in the drawings. The Smithsonian Institution provided financial support through Research Award Sg0625005.

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DIVERSE NODAL TYPES IN RHODODENDRON

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RHODODENDRON IS ONE of the largest of the angiosperm genera. In spite of obvious diversity in habit, flower form, and many other characters, there is little doubt that the group is a natural one. The only serious reservation to this view is that the three species forming the subgenus THERORHODION might be better regarded as a distinct genus (Sleumer, 1949). Proposals to subdivide the genus in recent years have been based on expediency in the face of such large numbers rather than on botanical merit (Copeland, 1943).

It might be expected, therefore, that studies of the range of form shown by various features of ***Rhododendron*** would reveal interesting examples of diversity within a coherent group. This is the first in a series of investigations into the anatomy of the genus. Here the anatomy and development of the nodes of foliage leaves and cataphylls is considered.

Previous studies by others have brought to light striking examples of such diversity. Maximowicz (1870) defined subgenera by the relationships between floral and vegetative buds. Sinclair (1937) demonstrated two well-defined types of vegetative bud, and Cowan (1950) published a detailed survey of trichome types within the genus. Kingdon-Ward (1947) makes some further suggestions, especially concerning characters of the seed. Hayes et al. (1951) thoroughly investigated the anatomy of the leaf blade and discussed its relation to the subdivisions of the genus.

In 1914 Sinnott demonstrated that three types of node occurred in dicotyledons, and that in many families one type only was found to be present. He also noted several families in which more than one type of node was present, and further examples have been recorded, e.g. Icacinaceae (Bailey & Howard, 1941), Epacridaceae (Dormer, 1945; Watson, 1967), Monimiaceae (Money, Bailey & Swamy, 1950), Escalloniaceae (Swamy, 1954). These findings did not seriously affect the importance of the node in classification, because different nodal types usually were found to correspond to major subdivisions within a family.

The need for comparisons to be made between appendages of similar age was brought out by Swamy (1949), working with *Degeneria*, who found that the complexity of the node might increase as successive leaves formed in the seedling. Canright (1955) found a similar ontogenetic sequence in members of the Magnoliaceae. Bailey (1956) also compared the nodes of seedlings and mature shoots and found that while sequences from the unilacunar to the tri- or multilacunar condition were frequent the reverse transition was not observed. This limitation is generally of little significance when the foliage of mature woody plants is being compared, though the work of Kato (1966, 1967) shows that variation may occur between successive nodes of some genera. Work by Müller (1944), Philipson (1948), and Post (1958) also demonstrated the need for considerable caution in comparing nodal types in herbaceous plants. For example, in *Helleborus foetidus* L., Müller found mature foliage leaves to possess seven to eleven traces, but this number diminished in higher leaves until bracts with a single trace were reached. Post found uni-, tri-, and multilacunar nodes in the genus *Frasera*, with reduction series up the appendages of the flowering stem. In the related *Swertia perennis* L. the multilacunar nodes diminished in complexity upwards, and also downwards in the basal cataphylls.

Records of different nodal types within one genus of woody plants are few. Pellegrin (1908) records tri- and unilacunar nodes in *Genista*, and Saha (1952) tri-, bi-, and unilacunar nodes in *Citrus*. The Araliaceous genus *Pseudopanax*, with most species multilacunar, has at least one trilacunar species (Philipson, 1965) and the South American members of *Griselinia* are trilacunar whereas the New Zealand species are pentalacunar (Philipson, 1967).

The occurrence of the five types of node here described in the mature foliage of a genus of woody plants is therefore of interest. Their relationship with other characters which have been used in the classification of the genus is discussed in the last section of this paper.

SCOPE AND METHODS

This investigation is concerned principally with the pattern of the vascular supply to mature foliage leaves. The node and petiole have been examined in 264 species, as listed in the last column of the APPENDIX. These were selected from all the subdivisions of the genus recognized in Sleumer's "Ein System der Gattung *Rhododendron*, L." (1949), as modified by him (Sleumer, 1958 and 1964), as well as from all the series and subseries recognized in the *Rhododendron Handbook*, Part I (Synge, 1963).[1] Subsidiary observations relate to the development of these patterns during the growth of the primordium and also to the acquisition of the mature pattern in successive leaves of seedlings. The nodal patterns of other lateral appendages (cotyledons, bud scales, and perulae) have also been examined.

A series of hand sections at right angles to the main axis was made to determine nodal types. For a few selected examples of each nodal type, tangential and radial series of longitudinal sections were also cut to clarify the interrelations of the traces. Petioles were sectioned, always at the base and mid-point, but often also distally. All these sections were stained in an aqueous solution of aniline sulphate and mounted in glycerine jelly.

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[1] Throughout the text the classification proposed by Sleumer has been used, but where it has been necessary to refer to smaller units the subseries of the Handbook have been employed. *Therorhodion* (Series *Camtschaticum*) was investigated as most authors have included it in *Rhododendron*. Authorities for specific names of Rhododendrons are omitted from the text but appear in the APPENDIX.

THE NODE OF THE MATURE FOLIAGE LEAF

The patterns of vascular supply to the foliage leaves fall into five types as follows:

I. Simple Unilacunar Node (Fig. 1)

The simplest type of node found consists of a single trace which departs from the stele of the axis leaving a single gap. The vascular supply

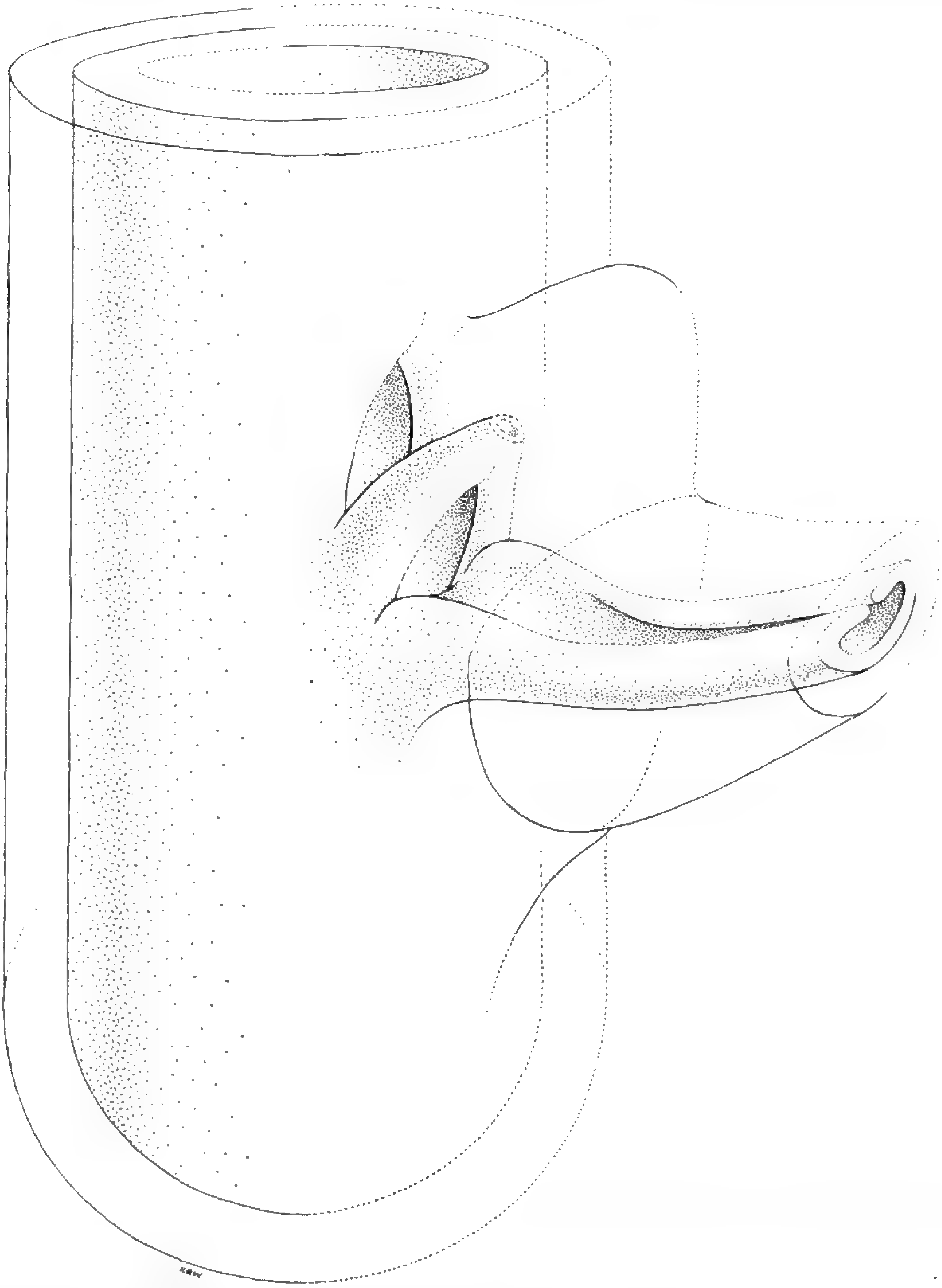

Fig. 1. Simple Unilacunar Node (semi-diagrammatic). The single leaf trace and the bud trace depart from one gap.

normally continues across the cortex and into the petiole as a single unit and remains unbranched as far as the base of the lamina. Rarely, lateral branches may occur as the petiole approaches the lamina. Such branches have been observed in *Rhododendron camelliaeflorum, R. tsangpoense, R. maddenii,* and *R. scabrifolium.*

This simple type of node, or slight modifications of it presently to be described, occurs in all the 136 species examined from the groups listed in TABLE 1. These groups comprise approximately 55 percent of the species in the whole genus.

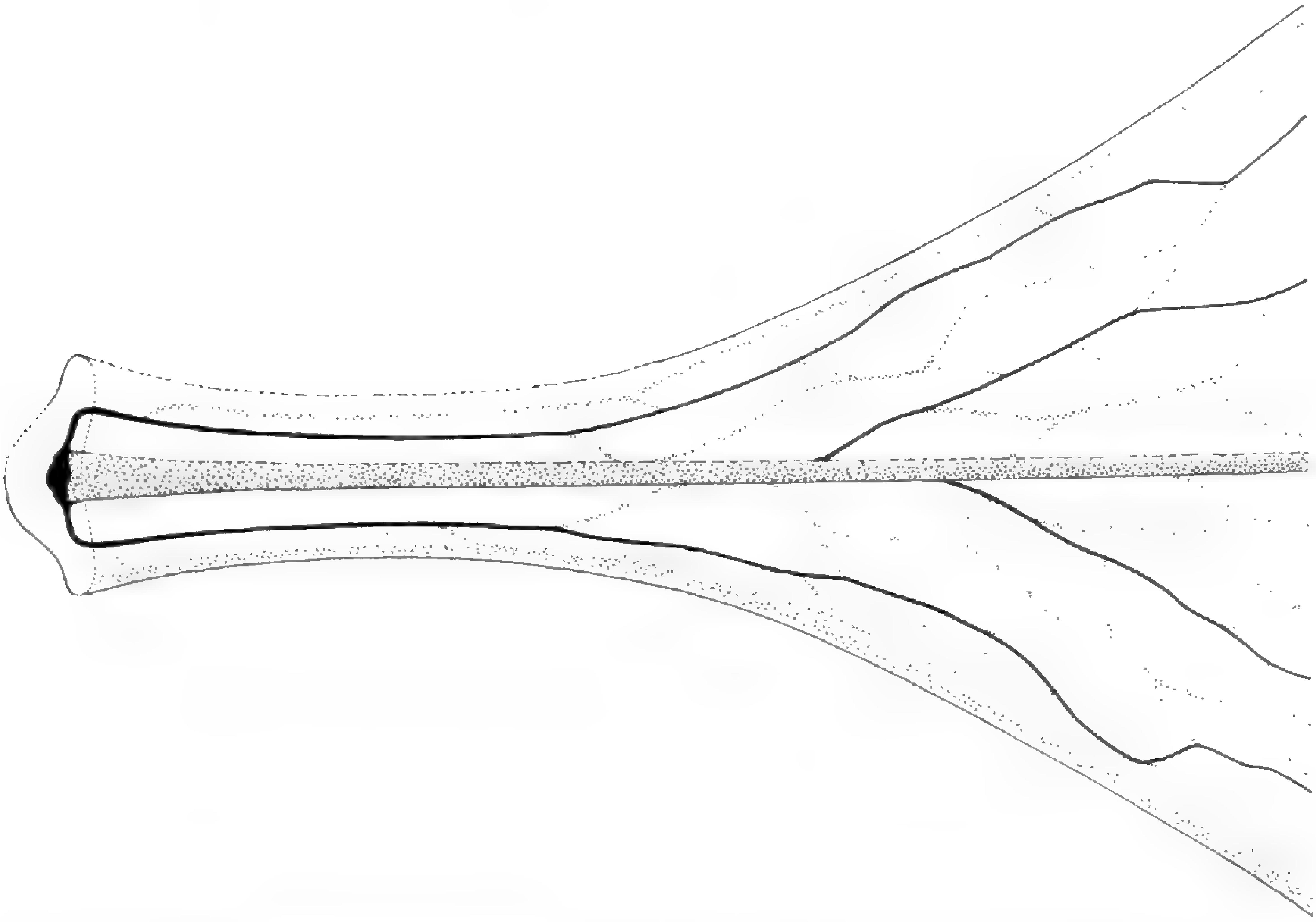

FIG. 2. *Rhododendron albiflorum.* Leaf base, showing origin of two accessory bundles outside the abscission layer.

TABLE 1. **Distribution of the Simple Unilacunar Node**

SUBGENERA (Sleumer's system)	EQUIVALENT SERIES (Handbook, 1963)
PENTANTHERA TSUTSUTSI	Azalea
AZALEASTRUM (except Sect. CHONIASTRUM)	Albiflorum Ovatum Semibarbatum
RHODORASTRUM PSEUDORHODORASTRUM RHODODENDRON PSEUDAZALEA	All the "lepidote" Series

Modifications of this simple type occur in a small proportion of the species. The variants fall into a number of categories, which are summarized below.

a) The leaf trace branches in the proximal half of the petiole, or near the abscission layer (FIG. 2). Examples are listed in TABLE 2.

b) The leaf trace divides into separate strands while still in the cortex of the axis. These subdivisions reunite after passing the abscission layer. This fragmentation of the leaf trace into distinct strands which form an arc is very clearly developed in *R. nuttallii* and occurs in some other large-leaved members of MADDENIA and VIREYA, but not in all. In very large leaves of *R. nuttallii* one or two bundles may remain as distinct strands in the petiole for some distance, even as far as the mid-point, but they eventually merge into the central bundle. The leaf trace is fragmented into distinct strands in leaves examined of the following species of VIREYA: *R. intranervatum*, *R. javanicum*, *R. brookeanum*, *R. lowii*, *R. crassifolium*, and *R. retivenium*. However, some species of this section with very large leaves were found to have very little, if any, fragmentation. Examples are *R. superbum* and *R. leucogigas*.

c) The accessory branches in the petiole originate from the stele of the axis independently of the central leaf trace. This condition was observed in one leaf of *R. schlippenbachii* and applied to the accessory on one side only. The other accessory arose, as in other leaves of this species, as a branch of the central trace. This particular node, therefore, was bilacunar.

d) Small adaxial strands of vascular tissue accompany the petiole bundle (FIG. 3). This was observed in species of the subsection MADDENIA belonging to subseries *Ciliicalyx* (*R. johnstoneanum*) and *Megacalyx* (*R. lindleyi*, *R. megacalyx* and *R. nuttallii*).

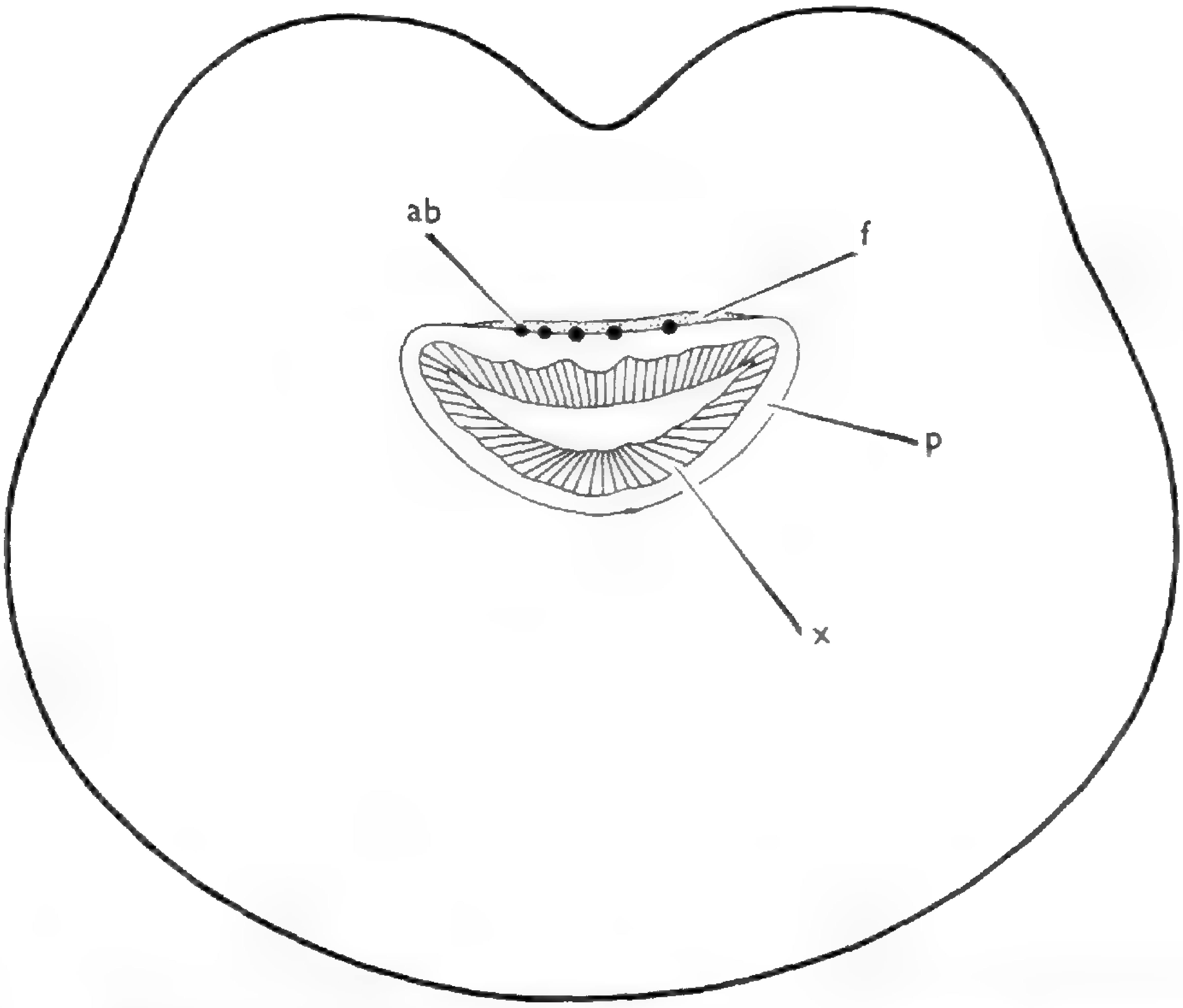

FIG. 3. *Rhododendron megacalyx*. Transverse section showing adaxial bundles in petiole. *ab*, adaxial bundles; *f*, fibers; *p*, phloem; *x*, xylem.

TABLE 2. **Simple nodes with accessory bundles**

GROUP	SPECIES	REMARKS
BOOTHIA	*sulfureum*	branches at base, or mid-petiole, or unbranched
PHAEOVIREYA	*superbum*	branches at base
PSEUDOVIREYA	*invasiorum*	branches near base
SOLENOVIREYA	*jasminiflorum*	branches near base
EUVIREYA		
BUXIFOLIA	*commonae*	branches at base
JAVANICA	*culminicolum*	branches at base
	leucogigas	branches at base
CANDIDASTRUM	*albiflorum*	branches at base
VISCIDULA	*nipponicum*	branches at base
PENTANTHERA	*luteum*	branches at base
	occidentale	branches near base
BRACHYCALYX	*schlippenbachii*	branches at base
TSUTSUTSI	*yedoense*	branches near base
	kaempferi	branches at base in sucker shoots: normal foliage unbranched

A review of these modifications indicates that the occurrence of branch traces (accessories) is not unusual in azaleas. Although this condition is not rare in VIREYA, it occurred in only one species of the other lepidote groups, namely *R. sulfureum*, though not in all leaves examined. The largest leaves among lepidote species are found in Section VIREYA and Subsection MADDENIA, and in both groups fragmentation of the trace occurs. In MADDENIA subdivisions of the trace may persist well into the petiole. In that event the transverse section of the petiole bears a resemblance to that of more complex nodal types (see below). This resemblance is superficial because the lateral bundles in the petiole always reunite with the central bundle, whereas in the complex type they remain distinct and enter the lamina.

II. **Intermediate Node** (FIG. 4)

In general there is a clear distinction between the simple node just described and the more complex type found in *Rhododendron* subgenus *Hymenanthes*. However, the nodes of all the species examined of the section CHONIASTRUM (series *Stamineum*) exhibited features of both these nodal types. Because of the difficulty in placing the CHONIASTRUM node, it was felt that its aberrant nature was best emphasized by referring it to a separate type, here designated the Intermediate Node. The

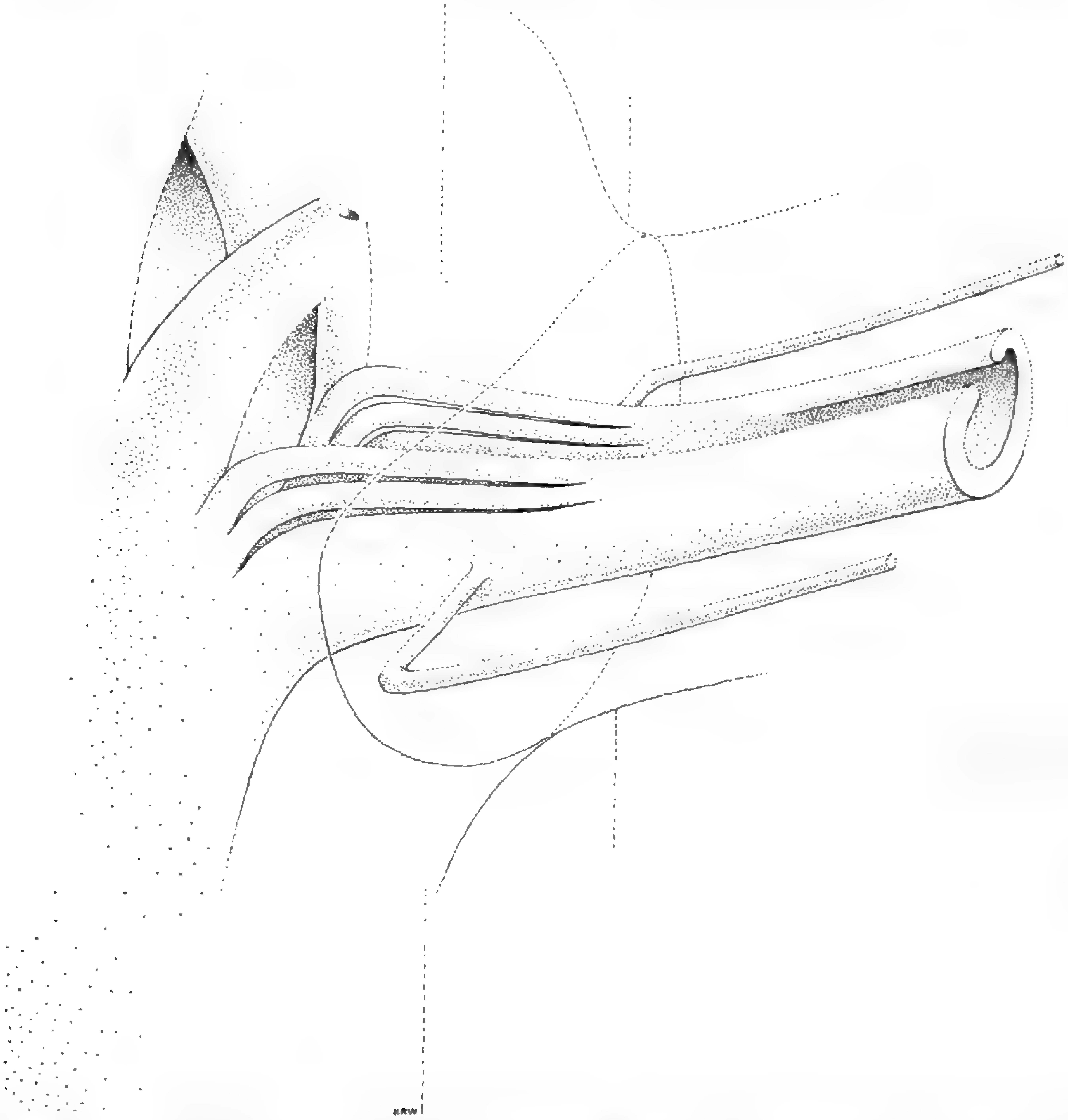

FIG. 4. INTERMEDIATE NODE (semi-diagrammatic). While in the cortex the leaf traces are closely aggregated into a central cylinder. In the petiole these traces unite to form a central strand to each side of which is an accessory bundle.

recognition of the peculiarity of this nodal type appears to be justified, as the section CHONIASTRUM has been considered aberrant within the genus on several grounds (see, for example, Kingdon-Ward (1947) on fruit and seed characters).

In nodes of this type, the leaf trace, which arises from a single gap in the stele, is composed of a number of bundles (typically five) at the level of the abscission layer. These soon unite to form a central arc-shaped strand within the petiole. Immediately outside the abscission layer accessory bundles arise from this central strand and follow a course parallel to the abscission layer before turning along the petiole.

The above description would apply almost as well to the Complex Unilacunar Node to be described below. However, it is considered that the CHONIASTRUM node (invariably present in all species of this section examined — see APPENDIX) would be wrongly placed in the complex type. This opinion is based on the fact that the separate portions of the central trace do not diverge, as in the typical complex type, but remain throughout their course as a compact arc. And again, this node differs from the simple type in the presence of accessories together with the division of the central trace. It is of interest that this small, very aberrant and natural group displays a vascular pattern which does not conform to any of the major nodal types.

The term Intermediate is used in a descriptive sense, without phylogenetic implication.

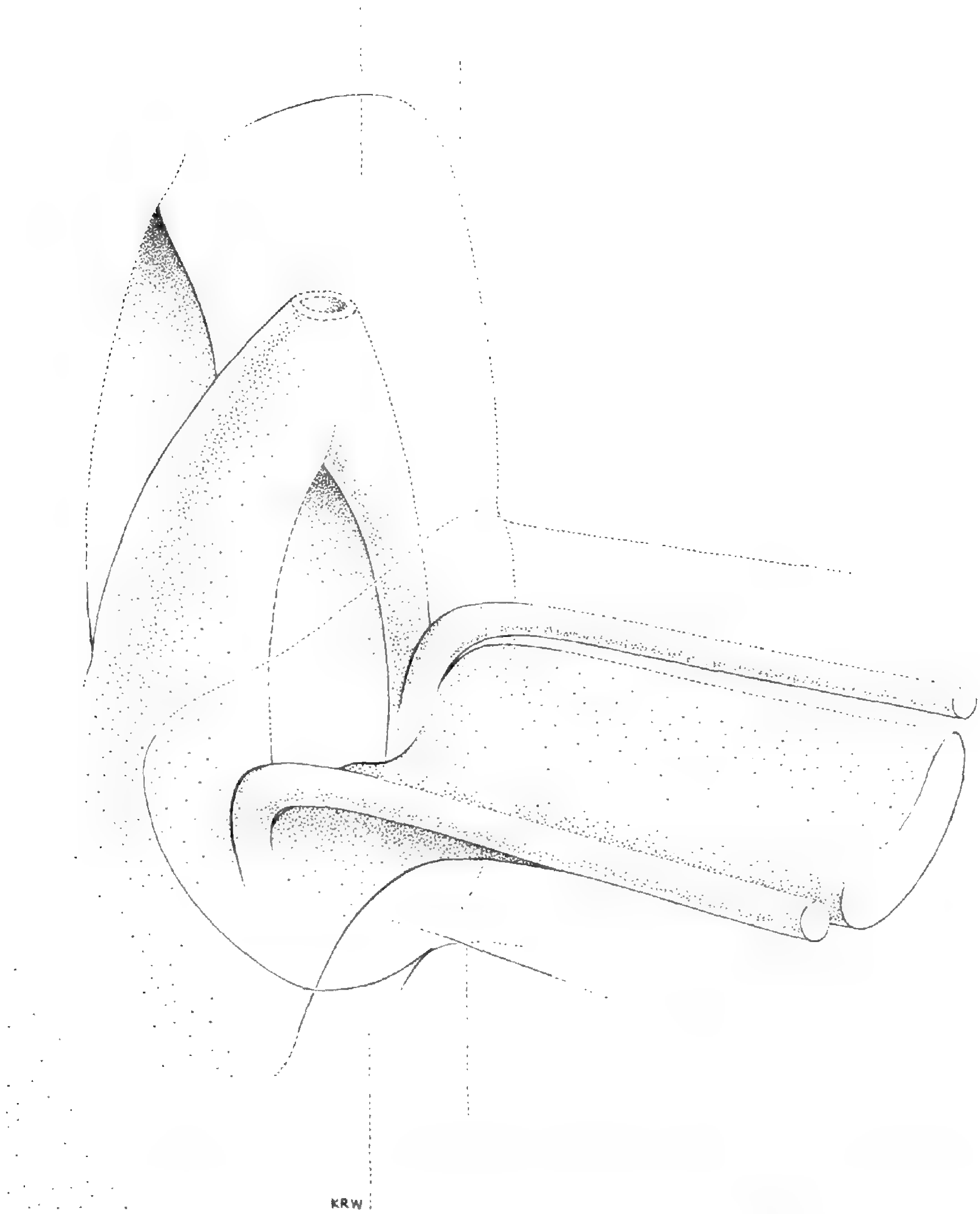

FIG. 5. THREE-TRACE UNILACUNAR NODE (semi-diagrammatic). Three strong traces diverge from a single gap.

III. Three-trace Unilacunar Node (FIG. 5)

The foliage leaves of *Rhododendron camtschaticum* are borne on lateral shoots which arise from buds situated below the terminal inflorescence buds. These terminal buds open to reveal shoots which bear a small number of flowers. Each flowering branch is subtended by a large leafy bract somewhat different in shape from the foliage leaves. Both the bracts and the foliage leaves are characterized by a type of leaf trace distinct from that of all other species examined. The nodal structure varies in detail, but the most distinctive form is found in the leafy bracts where three strands diverge from a single gap in the stele. These traverse the cortex and enter the petiole separately. The mid-trace is larger than the two laterals, but these are noticeably stronger than the accessory bundles found in the petioles of many Rhododendrons. In foliage leaves a single arc diverges from the stele before dividing into three separate strands (FIG. 5). The point at which the laterals diverge varies considerably, and frequently the two laterals at one node separate from the mid-trace at different distances from the gap. Indeed, in some leaves one or both laterals may not separate until the trace has passed beyond the abscission layer.

This type of node, with three strong traces arising from a single gap, was observed only in the very distinctive species *R. camtschaticum*. Two other closely related species are placed in THERORHODION but no material of these was available for study.

IV. Complex Unilacunar Node (FIG. 6)

In contrast to the simple node, this is a type with a highly complex structure. A number of strands (often five) leave the edge of a single leaf gap. If an axillary bud is present, the upper strands characteristically diverge from the bud trace and may branch during their passage through the cortex. As the strands approach the abscission layer they splay out, often widely, before entering the petiole. Within the petiole the strands converge, uniting to form a large central arc-shaped or cylindrical bundle. Immediately outside the abscission layer accessory bundles arise from this central bundle, as in the Intermediate Node, and follow a course parallel to the abscission layer before turning along the petiole. Alternatively, in species with a very widely splayed central complex, the accessories arise from its lateral extremities without further divergence.

The relationship between the origin of the lateral strands of the central complex and that of the bud trace varies. In many species the laterals diverge from the edges of the bud trace (FIG. 7, a); in others they arise from the stele of the axis, and enclose the bud trace (FIG. 7, b). These relationships vary according to the development of the axillary bud and probably also according to the amount of secondary growth which has taken place. Developmental studies will be required to evaluate this feature, but the character of enclosed bud traces was found to be prevalent in certain subsections, notably LACTEA and THOMSONIA.

Without exception, this Complex Unilacunar Node has been observed

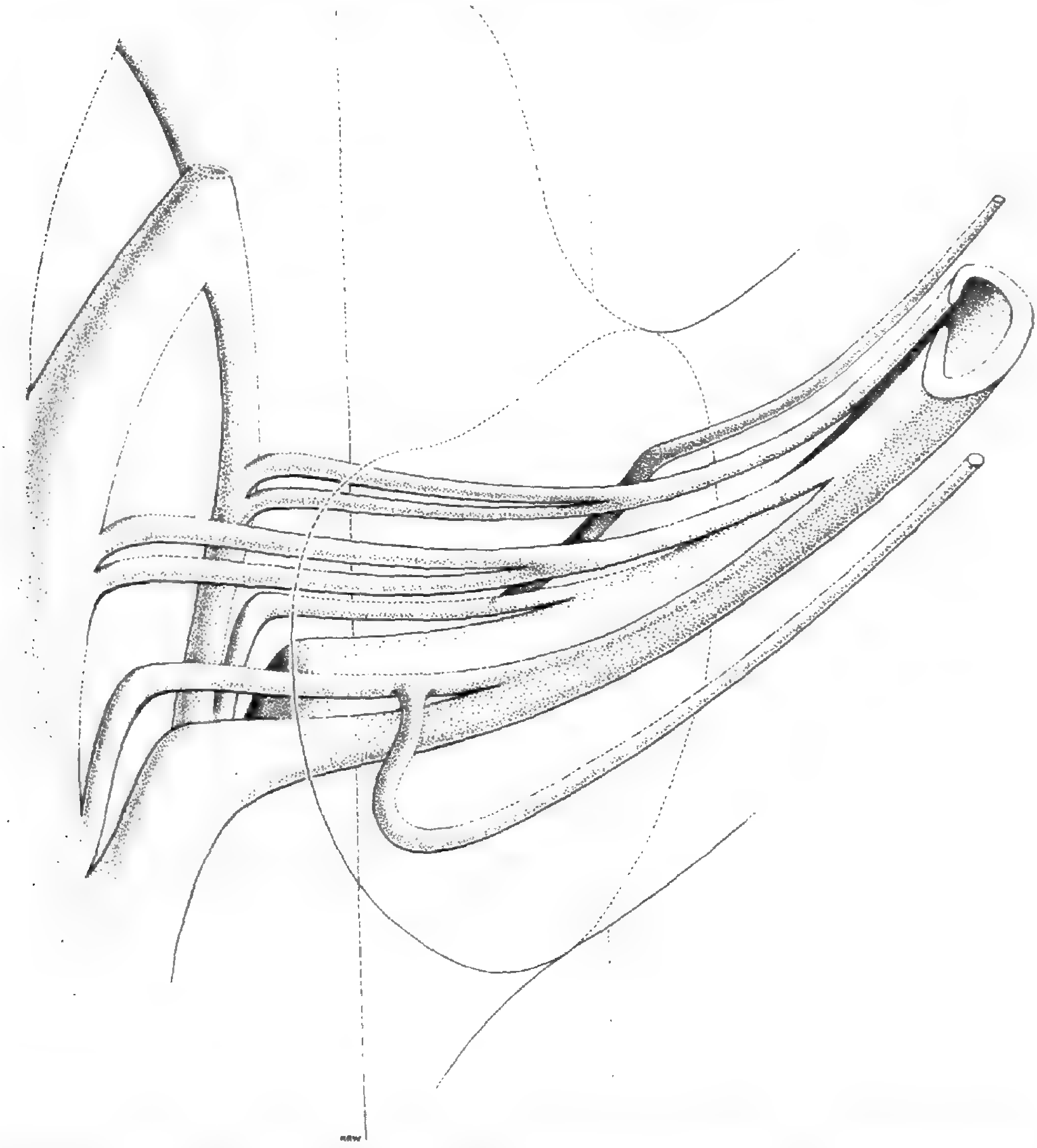

FIG. 6. COMPLEX UNILACUNAR NODE (semi-diagrammatic). Several leaf traces unite to form the central bundle of the petiole, to each side of which is an accessory bundle.

in all subdivisions of the subgenus HYMENANTHES. Indeed, all three previously described nodal types are unknown in this large subgenus. Some variants of the Complex Unilacunar Node are described below, as is the basically similar Complex Trilacunar Node, which is the only other nodal type known in HYMENANTHES.

The species in which trilacunar nodes occur will be considered in the next section. Here some interesting variations of the Complex Unilacunar Node will be described. They are confined to the following subsections.

TALIENSIA. In *R. pronum* (subseries *Roxieanum*) no accessory bundles were present in the petiole. However, the widely splayed and fragmented central strand is very similar to that of *R. gymnocarpum* which is considered to be closely related.

NERIIFLORA. In *R. forrestii* no accessories were observed, though these occurred in the varieties *repens* and *tumescens*. In the lowest foliage leaf of a

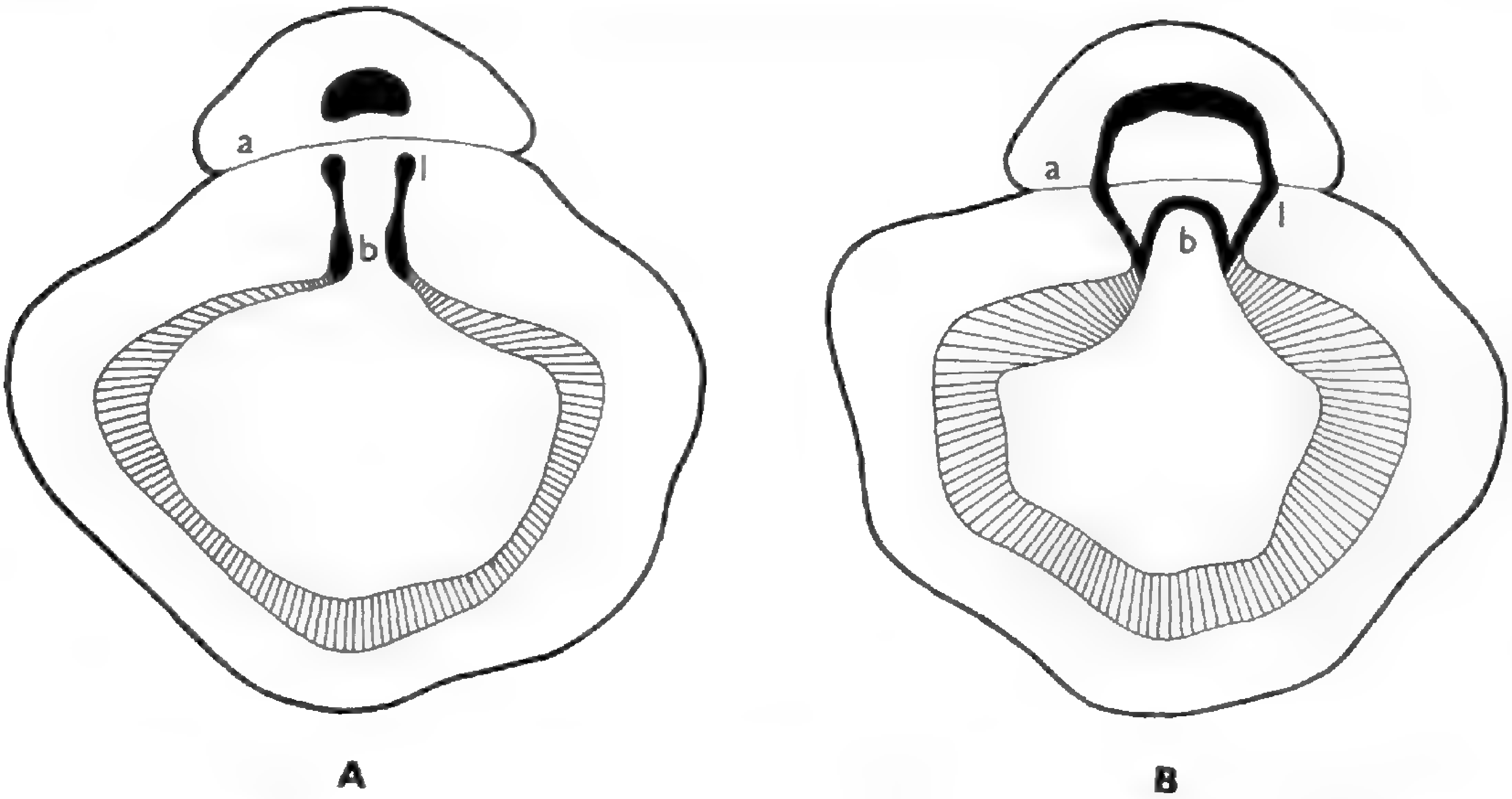

FIG. 7. Relation of lateral leaf traces to bud trace. A, *Rhododendron arboreum*, laterals unite to outer edge of bud trace; B, *R. fulvum*, laterals inserted at inner edge of bud trace (semi-diagrammatic) *a*, abscission layer; *b*, bud trace; *l*, lateral trace of leaf.

branch of *R. sperabile* only one accessory was present, and in *R. neriiflorum* one accessory became weak towards the base of the petiole and made no junction with the central complex. In *R. haematodes* one accessory diverged gradually from the central complex instead of making the usual abrupt departure.

CAMPANULATA. In *R. tsariense* no accessories were present. In a leaf with no axillary bud the central strand was inserted in the gap without obvious fragmentation. This node therefore could be placed in the simple type. However, when buds were present, parts of the central strand arose from the bud trace, a feature which reveals the undoubted relationship of this species. The patterns found in *R. campanulatum* were extraordinarily various. While the typical state of the complex type occurred, in some leaves the accessories failed to diverge from the central complex, arising *de novo* in the petiole base, sometimes with a swollen sheath of dense parenchyma around them. In one example (from seed collected on Mt. Everest by Wilkins, and grown at Dunedin Botanic Garden), most nodes were of the trilacunar type (see below) but one leaf of this plant varied in having only one accessory bundle which did not appear until halfway along the petiole. And again, a leaf of *R. succothii* with only one accessory bundle was found to have a bilacunar node.

THOMSONIA, SELENSIA, CAMPYLOCARPA, SOULIEA. All these related subsections exhibited some variants. The accessory bundles either arose *de novo* outside the abscission layer or diverged from the central complex in the typical manner in *R. campylocarpum*, *R. telopeum*, *R. selense* and *R. wardii*. In *R. dasycladum* and *R. wardii* some accessories diverged gradually from the central strand well above the abscission layer. In some nodes of *R. campylocarpum* one of the accessories arose from a separate gap in the stele, that is to say, such nodes were bilacunar; occasionally the accessory arose *de novo* in the cortex of the stem before continuing through the abscission layer into the petiole. In *R. caloxanthum* the central complex remained as three distinct bundles nearly as far as the mid-point of the petiole. As noted earlier the lateral strands of the central complex characteristically enclose the bud traces in this series, in which case these bundles appear to be inserted by separate gaps in the stele. This feature becomes exaggerated as further secondary growth occurs. In two species of this series, namely *R. hookeri* and *R. stewartianum* (both subsection THOMSONIA) the nodes were undoubtedly trilacunar, at least in the sense employed in this paper (see next section).

The variation within the species *R. williamsianum* is so great that it warrants separate description (FIG. 8). In some leaves the node was of the typical Complex Unilacunar type; in others no accessory bundles were present in the petiole; in others a single accessory occurred and was either confined to the distal portion

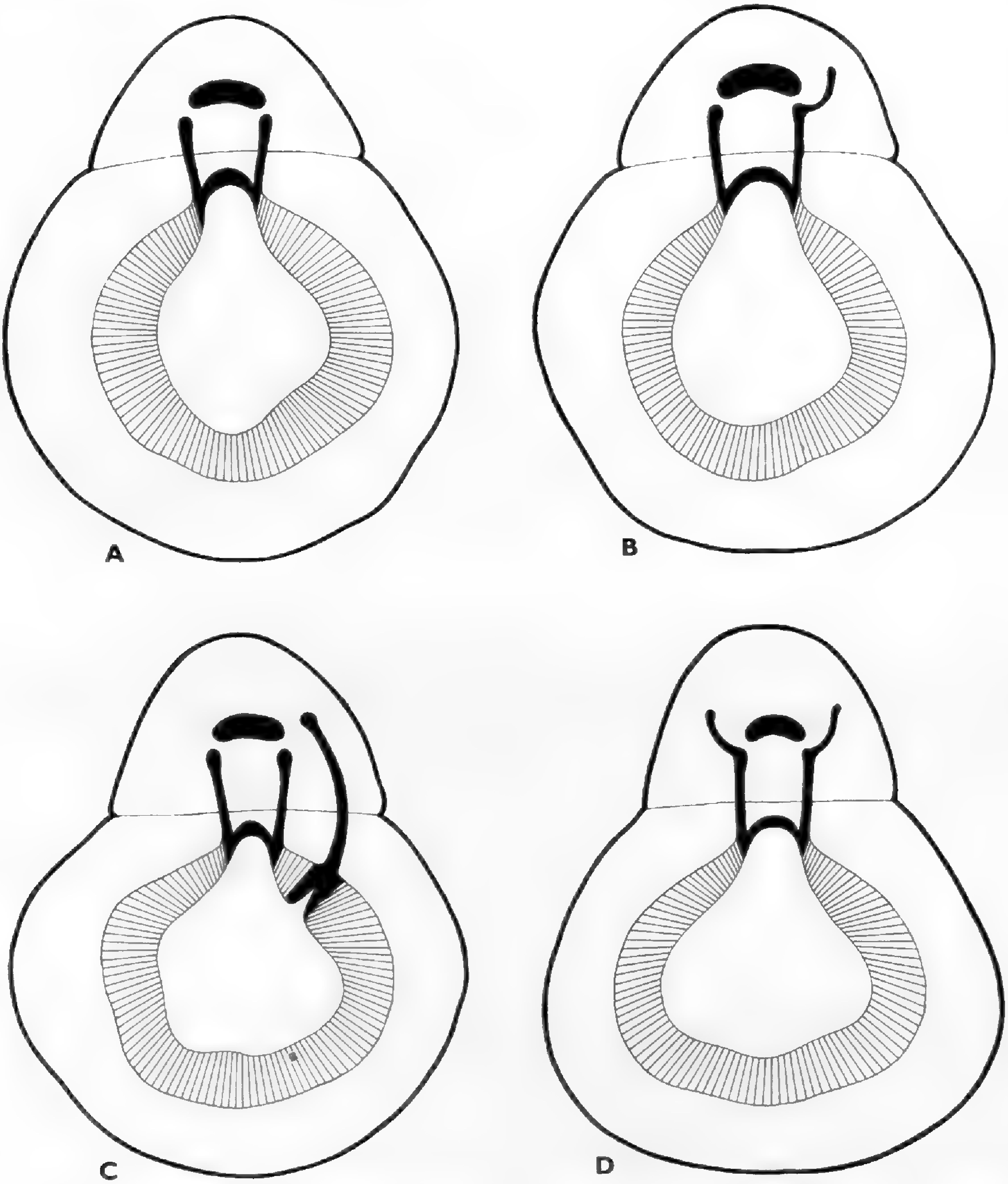

FIG. 8. *Rhododendron williamsianum*, diagrammatic representation of four types of node. A, petiole without accessories; B, petiole with one accessory which fuses with lateral bundle; C, petiole with one accessory which enters stele independently; D, petiole with two accessories, each fusing with its lateral bundle.

only or arose from the central strand at the base of the petiole; while in others the nodes were bilacunar, the accessory arising from a separate gap in the stele.

BARBATA. In one petiole of *R. bainbridgeanum* (subseries *Crinigerum*) only one accessory bundle was present and this diverged gradually from the central complex. Other nodes of the same shoot were normal.

To summarize, the Complex Unilacunar Node is found in all species of the subgenus HYMENANTHES except those with the even more elaborate Complex Trilacunar Node, still to be considered. Considerable variation is found in a few subsections of this subgenus. When accessories are not present this Complex Unilacunar Node can be defined by the complexity of the bundles at the abscission layer. Very rarely this feature may be lacking in leaves without buds, but no species of this subgenus has been found where this complexity never occurs. However, since fragmentation of the central trace occurs in *R. nuttallii* and some species of VIREYA (see above) no absolute distinction can be maintained between the nodal type of the lepidote subgenera as compared with those of the subgenus HYMENANTHES. Nevertheless, these two groups, each with over 400 species can be separated by their nodal structure, almost without exception. The intermediate nature of the node in the section CHONIASTRUM (series *Stamineum*) has been discussed previously. In the subgenus HYMENANTHES only three species were found to lack accessory bundles and in them the central strand becomes divided in at least some nodes. When it is recalled that the node of the subgenera TSUTSUTSI, PENTANTHERA (azaleas) and AZALEASTRUM can also be distinguished from that of the subgenus HYMENANTHES without exception, the taxonomic importance of the node in this genus becomes evident.

V. **The Complex Trilacunar Node** (FIG. 9)

In several different taxonomic groups within the subgenus HYMENANTHES the accessory bundles in the petiole do not diverge from the central system as in the Complex Unilacunar Node just described. Instead, they arise from strong bundles which leave the stele by independent gaps and link up with the central system just outside the abscission layer. The gaps left in the stele by the origin of these bundles are defined by primary as well as by secondary xylem. The term trilacunar, therefore, is applied to these nodes. However, since all the strands of a leaf trace are included within the same mesh of the original primary pattern of protoxylem, it is perhaps arguable that the pattern is still basically unilacunar. Nevertheless, for comparative purposes this is a most distinctive nodal type, and will be regarded here as trilacunar.

This type of node is characteristic of the subsection GRANDIA where it occurs in all species examined, though not necessarily in all leaves (see below). It also occurs in some species of the following five subsections: BARBATA (*R. argipeplum*, *R. barbatum*, *R. erosum*, *R. exasperatum* and *R. smithii*); FALCONERA (*R. arizelum*, *R. basilicum*, *R. falconeri* and *R. hodgsonii*); FORTUNEA (*R. griffithianum*); LACTEA (*R. wightii*), and

THOMSONIA (*R. hookeri* and *R. stewartianum*). The nodes of other members of these five subsections examined (see APPENDIX) were of the complex unilacunar type. In addition, the Complex Trilacunar Node was observed exceptionally in *R. campanulatum*.

An interesting consistent feature distinguishes the trilacunar node of the subsection BARBATA. The strong flanking bundles run horizontally across the cortex, so that their gaps occur higher in the stele than the gap of the midrib. In the remaining groups with trilacunar nodes the flanking bundles arise from gaps some distance below that of the midrib and ascend sharply while crossing the cortex to the abscission layer. The only exception found occurred in *R. basilicum* (FALCONERA) where the node resembles the BARBATA type.

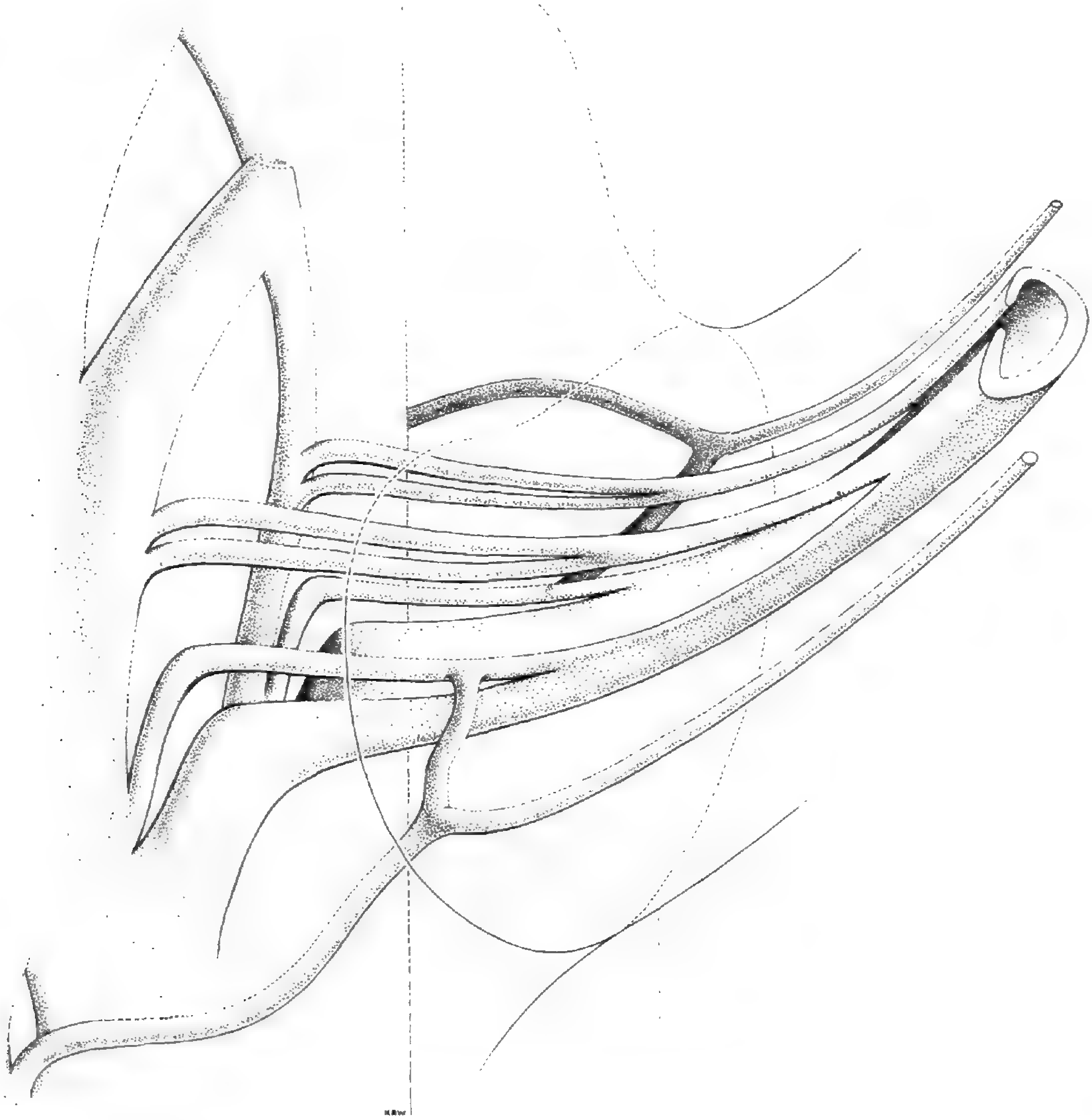

FIG. 9. COMPLEX TRILACUNAR NODE (semi-diagrammatic). Bundles leave the stele by independent gaps and join the central complex in the base of the petiole. From them the accessory bundles arise.

Such complex nodes are subject to considerable variation of detail. In particularly large specimens of *R. griffithianum* (subsect. FORTUNEA) and *R. magnificum* (subsect. GRANDIA), the central complex of bundles is convoluted so that the appearance of a double midrib is produced, and, in the latter, ventral branches of the laterals join the additional ventral fold of the midrib. On the other hand a plant of the Trinwald variety of *R. griffithianum* grown at the Dunedin Botanic Garden had asymmetrical nodes which were bilacunar, and the same condition was found in *R. monosematum* (subsect. MACULIFERA). Shoots of *R. grande* and *R. griffithianum* had successive nodes which were unilacunar (complex), bilacunar and trilacunar.

In summary, the trilacunar node occurs in some species of five subsections (BARBATA, FALCONERA, FORTUNEA, LACTEA, THOMSONIA); occasionally in one species of another (CAMPANULATA); and in all the species examined (though not all the nodes) of the subsect. GRANDIA.

VI. Nodes of Subgeneric Hybrids

Hybrids between species of the subgenus HYMENANTHES and those of other subgenera are rare (Martin, 1963). In view of the distinctive features of the node of HYMENANTHES, the nodal patterns of two such hybrids, from species belonging to two subgenera, were investigated. Specimens of *Azaleodendron* (hybrids between species of HYMENANTHES and PENTANTHERA) growing at the University of Canterbury and in the Botanic Garden, Dunedin, were found to have simple nodes similar to those of the subgenus PENTANTHERA. On the other hand, the hybrid 'Grierdal' (*R.* (subgen. *Hymenanthes*) *griersonianum* × *R.* (subgen. *Rhododendron*) *dalhousiae*), from the Savill Gardens, Windsor Great Park, had nodes similar to those of the subgenus HYMENANTHES, that is, of the Complex Unilacunar type.

Two hybrids between the subgenera RHODODENDRON and RHODORASTRUM were provided by the Arnold Arboretum. These were the hybrid 'P.J.M.' (*R. dauricum* var. *sempervirens* × *R. carolinianum*) and another unnamed hybrid (*R. mucronulatum* × *R. carolinianum*). Both were found to have nodes of the simple type. This would be expected as both species belong to subgenera with this type of node.

VARIABILITY IN NODAL PATTERNS

I. Within-plant variation

a. FOLIAGE LEAVES. Since the principal object of this investigation was to compare the nodes of typical foliage leaves, no systematic study of the variation over the full range of leaf size was undertaken. However, our observations were extensive enough to enable us to conclude that little variation does in fact occur. That is to say, the nodes of plants with characteristically simple nodes are all simple, as would be expected, though some variation in minor features was noted. Similarly, species with complex nodes in general have all their nodes complex, though the greater scope for variation possibly leads to more frequent modification. A few specific instances of within-plant variation follow, though most have already been mentioned when describing the various nodal types.

R. schlippenbachii. Accessory bundles normally leave the central strand above the abscission layer, but at one node one accessory left the stele by its own gap (bilacunar).

R. kaempferi. Accessory bundles are absent from normal foliage, but in leaves of strong sucker shoots accessories arose at the base of the petiole.

R. grande and *R. griffithianum.* Successive nodes on the same shoot were uni-, bi-, and trilacunar.

R. sperabile and *R. succothii.* Very small accessory bundles are normally present at each side of the petiolar strand. In one leaf only one of these occurred.

R. campanulatum. In one plant, accessory bundles normally branched from the central strand at the base of the petiole, but in one leaf they did not occur until mid-petiole.

R. sulfureum. In one plant, accessory bundles normally arose at the base of the petiole, though they did not all persist as far as the blade. In one leaf these basal accessories were joined by a pair of bundles which branched from the central strand at mid-petiole.

R. williamsianum. In leaves of the same plant accessory bundles may be absent or one may be present. The accessory, if present, may leave the central complex at the base of the petiole or leave the stele by an independent gap.

b. OTHER LATERAL APPENDAGES.

Cotyledons. The cotyledonary node was not investigated in detail. However, the cotyledons of several species of diverse affinity have been examined and all were found to receive a single bundle.

Bud scales. The nodes of the scales which enclose the buds of Rhododendrons are characteristically unilacunar. An exception occurred in a series cut through the scales of a plant of *R. magnificum* which had a very complex pattern of bundles in the nodes of its foliage leaves. The bud scales of this plant had several veins which united with the midrib at the base of the scale: only one bundle entered the axis. In one inner scale, however, a lateral bundle entered the axis independently so that the node of this scale was bilacunar.

Perulae. A feature of many *Rhododendron* leafy shoots is that a terminal group of foliage leaves is separated from the scars of the bud scales by several internodes which bear no foliage leaves. The appendages borne at these nodes are strap-shaped scales, or perulae, which are usually early deciduous, leaving a bare axis below the foliage leaves. In some species, however, these perulae are persistent. The nodes of the perulae were investigated in many species of diverse affinity, including those with the most complex foliage traces, and in all they were found to consist of a single trace. This branches immediately it enters the perula into several parallel veins. A curious feature of these perula-traces is that they are frequently decurrent in the cortex, arising from the stele by gaps as much as 2.5 cm. below the appendage (FIG. 10). The internodes separating the perulae grade from short at the base (i.e. next to the bud-scale scars)

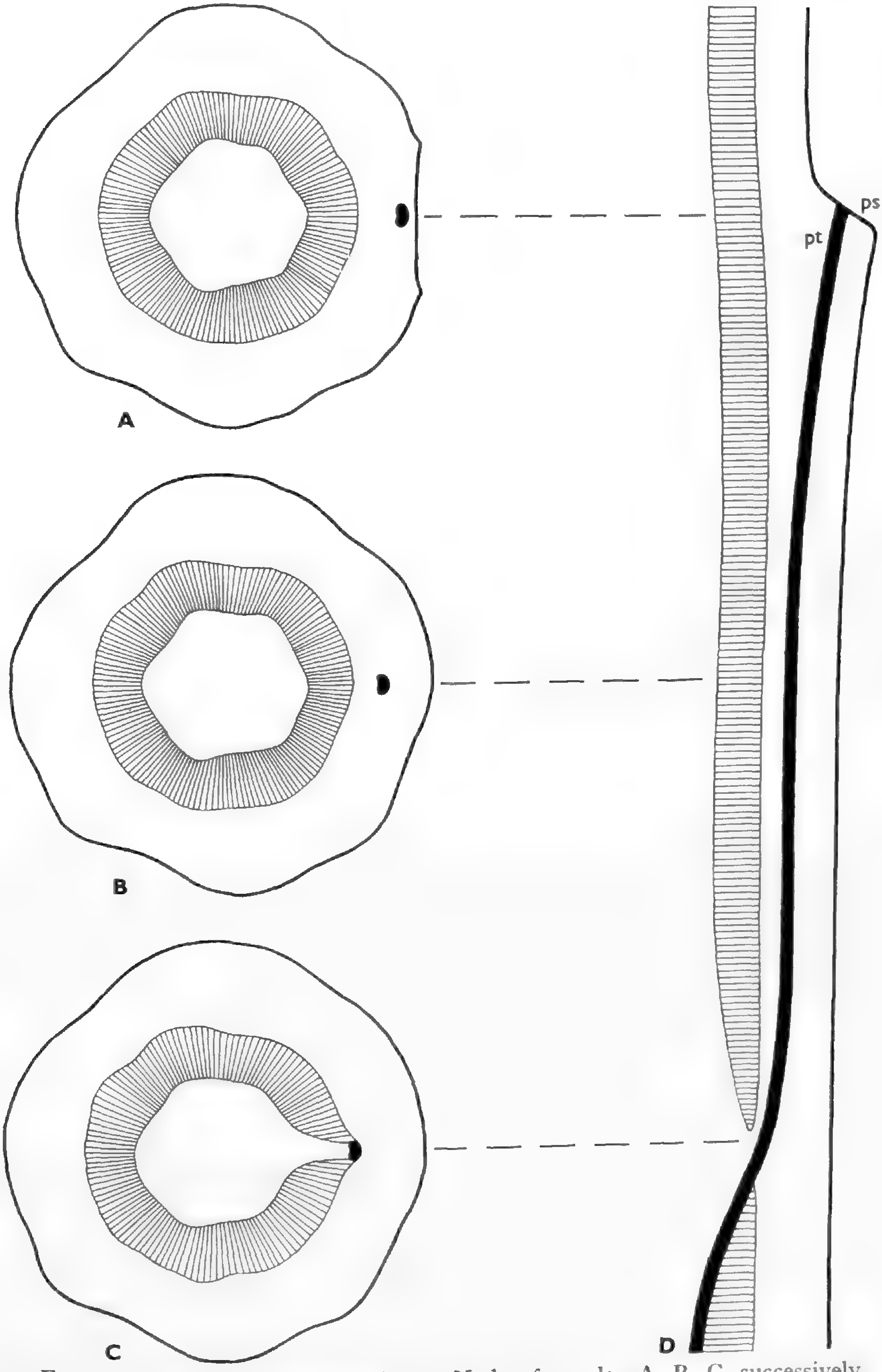

FIG. 10. *Rhododendron magnificum*. Node of perula. A, B, C, successively lower transverse sections at levels indicated on D, longitudinal section. *ps*, scar of perula; *pt*, trace of perula. Secondary xylem hatched, trace in solid black.

to a maximum about three-quarters of the way up the shoot. Above this they decrease in length. The length of the decurrent trace reaches a maximum in the longest internodes, but no simple relationship exists between internode length and degree of decurrence.

II. Within-species variation

Several instances of differences between individuals of the same species were noted. In view of the within-plant variation just described, and since no extensive surveys were undertaken, little can be concluded about the range of variation which may exist among members of the same species. However, the number of species examined, and the great consistency of the findings, with mainly trivial within-plant variation, make it safe to conclude that most species exhibit little variation. Some notable exceptions were encountered, three species standing out as most variable in their nodal structure. The variations noted in different plants of *Rhododendron williamsianum* have already been described and figured (FIG. 8). It is surprising that a species so distinct and so constant in most morphological features as *R. williamsianum* should exhibit such wide variation in nodal structure. The variation may be found between nodes of the same plant and between those of different individuals. Almost as great a range of variation was observed in *R. campanulatum* and *R. campylocarpum*.

DEVELOPMENT OF NODAL PATTERNS

I. Development in Seedling Leaves

An examination of a series of seedlings of the subsect. FALCONERA (in which the mature leaf has a trilacunar node) established that the earliest leaves, ranging in length from 0.7–1.5 cm. were unilacunar. The trilacunar state was reached in the node of a leaf only 2.6 × 1.2 cm. and still without the mature indumentum. However, some longer leaves, between 5 and 7 cm. long and with the mature indumentum were only bilacunar.

One seedling from this same suite of specimens exhibited some interesting nodes intermediate between the simple and the trilacunar state. The leaves did not form a graded series up the stem because their size varied considerably and irregularly. Four leaves in ascending sequence were as follows:

(i) blade 1.8 × 1.25 cm., node bilacunar with one very faint accessory bundle in the petiole;
(ii) blade 0.9 × 0.75 cm., node simple, with one faint accessory bundle in the petiole;
(iii) blade 0.8 × 0.55 cm., node simple, with two accessory bundles in the petiole;
(iv) blade 2.0 × 1.3 cm., node bilacunar with one accessory bundle in the petiole.

In all these nodes the central (or only) trace was undivided. It is of interest to note that the bilacunar and trilacunar conditions arise so early in the development of the seedling. In contrast to these specimens, seedlings of *R. sinogrande* of comparable size had nodes which were of the Simple Unilacunar type. Leaves with blades 2.0 × 1.0 cm. showed no sign of accessory bundles in the petiole nor of extra bundles in the cortex. Their only departure from the simple condition was the separation from the central strand of one or two subsidiary traces, which arose in the cortex, passed through the abscission layer, and then reunited with the central strand to form the single bundle of the petiole. In smaller leaves the central bundle remained entire, although the individual vessels could be seen to diverge at the abscission layer. This dilation of the trace as it passes from the stem into the petiole is never observed in typical simple nodes, and can be regarded as the first sign of the development of the complex node of the subgenus HYMENANTHES.

II. Development in the Leaf Primordium

Sections were taken through resting vegetative buds in autumn. The species investigated (*Rhododendron magnificum* and *R. griersonianum*) have mature nodes with Complex Trilacunar and Complex Unilacunar nodes respectively. No time-sequence study of primordia was undertaken, so that the detailed development of the complex node can not be described. The foliage-leaf primordia of both species examined were at an early stage of development with lamina formation only beginning. In each the primordium contained a single procambial strand, representing the midrib, and this was traced downwards until it entered the axis. No rudiment of any other part of the nodal complex was present, thus showing, as might be expected, that the supply of each leaf passes through a simple stage, no matter how complex its final condition may be.

DISCUSSION

The presence within one genus of such diverse nodal structure is, we believe, unique among woody plants. Following the pioneer work by Sinnott (1914), the node was long considered a conservative character, often stable in all members of large taxonomic groups within the dicotyledons. Latterly, this view has been seen to require modification, since considerable variation in nodal structure has been reported within families and even genera (Saha, 1952; Post, 1958). However, until the present time, the unilacunar condition has been regarded as a constant feature of the Ericaceae, although variation has been recorded in the closely related Epacridaceae (Dormer, 1945; Watson, 1967).

The variation in nodal structure observed in the genus *Rhododendron* has been presented here as falling into five types. One of these occurs in a group of three species which have been regarded as forming a distinct genus, *Therorhodion* (e.g. by Sleumer, 1949). We consider that the distinctive nodal anatomy of *R. camtschaticum* provides further evidence for the recognition of this genus. The nodal types found in the genus *Rhododendron*, ranging from simple to complex, form a natural and coherent sequence into which the three strong, divergent traces of the camtschaticum type have no place.

The remaining four groups fall into two major categories. The Complex Unilacunar and the Complex Trilacunar nodes are clearly very similar morphologically and taken together are found in all the species of the subgenus HYMENANTHES and in no other group. The morphological similarity evident from a comparison of FIGS. 6 and 9 is strengthened by two other considerations. Firstly, these two nodal types may occur together in different species of the same taxonomic group, in different plants of the same species, and even in different nodes of the same shoot. Secondly, a few species with otherwise typical Complex Unilacunar nodes have the lateral parts of the leaf trace inserted so widely that they approach the trilacunar state, or one bundle may clearly enter by its own gap, giving a bilacunar node.

The Simple Unilacunar Node and the Intermediate Node also appear to be linked by similar features. These two nodal types are found in all species of the seven subgenera listed in TABLE I but including CHONIASTRUM. They stand, therefore, in sharp contrast to the eighth subgenus HYMENANTHES, in which the node is complex. Apart from the section CHONIASTRUM which will be considered presently, the distinction between simple and complex nodes presents no real problems. It is true that some leaf traces of the subsection MADDENIA divide in the cortex as they pass into the petiole but accessories are not developed in this group. Similarly, in some species of section VIREYA the leaf trace divides in the cortex, and in addition in this section accessory bundles may occur in the petiole. On the other hand, in the few members of HYMENANTHES which lack accessory bundles, the leaf trace is divided in the cortex in the manner typical of that subgenus. These aberrant forms are closely related to species with nodes of the typical Complex Unilacunar form. That is to say, most species of the subsection TALIENSIA, for instance, are complex, though one of its species lacks accessory bundles. It is concluded, therefore, that these instances of approach between the two types are secondary modifications resulting from convergent evolution.

The Intermediate Node, found in the section CHONIASTRUM, is possibly nearer to the simple than to the complex node since the central strand, though divided, does not lose the compactness of form characteristic of the simple type. Therefore, it is probably correct to regard it as a modification of that form, though sufficiently distinctive to be considered a separate nodal type.

The other three sections of AZALEASTRUM, namely CANDIDASTRUM, MUMEAZALEA and EUAZALEASTRUM were found to share certain features which contrast strongly with those of CHONIASTRUM. They all bear minute, often strongly curved, simple hairs on the petiole; the petiolar strand is fan shaped in section, not incurved; and some species (e.g. *R. semibarbatum* and *R. ovatum*) have serrated leaf margins. It is suggested that the subgenus AZALEASTRUM might well be subdivided in order to accentuate the evident close relationship of these three sections, and their equally evident lack of relationship to CHONIASTRUM.

It is probable that a close study of the histology of the nodes and petioles of the azaleas (subgenera PENTANTHERA and TSUTSUTSI) would reveal characters distinguishing them from the nodes of scale-bearing rhododendrons. While it was noticed that branches of the central trace were not infrequent in azaleas but very rare in lepidote species, no diagnostic feature was recorded.

It will be clear from the foregoing discussion that the node offers a character of taxonomic importance. The coincidence between nodal types and the major subdivisions recognized within the genus is striking. That a completely new set of characters indicates groups that accord with existing classification is encouraging, and the validity of the groups is strengthened by this new evidence. The classification of the genus is at present in a transitional state. On the one hand there is an old-established classification in traditional botanical form. This may be seen, for example, in Rehder (1902), where major subdivisions of the genus are defined. This system has the grave practical disadvantage that most of the species, including the majority of interest to horticulturists, fall within two of the major groups. It was for this reason, no doubt, that an empirical, informal classification into series was adopted in *The Species of Rhododendron* (Stevenson, 1930). These series form the most comprehensive and discriminating grouping of the temperate species yet devised. However, the already established major subdivisions of the genus were not employed, the series being presented in alphabetical sequence. A much clearer appreciation of the genus results if the systems are united, giving the advantages of both. This was done by Sleumer in 1949.

While we wish to emphasize this close correspondence between nodal anatomy and classification, we would also draw attention to the interesting variation in detail to be found between members of taxonomic groups, both large and small, between the nodes of different categories of appendages, and between nodes of the same order within one individual. Clearly, the adult anatomy of a node may vary, particularly in some species and some subsections. Nevertheless, the range of variation is limited so that the definition of the major types remains clear, with very few exceptions. The interest of these exceptions must not be allowed to detract from the taxonomic significance of the nodal types which is based on the vast majority of the species.

The anatomical evidence presented here reinforces the view that major groupings are present within the genus. Indeed it provides further evidence for those who would raise these groups to generic rank (Copeland, 1943). The distinctness of the subgenus HYMENANTHES from the remaining groups is suggested by nodal anatomy. It is reinforced by the absence of scales, though this feature is also lacking in several groups with simple nodes. These same groups (azaleas and *Azaleastrum*), moreover, resemble subgenus HYMENANTHES in the aestivation of their foliage leaves (Sinclair, 1937). By employing these three anatomical features in combination, three major subdivisions can be defined (TABLE 3). However, the definition of the resulting groups, whether by anatomy or by external features, such as the position of flower and foliage buds, is complex. For this reason, and also in view of the long horticultural history of the genus, there appears to be little advantage in maintaining separate genera.

TABLE 3

SUBGENUS	ANATOMICAL FEATURES
PENTANTHERA TSUTSUTSI AZALEASTRUM	node simple scales absent aestivation revolute
HYMENANTHES	node complex scales absent aestivation revolute
RHODODENDRON PSEUDAZALEA RHODORASTRUM PSEUDORHODORASTRUM	node simple scales present aestivation convolute (except in subsect. EDGEWORTHIA)

The prevalence of the unilacunar node in so many genera of the Ericaceae suggests that this state is basic for the family and that the comparatively few species with trilacunar nodes in *Rhododendron* are derived from the simpler type. Indeed, the unilacunar node has come to be regarded as primitive for the dicotyledons as a whole, and there are convincing instances of the derivation within a family of trilacunar nodes from the unilacunar condition (Bailey, 1956). This view is supported in *Rhododendron* by the occurrence of two forms of trilacunar node, that occurring in the subsection BARBATA and that in other groups. Kingdon-Ward (1947) adopts the view that the lepidote rhododendrons are primitive and this would imply that the simple node is the original type. On the other hand, Hutchinson (1946) postulates that the subsection FALCONERA resembles the ancestral form of the genus. This group is predominantly trilacunar. Hutchinson's opinion is based on his belief in a resemblance between the subsection FALCONERA and the Dilleniaceae, a family which he considered to be ancestral to the Ericaceae. The node in the principal subfamily of the Dilleniaceae is tri- or pentalacunar (Sinnott, 1914). In *Actinidia* and *Saurauia*, representing the other two subfamilies, the node is unilacunar. Since the majority of dicotyledonous families are characteristically trilacunar, the presence of this nodal type in two groups does not necessarily imply relationship. However, if the Ericaceae are, in fact, derived from the Dillenioideae, the trilacunar node is likely to be the original state in the family. In that event, the genus *Rhododendron* would be primitive within the Ericaceae, as only in this genus are trilacunar nodes known to occur. It must be emphasized that the opinions of Kingdon-Ward and Hutchinson are both speculative. While it is necessary to examine them in the light of the evidence relating to nodal anatomy, no final conclusion can be drawn.

Money, Bailey and Swamy (1950) have suggested that single arc-shaped leaf traces may in fact sometimes represent several concrescent strands. If the more complex type of node were primitive in *Rhododendron*, the very prevalent simple leaf trace which is characteristic of other genera in the family, would be of such a concrescent type.

In this investigation we have observed the node of a little more than one quarter of the species of the genus. A larger sample would undoubtedly have revealed greater variation in some groups. The types described are based on features of vascular patterns. Future studies will include histological characters, and preliminary observations suggest that these additional characters will allow differences between groups with simple traces to be recognized and also that distinct types of node and petiole will be found within the subgenus HYMENANTHES.

SUMMARY

1. The anatomy of the nodes of the mature foliage leaf has been investigated in 264 species of the genus *Rhododendron*. These are presented as falling into five types:

(i) *Simple Unilacunar*: the leaf receives a single trace; rarely, accessory bundles may be present in the petiole.

(ii) *Intermediate*: the trace, while in the cortex, consists of a few bundles closely aggregated into a central cylinder. In the petiole these bundles unite to form a central strand which is accompanied by two or more accessory bundles.

(iii) *Three-trace Unilacunar*: a single arc diverges from the stele before dividing into three separate strands. This division may be in the cortex or just outside the abscission layer.

(iv) *Complex Unilacunar*: several traces arise from a single gap and enter the petiole, where they unite to form a central strand which is accompanied by two or more accessory bundles.

(v) *Complex Trilacunar*: the pattern of traces is similar to type iv, but additional traces leave the stele by separate gaps.

2. Variations are recorded within the framework of these types as they occur in taxa and individuals.

3. The essential features of the Complex Trilacunar Node were found to be established very early in the development of seedlings.

4. All types, including the most complex, pass through a stage of development when only one leaf trace is present.

5. The nodes of cotyledons, cataphylls and perulae are unilacunar even in species with trilacunar foliage leaves.

6. The significance of these findings is discussed in relation to the taxonomic subdivision of the genus.

ACKNOWLEDGMENTS

This investigation was possible only with the assistance of the many persons who supplied specimens. All those to whom we appealed responded with willing and full co-operation, and to them we tender our sincere thanks. In particular, we wish to record the generosity of Mr. R. B. Cooke of Corbridge, Northumberland, England, and Mr. H. J. Marchant of Stratford, New Zealand, who each contributed a large number of specimens which together formed the basis of this investigation. In addition, we are indebted to Mr. T. H. Findlay and the Crown Commissioners, Great Park, Windsor; to Mr. J. R. Sealey and the Royal Botanic Gardens, Kew; to Dr. H. R. Fletcher, Dr. B. L. Burtt, Mr. H. H. Davidian and Mr. P. J. Woods of the Royal Botanic Garden, Edinburgh; to Dr. D. Wyman and the Arnold Arboretum; to Mr. R. W. Balch and the Botanic Garden, Dunedin; to Mr. C. Puddle and Bodnant Gardens, North Wales; to Mr. E. H. Lohbrunner, Victoria, Canada; to Mr. David G. Leach, Brookville, Pennsylvania, U.S.A.; and to Mrs. H. A. Hearn, Mr. R. Wilson, and Mrs. N. G. Mitchell of Christchurch, New Zealand. We are indebted to Dr. R. D. Hoogland of the Department of Land Research, C.S.I.R.O., Canberra; Dr. H. M. Burkill of the Botanic Gardens, Singapore; Dr. H. Sleumer of the Rijksherbarium, Leiden; and Dr. R. A. Howard of the Arnold Arboretum, who all generously contributed herbarium material of otherwise unobtainable species; to Mr. G. D. Smith of the Northern Horticultural Society, Harlow Car, Harrogate, England, and Mr. G. B. Petterson of the N. Z. Rhododendron Association, who kindly supplied series of seedlings for developmental studies; and to Mr. K. R. West of the Botany Division, D.S.I.R., Christchurch, New Zealand, who with patience and skill prepared the illustrations for publication.

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Appendix: Comparison of Classifications, and Species Examined

SLEUMER, 1949 and 1958			HANDBOOK, 1963		SPECIES EXAMINED	
Subgenus	Section	Subsection	Series	Subseries		
(Excluded)	—	—	Camtschaticum	—	*camtschaticum* Pallas	
PENTANTHERA	RHODORA	—	Azalea	Canadense	*albrechtii* Maxim.	*vaseyi* A. Gray
	VISCIDULA	—		Nipponicum	*nipponicum* Matsuma	
	PENTANTHERA	—		Luteum	*luteum* Sweet *roseum* (Loisel.) Rehd.	*occidentale* A. Gray
TSUTSUTSI	BRACHYCALYX	—		Schlippenbachii	*schlippenbachii* Maxim.	
	TSUTSUTSI	—		Obtusum	*kaempferi* Planch.	*yedoense* Maxim.
	TSUSIOPSIS	—		Tashiroi	*tashiroi* Maxim.	
AZALEASTRUM	CANDIDASTRUM	—	Albiflorum	—	*albiflorum* Hook.	
	MUMEAZALEA	—	Semibarbatum	—	*semibarbatum* Maxim.	
	CHONIASTRUM	—	Stamineum	—	*cavaleriei* Lévl. *hancockii* Hemsl. *latoucheae* Franch. *moulmainense* Hook.	*esquirolii* Lévl. *henryi* Hance *oxyphyllum* Franch. *stamineum* Franch.
	EUAZALEASTRUM	—	Ovatum	—	*leptothrium* Balf. f. & Forrest	*ovatum* Planch.
HYMENANTHES	—	AURICULATA	Auriculatum	—	*auriculatum* Hemsl.	
			Griersonianum	—	*griersonianum* Balf. f. & Forrest	
		BARBATA	Barbatum	Barbatum	*argipeplum* Balf. f. & Cooper *smithii* Nutt. ex Hook.	*barbatum* Wall.
				Glischrum	*erosum* Cowan *glischroides* Tagg & Forrest *habrotrichum* Balf. f. & W.W. Sm.	*exasperatum* Tagg *glischrum* Balf. f. & W.W. Sm.
				Crinigerum	*bainbridgeanum* Tagg & Forrest	*crinigerum* Franch.
		MACULIFERA		Maculiferum	*longesquamatum* C. K. Schneid. *morii* Hayata *strigillosum* Franch.	*monosematum* Hutch. *pachytrichum* Franch.
		ARBOREA	Arboreum	Arboreum	*arboreum* Smith *niveum* Hook. f.	*delavayi* Franch. *zeylanicum* Hort. ex Loud.
		ARGYROPHYLLA		Argyrophyllum	*argyrophyllum* Franch.	*insigne* Hemsl. & Wils.
		FLORIBUNDA			*floribundum* Franch.	*hunnewellianum* Rehd. & Wils.
		THOMSONIA	Thomsonii	Thomsonii	*cyanocarpum* (Franch.) W.W. Sm. *hookeri* Nutt. *thomsonii* Hook. f.	*eclecteum* Balf. f. & Forrest *stewartianum* Diels *viscidifolium* Davidian
				Cerasinum	*cerasinum* Tagg	
		SELENSIA		Selense	*selense* Franch.	*dasycladum* Balf. f. & W.W. Sm.
		MARTINIANA			*eurysiphon* Tagg & Forrest	*martinianum* Balf. f. & Forrest
		CAMPYLOCARPA		Campylocarpum	*callimorphum* Balf. f. & W.W. Sm. *campylocarpum* Hook f.	*caloxanthum* Balf. f. & Farrer *telopeum* Balf. f. & Forrest
		SOULIEA		Souliei	*litiense* Balf. f. & Forrest *wardii* W.W. Sm.	*souliei* Franch.
				Williamsianum	*williamsianum* Rehd. & Wils.	
		IRRORATA	Irroratum	Irroratum	*aberconwayi* Cowan *irroratum* Franch. *wrayi* King & Gamble	*eritimum* Balf. f. & W.W. Sm. *pankimense* Cowan & Ward

Appendix: *(Continued)*

SLEUMER, 1949 and 1958			HANDBOOK, 1963		SPECIES EXAMINED	
Subgenus	Section	Subsection	Series	Subseries		
		Parishia		Parishii	*cookeianum* Davidian *venator* Tagg	*elliottii* Watt. ex W.W. Sm.
		Lactea	Lacteum	—	*beesianum* Diels *phaeochrysum* Balf. f. & W.W. Sm. *traillianum* Forrest & W.W. Sm.	*lacteum* Franch. *przewalskii* Maxim. *wightii* Hook. f.
		Falconera	Falconeri	—	*arizelum* Balf. f. & Forrest *coriaceum* Franch. *falconeri* Hook. f. *hodgsonii* Hook. f.	*basilicum* Balf. f. & W.W. Sm. *eximeum* Nutt. *fictolacteum* Balf. f. *rex* Lévl.
		Grandia	Grande	—	*coryphaeum* Balf. f. & Forrest *macabeanum* Watt ex Balf. f. *praestans* Balf. f. & W.W. Sm. *sinogrande* Balf. f. & W.W. Sm.	*grande* Wight *magnificum* Ward *sidereum* Balf. f.
		Fulva	Fulvum	—	*fulvum* Balf. f. & W.W. Sm.	*uvarifolium* Diels
		Campanulata	Campanulatum	—	*campanulatum* D. Don *lanatum* Hook. f. *succothii* Davidian	*fulgens* Hook. f. *sherriffii* Cowan *tsariense* Cowan
		Taliensia	Taliense	Adenogynum	*bureavii* Franch.	*detonsum* Balf. f. & Forrest
				Roxieanum	*gymnocarpum* Balf. f. & Tagg *roxieanum* Forrest	*pronum* Tagg & Forrest
				Taliense	*sphaeroblastum* Balf. f. & Forrest	
				Wasonii	*inopinum* Balf. f.	*rufum* Batal.
		Neriiflora	Neriiflorum	Forrestii	*chamae-thomsonii* (Tagg & Forrest) Cowan & Davidian	*forrestii* Balf. f. ex Diels
				Haematodes	*chaetomallum* Balf. f. & Forrest *mallotum* Balf. f. & Ward	*haematodes* Franch.
				Neriiflorum	*neriiflorum* Franch.	*sperabile* Balf. f. & Farrer
				Sanguineum	*aperantum* Balf. f. & Ward *sanguineum* Franch.	*dichroanthum* Diels
		Pontica	Ponticum	Caucasicum	*degronianum* Carriere *makinoi* Tagg *yakusimanum* Nakai	*hyperythrum* Hayata *ungernii* Trautv.
				Ponticum	*catawbiense* Michaux *ponticum* L.	*macrophyllum* D. Don
		Fortunea	Fortunei	Calophytum	*calophytum* Franch.	
				Davidii	*planetum* Balf. f. *sutchuenense* Franch.	*praevernum* Hutch.
				Fortunei	*decorum* Franch. *discolor* Franch. *vernicosum* Franch.	*diaprepes* Balf. f. & W.W. Sm. *fortunei* Lindl.
				Orbiculare	*orbiculare* Decaisne	
				Griffithianum	*griffithianum* Wight	
				Oreodoxa	*fargesii* Franch.	*oreodoxa* Franch.

SLEUMER, 1949 and 1958			HANDBOOK, 1963		SPECIES EXAMINED	
Subgenus	Section	Subsection	Series	Subseries		
Pseudazalea	—	—	Trichocladum	—	*chloranthum* Balf. f. & Forrest	*lepidostylum* Balf. f. & Forrest
					melinanthum Balf. f. & Ward	*trichocladum* Franch.
Rhodorastrum	—	—	Dauricum	—	*dauricum* L.	*mucronulatum* Turcz.
Pseudorhodorastrum	Trachyrhodion	—	Scabrifolium	—	*mollicomum* Balf. f. & W.W. Sm.	*pubescens* Balf. f. & Forrest
					scabrifolium Franch.	*spiciferum* Franch.
	Rhodobotrys	—			*racemosum* Franch.	
	Rhabdorhodion	—	Virgatum	—	*virgatum* Hook. f.	
Rhododendron	Lepipherum	Camelliaeflora	Camelliaeflorum	—	*camelliaeflorum* Hook. f.	
		Boothia	Boothii	Boothii	*chrysodoron* Tagg ex Hutch.	*sulfureum* Franch.
				Megeratum	*leucaspis* Tagg	*megeratum* Balf. f. & Forrest
		Tephropepla		Tephropeplum	*auritum* Tagg	*tephropeplum* Balf. f. & Farrer
					xanthostephanum Merr.	
		Edgeworthia	Edgeworthii	—	*edgeworthii* Hook. f.	*pendulum* Hook. f.
		Glauca	Glaucophyllum	Glaucophyllum	*brachyanthum* Franch.	*charitopes* Balf. f. & Farrer
					glaucophyllum Rehd.	*tsangpoense* Hutch. & Ward
		Genesteriana		Genesterianum	*genesterianum* Forrest	
		Maddenia	Maddenii	Ciliicalyx	*burmanicum* Hutch.	*ciliatum* Hook. f.
					ciliicalyx Franch.	*formosum* Wall.
					johnstoneanum Watt	*scopulorum* Hutch.
					valentinianum Forrest	*veitchianum* Hook.
				Maddenii	*crassum* Franch.	*maddenii* Hook. f.
				Megacalyx	*lindleyi* Moore	*megacalyx* Balf. f. & Ward
					nuttallii Booth	*taggianum* Hutch.
		Moupinensia	Moupinense	—	*moupinense* Franch.	
		Saluenensia	Saluenense	—	*calostrotum* Balf. f. & Ward	*keleticum* Balf. f. & Forrest
					nitens Hutch.	*radicans* Balf. f. & Forrest
					saluenense Franch.	
		Triflora	Triflorum	Augustinii	*augustinii* Hemsl.	
				Hanceanum	*hanceanum* Hemsl.	
				Triflorum	*ambiguum* Hemsl.	*bauhiniiflorum* Watt ex Hutch.
					lutescens Franch.	*triflorum* Hook. f.
				Yunnanense	*concinnum* Hemsl.	*davidsonianum* Rehd. & Wils.
					oreotrephes W.W. Sm.	*yunnanense* Franch.
		Campylogyna	Campylogynum	—	*campylogynum* Franch.	
		Caroliniana	Carolinianum	—	*carolinianum* Rehd.	*minus* Michaux
					chapmanii A. Gray	
		Ferruginea	Ferrugineum	—	*ferrugineum* L.	*kotschyi* Simonk.
		Heliolepida	Heliolepis	—	*desquamatum* Balf. f. & Forrest	*heliolepis* Franch.
					rubiginosum Franch.	
		Lapponica	Lapponicum	—	*edgarianum* Rehd. & Wils.	*fastigiatum* Franch.
					flavidum Franch.	*hippophaeoides* Balf. f. & W.W. Sm.
					idoneum Balf. f. & W.W. Sm.	*microleucum* Hutch.
					russatum Balf. f. & Forrest	
		Micrantha	Micranthum	—	*micranthum* Turcz.	
		Cinnabarina	Cinnabarinum	—	*cinnabarinum* Hook. f.	*concatenans* Hutch.
					keysii Nutt.	*xanthocodon* Hutch.
		Lepidota	Lepidotum	Lepidotum	*lepidotum* Wall.	
		Baileya		Baileyi	*baileyi* Balf. f.	
		Uniflora	Uniflorum	—	*ludlowii* Cowan	*patulum* Ward
					pemakoense Ward	*uniflorum* Hutch. & Ward

Appendix: *(Continued)*

SLEUMER, 1949 and 1958			HANDBOOK, 1963		SPECIES EXAMINED	
Subgenus	Section	Subsection	Series	Subseries		
	Pogonanthum	—	Anthopogon	—	*anthopogon* D. Don	*cephalanthum* Franch.
					sargentianum Rehd. & Wils.	*trichostomum* Franch.
	Vireya		Vaccinioides			
		Pseudovireya			*invasiorum* Sleum.	*perakense* King & Gamble
					saruwagedicum Foerster	*seimundii* J.J. Smith
					spathulatum Ridl.	*vaccinioides* Hook. f.
		Siphonovireya			*herzogii* Warb.	
		Phaeovireya			*beyerinkianum* Koord.	*konori* Becc.
					superbum Sleum.	
		Malayovireya			*malayanum* Jack	*vinicolor* Sleum.
		Albovireya			*yelliottii* Warb.	
		Solenovireya			*jasminiflorum* Hook.	*pleianthum* Sleum.
		Euvireya				
		Series				
		Linnaeoides			*gracilentum* F. v. Muell.	
		Saxifragoides			*saxifragoides* J.J. Smith	
		Taxifolia			*taxifolium* Merr.	
		Stenophylla			*purpureiflorum* J.J. Smith	
		Citrina			*citrinum* (Hassk.) Hassk.	
		Buxifolia			*commonae* Foerster	*pauciflorum* King & Gamble
					luteosquamatum Sleum.	
		Javanica			*brookeanum* Low ex Lindl.	*culminicolum* F. v. Muell.
					javanicum (Bl.) Benn.	*intranervatum* Sleum.
					lochae F. v. Muell.	*laetum* J.J. Smith
					macgregoriae F. v. Muell.	*leucogigas* Sleum.
						longiflorum Lindl.
						robinsonii Ridl.

A NEW HYDRANGEA FROM MEXICO

Lorin I. Nevling, Jr., and Arturo Gómez-Pompa

The genus *Hydrangea* is familar to both layman and scientist primarily through species which have ornamental value. Since the species most widely cultivated are shrubby, with the exception of the spectacular climbing *H. anomala* D. Don, and usually have been selected for inflorescences bearing large numbers of sterile flowers, one tends to have a distorted impression of the genus as a whole. In the recent monograph by Elizabeth McClintock (1957) two sections were recognized: Hydrangea and Cornidia, containing 11 and 12 species respectively. Section Hydrangea includes most of the cultivated species, all of which are shrubs, excepting *H. anomala*. Two species of this group, *H. arborescens* L. and *H. quercifolia* Bartram, are native to the southeastern United States, the remainder are Asiatic. In contrast, species of section Cornidia seem to be more flexible in growth form with many species occurring both as shrubs and climbers, depending on circumstances of position and, perhaps, age. The normal mature form, however, is a root climber. The species of this section are native to the New World, excepting *H. integrifolia* Hayata of Formosa and the Philippines. Thus 13 of 23 species are climbers.

In this paper a new climbing species of section Cornidia is described as *Hydrangea nebulicola* (Figs. 1 and 2). It was discovered in the deciduous liquidambar-oak forest of the Sierra de Chiconquiaco north of Jalapa, Veracruz, México. This zone can be characterized floristically by the abundance of individuals of *Alnus, Clethra, Cyathea, Hedyosmum, Liquidambar, Magnolia, Meliosma, Podocarpus*, and *Quercus* (see Gómez-Pompa, 1966). The climate in this region is temperate due to altitude (ca. 1500 m.) and extremely humid, not only because of high rainfall (250–300 cm. annually), but also because of the many clouds which sweep through the forest. It is difficult to determine the temperature in this zone exactly. However, from data obtained from a climatological station nearby (Naolinco, Ver.) we are able to give a mean temperature of between 17° and 18° C. The coldest month is January with an average of 12° to 14° C, the extreme minimum temperatures during this period being some degrees below 0° C. The topography is rather rugged with slopes of 10 to 40 percent. The soil, which is derived from volcanic rock, contains abundant organic matter. The new species is abundant only locally, and it possesses several characteristics which we believe to be of important evolutionary significance within the genus and which mark it as a very specialized member of section Cornidia. One of the most interesting aspects of this species is its vegetative reproduction. We believe that this type of reproduction has an adaptive value sufficient for the species even though the scarcity of individuals is notable. Several trips have been made without

FIG. 1. *Hydrangea nebulicola.* (*Gómez-Pompa 1541*). Flowering branch with details of inflorescence and pubescence of lower leaf-surface.

success to search for pistillate specimens. All that we have observed is that the flowering of the species is rare although it may continue over several months. With these considerations in mind and the realization that the species is both rare and dioecious we can understand the importance of vegetative reproduction and its rôle in survival.

In climbing species of this genus, three kinds of shoots are generally found: juvenile, found only in young plants; the terminal one, which functions as a climbing shoot; and the lateral shoot, which supports the reproductive functions and the primary photosynthetic activity. When a tree is the substrate the climbing often is restricted to a single individual. In this new *Hydrangea* several deviations from the general ground plan just mentioned are to be found. Although no juvenile plants were located in spite of a careful search, a fourth type of shoot bearing a marked re-

FIG. 2. Flowering branch of *Hydrangea nebulicola* showing paired inflorescences at anthesis and young inflorescences enclosed by cucullate bracts. Photograph from *Nevling & Gómez-Pompa 39.*

semblance to juvenile shoots was found. These, termed runner-shoots, were discovered along the forest floor, sometimes covered by leaf-litter. They permit a single plant to climb several individual trees simultaneously. Runner-shoots (FIG. 3) were quite common and are characterized morphologically by reduced bract-like deciduous leaves and adventitious roots on the lower and lateral surfaces, similar in external appearance to those found in *Hedera helix* L. These peculiar shoots seem to be selective as to the substrate tree, for they were found ascending only relatively mature tree trunks, although no selection as to substrate species is obvious. As a runner-shoot begins an ascent the reduced leaves become larger with a few marginal serrations above the middle of the lamina but very soon become similar to the mature leaf in form and size. The climbing shoot (FIG. 3) is characterized by a very marked unequal production of secondary xylem, the mass of the new wood being produced in the direction of the substrate. This apparently permits the continuing production of the adventitious roots necessary for attachment to the substrate. It is believed that detailed comparison of the wood anatomy of climbing *vs.* non-climbing species of *Hydrangea* might prove useful in the determination of evolutionary direction within the genus.

The inflorescences of species of *Hydrangea* are marked by having either monomorphic or dimorphic flowers. These two conditions are denoted by students of the genus as fertile and sterile flowers: fertile flowers being bisexual with androecium and gynoecium normally developed; sterile

FIG. 3. Young climbing shoot of *Hydrangea nebulicola* showing side normally appressed to substrate. Note adventitious roots and lateral branches. × approximately 3/4.

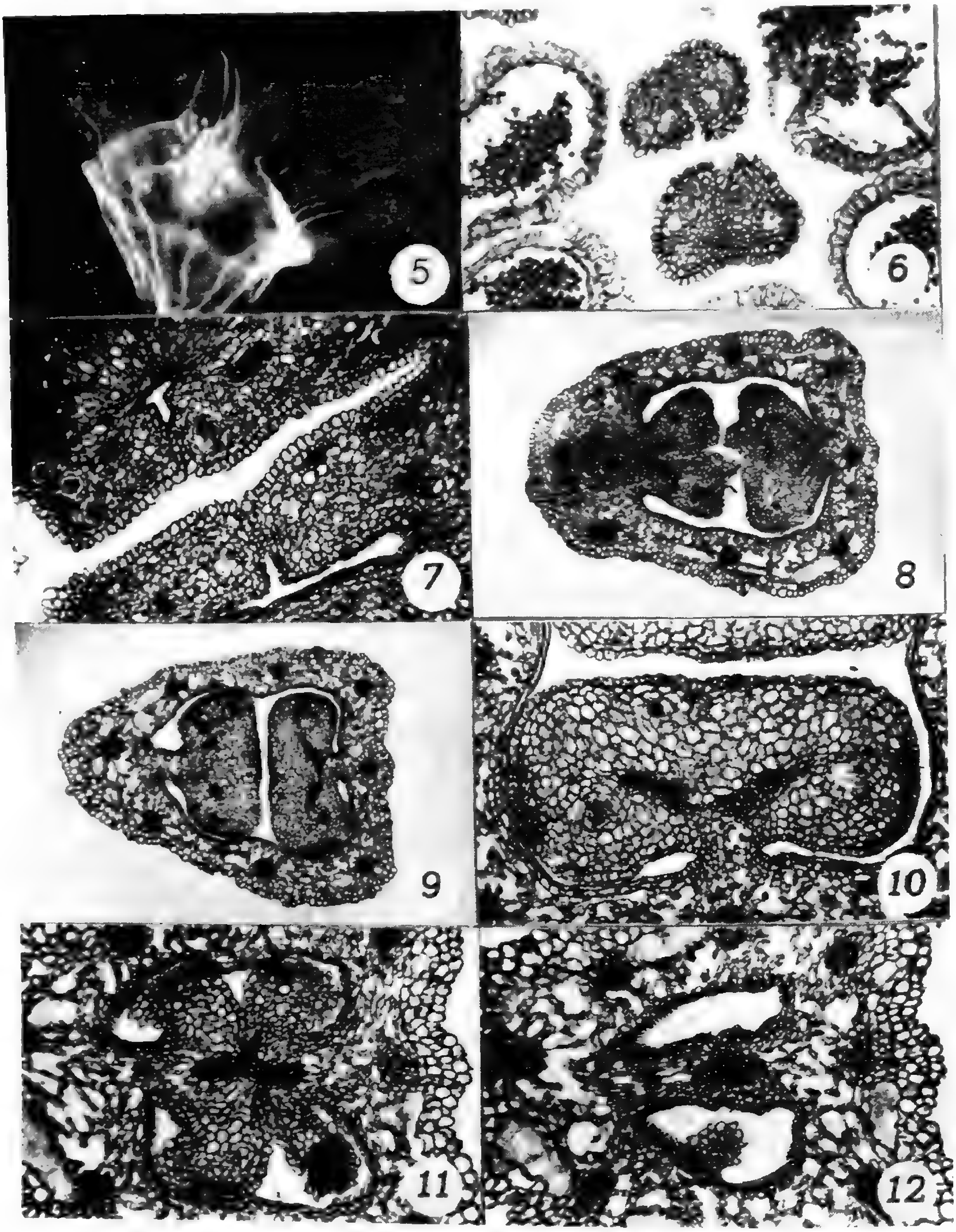
FIG. 4. Apex of runner-shoot of *Hydrangea nebulicola* showing reduced bract-like leaves, approximately natural size.

flowers having neither androecium nor gynoecium normally developed but with the calyx lobes becoming greatly enlarged and showy. An intermediate type with enlarged calyx lobes and functional reproductive organs is found in *H. scandens* (L.f.) Seringe. The inflorescence in this species also contains "normal" fertile flowers. Inflorescences containing both fertile and sterile flowers generally are considered more specialized than those composed of fertile flowers only. The addition of sterile flowers or the conversion of fertile flowers to sterile ones probably is related to increased efficiency in terms of insect attraction. Although in some species such as *H. anomala* D. Don the number of sterile flowers per inflorescence varies somewhat from year to year, the presence or absence of sterile flowers appears to be a relatively reliable taxonomic character. Two notable exceptions are *H. arborescens* L. and *H. scandens* in which considerable variability occurs.

In *Hydrangea nebulicola* another floral condition is present: the inflorescences contain only fertile flowers which appear to be functionally unisexual. In our field studies one mature plant has been observed to be staminate through two flowering cycles and for this reason we are inclined to believe that the plants are dioecious rather than monoecious. Although McClintock has suggested proterandry for *H. serratifolia* (Hook. & Arn.) Phil. f., we do not make a similar interpretation for *H. nebulicola*. In the flowers examined, pollen stainability with cotton blue in lactophenol is approximately 98 percent and all grains appear to be properly formed. Ovules have not been observed and the sterile placentae are enlarged, filling the locule, and leaving little room for ovule development. In addition, no discernible stigmatic surface was found on the styles. Curiously, the placentation at the base of the ovary is of the axile type noted by McClintock but the massive central trace divides almost immediately into two smaller traces which supply the two large parietal placentae, the ovary being bicarpellate and uniloculate (FIGS. 5–12). Near the apex of the ovary the two placentae divide so that the two carpels are open and their margins free from one another. At the roof of the hypanthium the carpels are open (the opening in the form of a linear slit). It is at such a minute opening that the terminal poricidal dehiscence of *Hydrangea* fruits takes place in other species. The two styles reflect the open condition by being obviously grooved nearly to their apices. Unfortunately, it must be recalled that the situation described applies only to staminate flowers and confirmation must await discovery of pistillate flowers (although in the bisexually flowered *H. arborescens* the placental configuration is identical with that of *H. nebulicola*). If we are correct in our interpretation of sexual dimorphism in this species, the pistillate flowers should have smaller petals, shorter stamens, no stainable pollen, longer styles, papillate stigmatic surfaces, and many ovules borne on parietal placentae.

The evolutionary significance of the "advancement" of bisexual flowers to unisexual ones is difficult to estimate in *Hydrangea* because of the few floral characteristics in which the species vary and the small degree of the variation. The recognition of sexual differences among fertile flowers may be helpful in defining evolutionary pathways. Solely on the basis of the unisexuality of the flowers, *H. nebulicola* would seem to be a specialized member of section CORNIDIA which is in turn more advanced than section HYDRANGEA.

A case of sexual dimorphism similar (but not precisely identical because of the presence of sterile flowers) to that just described appears to be found in *Hydrangea oerstedii* Briquet and *H. peruviana* Moricand. The characters which McClintock employs in her key to *Hydrangea* to dis-



FIGS. 5–12. *Hydrangea nebulicola (Nevling & Gómez-Pompa 39).* FIG. 5. Cleared flower showing grooved style, × 20. FIGS. 6–12. Transverse sections of flower. FIG. 6. Section at level through style apices, note grooves. × ca. 58. FIG. 7. Section at level of hypanthium roof showing open carpels and stylar canals, × ca. 58. FIG. 8. Section of ovary immediately below hypanthium roof showing free margins of placentae. × ca. 25. FIG. 9. Section at mid-ovary showing the large, sterile, parietal placentae, × ca. 25. FIG. 10. Magnification of one placenta (inclined 90° from previous figure) showing vascularization and absence of ovules. × ca. 58. FIG. 11. Section at base of placentae. Note fusion of ventral traces with each carpel becoming closed. × ca. 58. FIG. 12. Section at base of ovary demonstrating bilocular condition and compound ventral trace, × ca. 58.

tinguish these species are (in part) the relative length of stamens and styles of fertile flowers. In *H. oerstedii* the stamens are 2–4.5 mm. long and the styles are 0.3–1 mm. long, while in *H. peruviana* they are 0.4–1.6 mm. long and 1–2 mm. long, respectively. McClintock suggests in her discussion that the two may represent two forms of a dimorphic species. It is our suggestion that these two species do reflect two sexual forms of the same species. In addition to the larger stamens in *H. oerstedii* is accompanying high pollen stainability (with cotton blue in lactophenol). The short-styled flowers lack both papillate stigmatic surface and functional ovules. In *H. peruviana* the short stamens have no stainable pollen, although the anthers appear reasonably well formed. The long-styled flowers have a papillate stigmatic surface and produce many well-developed ovules. The vegetative morphology and geographic distribution present no great difficulty in the interpretation of these two taxa as functionally staminate and functionally pistillate components of the same species.

Hydrangea nebulicola Nevl. & Gómez-Pompa, sp. nov.

Planta fruticosa scandens ad 30 m. alta, sempervirens; ramuli ferruginei, glabriusculi. Folia simplicia, opposita, elliptica, 7–16 cm. longa, 4–9 cm. lata, apice acuminata, basi cuneata, coriacea, pubescentia pilis stellatis, 6–8-nervia; petioli 1–4 cm. longi. Inflorescentia in umbellis oppositis, 5–10 cm. in diametro, omnino velutina; flores steriles 0. Bracteae cucullatae, 1.5–3 cm. longae et latae. Flores ♂: hypanthia turbinata, 1–1.25 cm. longa, 1.5 mm. in diametro; petala 4, alba, ovata, 2–2.5 mm. longa, 1.25–2 mm. lata, caduca; stamina 8 vel 9, libera, quam petala longiora; filamenta 2–2.5 mm. longa; antherae oblongae; pistillum 2-carpellatum, ovulis 0; stylis effusis, ca. 0.5 mm. longis; stigmatibus 0. Flores ♀ et fructus non visi.

Powerful root climber, evergreen, to 20 cm. in diameter at the base, to 30 m. tall; bark of mature trunk gray, smooth and non-peeling; young shoots stout, tomentose, the trichomes stellate but often only the basal stalk persistent and then appearing simple, ferrugineous. Leaves simple, opposite, coriaceous, broadly elliptic, 7–16 cm. long, 4–9 cm. broad, acuminate at the apex, more or less cuneate at the base, sparsely ferrugineous-pubescent to glabrescent above, moderately ferrugineous-pubescent beneath, the midrib plane above, emersed beneath, the primary lateral veins 6–8 pairs, slightly arcuate, the margin entire; petiole 1–4 cm. long. Inflorescences borne in opposite axillary pairs near the apex of lateral (non-climbing) shoots, the axillary shoots 3–7 cm. long, ferrugineously felted, the inflorescences compound, umbelliform, 5–10 cm. in diameter, enclosed in bud by cucullate bracts, the bracts nearly orbicular, 1.5–3 cm. long and broad, chartaceous, pubescent, caducous. Sterile flowers absent. Fertile flowers unisexual by abortion, plants functionally dioecious (?). Staminate flowers: creamy white, glabrous throughout; pedicel ca. 2.5 mm. long; hypanthium turbinate, 1–1.25 mm. long, 1.5 mm. in diameter; calyx lobes free, very shallowly deltate; petals 4, valvate, free, ovate, 2–2.5 mm. long, 1.25–2 mm. broad, caducous; stamens 8 or 9, free, the filaments folded in bud becoming erect at anthesis, the filaments 2–2.5 mm. long; anthers greatly exserted, oblong, ca. 2 mm. long, 1.5 mm. broad, basifixed, dehiscing by lateral slits; pistillode 2-carpellate, inferior, ovules 0, the 2 styles free, recurved, ca. 0.5 mm. long, slightly canaliculate, stigmatic surface not apparent. Pistillate flowers and fruit not seen.

México. VERACRUZ: región de Misantla, Sierra de Chiconquiaco y Misantla, a 1540 m. de altitud en bosque de encino-liquidambar, 9 de julio 1966, *A. Gómez-Pompa 1541* (holotype MEXU, isotype GH); *R. Hernandez M. 306* (MEXU), *Nevling & Gómez-Pompa 39* (GH, MEXU).

Although this new species is placed in section CORNIDIA without hesitation, its affinities with other species of the section are still uncertain. Prior to any speculation concerning affinities, the entire section should be reexamined in terms of problems of floral sexuality mentioned previously. In addition, there is at least one, possibly two, undescribed species of *Hydrangea* from Chiapas referable to this section. Until these species are studied, definitive placement seems fruitless.

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ARNOLD ARBORETUM AND GRAY HERBARIUM
CAMBRIDGE, MASSACHUSETTS

AND

INSTITUTO DE BIOLOGÍA
UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
MÉXICO, D.F.

A SYNOPSIS OF THE ASIAN SPECIES OF DELPHINIUM, SENSU STRICTO*

PHILIP A. MUNZ

GROUP X

Leaves rather coarsely lobed as in Groups VIII and IX, but the spurs strongly curved to make about a half circle.

This group, also, is an artificial one and does not agree with any taxonomic subdivision proposed for the genus.

KEY TO SPECIES

1. Sepals with subapical cornute appendages 1–2 mm. long; flowers purplish blue.
    2. The sepals 18–20 mm. long; spur 20–22 mm. long. (These two species treated in Group VIII).
        3. Ultimate leaf-lobules 5–8(–10) mm. wide. Yunnan, etc. . . . . 146. *D. ceratophorum.*
        3. Ultimate leaf-lobules 2–4 mm. wide. Tibet. 145. *D. ceratophoroides.*
    2. The sepals 15–18 mm. long; spur to 18 mm. long. Szechwan. . . . . 236. *D. campylocentrum.*
1. Sepals lacking subapical cornute appendages.
    4. Stem and axis of inflorescence largely glabrous.
        5. Sepals 10–11 mm. long.
            6. Inflorescence racemose; pedicels 3.5–9 cm. long. Szechwan. (This species treated in Group VIII). . . . . 154. *D. glabricaule.*
            6. Inflorescence a diffuse panicle; pedicels 1.5–3 cm. long. Yunnan, etc. . . . . 239. *D. polyanthum.*
        5. Sepals 15–25 mm. long.
            7. Bracteoles 7–15 mm. long. Yunnan. . . . . 237. *D. eriostylum.*
            7. Bracteoles shorter, 2–7 mm. long. Szechwan.
                8. Petals more or less dark; sepals more or less strigulose, 17–20 mm. long. . . . . 240. *D. potaninii.*
                8. Petals bluish; sepals more loosely pubescent, 13–17 mm. long. . . . . 244. *D. tongolense.*
    4. Stem and/or axis of inflorescence more or less hairy or pubescent.
        9. Sepals 18 mm. or more long.
            10. Sepals glabrous; spur 17–18 mm. long. Dagestania. (Treated in Group IX). . . . . 215. *D. mariae.*

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* Continued from volume 49, p. 166. With this section of the paper the long series of studies by Philip A. Munz on the genera *Delphinium* and *Consolida* is completed. The series was initiated in volume 48 of this Journal and includes: A synopsis of African species of *Delphinium* and *Consolida* **48:** 30–55. 1967; A synopsis of the Asian species of *Consolida* (Ranunculaceae), *ibid.* 159–202; and the first two portions of the present paper, *ibid.* 249–302, 476–545, which is continued in the first number of the present volume, **49:** 73–166. *Ed.*

10. Sepals more or less pubescent; spur 20–25 mm. long. China. . . . 243. *D. spirocentrum.*
9. Sepals shorter.
11. Leaf divisions long-acuminate; bracteoles at middle of pedicels. Szechwan. . . . . 241. *D. pseudo-tongolense.*
11. Leaf divisions not long-acuminate.
12. Upper petal bidentate at apex; upper sepal largely 15–18 mm. long.
13. Inflorescence racemose; leaves with coarse teeth; bracteoles near the flower. . . . . 235. *D. bulleyanum.*
13. Inflorescence paniculate; leaves with fine teeth; bracteoles near middle of pedicel. . . . . . 244. *D. tongolense.*
12. Upper petal entire to somewhat erose at apex.
14. Lamina of lower petal not divided.
15. Limb of the lower petal elongate-linear. Asia Media. (Treated in Group VIII). . . . . 159. *D. knorringianum.*
15. Limb of the lower petal oblong, 5 mm. wide. Szechwan. (Treated in Group VIII). . . . . 156. *D. hirticaule.*
14. Lamina of lower petal divided.
16. Upper sepal 20–25 mm. long, the spur 16–18 mm. long. Altai. (Treated in Group IX). . . . . 217. *D. mirabile.*
16. Upper sepal shorter.
17. Sepals with appressed hairs, spur almost twice as long as blade. Yunnan. 238. *D. hamatum.*
17. Sepals with spreading hairs. Szechwan. . . . . . 242. *D. sino-vitifolium.*

235. **Delphinium bulleyanum** G. Forrest ex Diels, Notes Bot. Gard. Edinb. **5**: 265. 1912. FIG. 19, A.

Delphinium spirocentrum Hand.-Mazz. var. *pauciflorum* Chen, Bull. Fan Mem. Inst. Biol. (n.s.) **1**: 170. 1943. Based on *Yü 15544*, (BM), taken on the east flank of the Lichiang Range, Yunnan, 2800 m.; seen.

Perennial from a woody root, the stem 3–14 dm. tall, glabrous below, spreading pubescent and more or less glandular in the inflorescence, often subglaucous and somewhat violet, simple at least below; leaves well distributed, but gradually reduced up the stem, the lower petioles to 2 dm. long, glabrous, slightly dilated at the base, the uppermost leaves becoming foliose bracts; blades rounded-pentagonal in outline, 3–10 cm. broad, glabrous to scattered strigulose on both surfaces, pale beneath, 5-fid into subcuneate incised-serrate triangular-ovate segments; inflorescence rather laxly racemose; upper bracts setose to lanceolate, lower foliose and divided; pedicels strict, 1–10 cm. long, pubescent; bracteoles setose to wider, usually 5–10 mm. long, located near the flower; sepals rich purple to deep blue-lavender, pubescent without; upper sepal 10–20 mm. long, 8–12 mm. wide, ovate, obtuse to acute, the spur 18–22 mm. long, 4 mm. wide at base, rather narrow at tip, recurved at the middle to make an almost complete circle; lateral sepals oblong, rounded at apex, 12–15 mm. long, 7–9 mm. wide, glabrous except on the midveins; lower sepals 12–18 mm. long, 8–10 mm. wide, acuminately obtuse, pubescent; petals bluish, the upper laminae slightly oblique, glabrous, 9–11 mm. long, cleft for 1 or 2 mm., the spur 18–20 mm. long; lower laminae oblong, 5 mm. long, cleft halfway into 2 lance-oblong ciliate lobes, bearded at base, claw 4.5–5 mm. long; stamens 6–7 mm. long, glabrous; anthers oblong, dark, 1.3 mm. long; follicles 3(–4), somewhat divergent toward apex, sparsely pilose, 10–12 mm. long, the styles an additional 3 mm. long; seeds dark, 1 mm. long, obpyramidal, covered with minute scales.

TYPE: Moist rocky places among scrub on eastern flank of the Lichiang Range, Yunnan, at 3500–3800 m., Aug. 1906, *G. Forrest 2694* (E); seen. Isotype (BM); seen.

RANGE. A species of western Yunnan and southwestern Szechwan, at elevations of 2800 m. to 5100 m.

EXAMPLES. **Yunnan:** *Rock 9924, 9669, 9766, 9755, 6082, 6085, 5696, 10797, 6091*; *K. M. Feng 1982, 2001*; *Forrest 6556, 11130*; *Kingdon Ward 995*. **Szechwan:** *Kingdon Ward 4846, 4811.*

236. **Delphinium campylocentrum** Maxim. Act. Horti Petrop. **11**: 31. 1889. FIG. 19, B.

Delphinium tongolense Rehd. & Kobuski, Jour. Arnold Arb. **14**: 11. 1933, *pro parte*, not Franchet, 1893.

To about 7 dm. tall, the stem simple below, with a few scattered upcurved branches in the inflorescence, scattered-pilose below, more densely so above and more or less glandular, leafy, the leaves rather evenly developed; petioles slender, with somewhat dilated base; blades mostly 3-fid, the segments subsessile, cuneate, mostly 3–5 cm. long, the 2 lateral bilobed, then pinnately incisely lobed or coarsely toothed, the central palmately lobed or toothed, these lobes broadly lanceolate, mucronate, strigulose, paler beneath than above; inflorescence open, paniculate, several flowered; bracts mostly narrowly linear, entire, to ca. 10 mm. long; pedicels 2–5 cm. long, slender, with 1 to 3 bracteoles ca. 4–6 mm. long; sepals purplish blue, 15–18 mm. long, glabrous in original description, strigose in specimens seen, cornigerous below apex with terete outgrowths mostly 2-lobed and 2–4 mm. long; upper sepal elliptic-oval, 15 mm. by 8 mm., the spur coarse, strongly incurved (half circle or more), almost 2 cm. long, 4 mm. wide at base; lateral sepals broadly oblong, 13 mm. by 6.5 mm., pubescent along the midrib; lower sepals oblong, 18 mm. by 5 mm.; upper petal laminae glabrous, 11–12 mm. long, slightly 2-lobed, the strongly curved spur as long as the blade; lower petal laminae 11 mm. long, pilose, deeply cleft, oblong, clawed; stamens 5–7 mm. long, glabrous; anthers yellowish, 1.5 mm. long; follicles 3, glabrous.

TYPE: "Ad limites Kansu et Szetschuan, Valle fl. Heiho, 24 Julii 1885," *Potanin* (LE); seen.

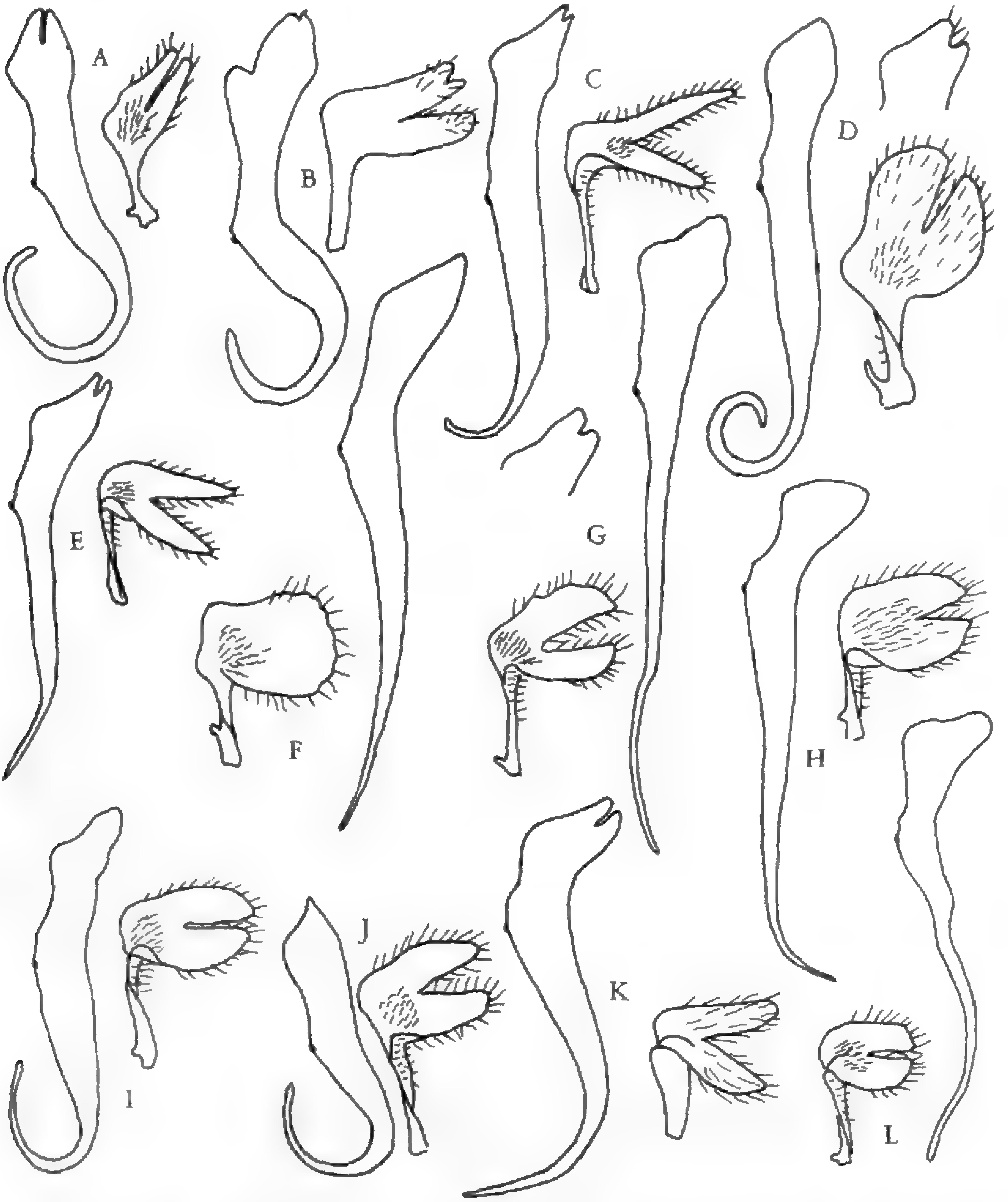

Figure 19. **Delphinium,** Group X. Petals, the upper spurred, the lower clawed. A. *D. bulleyanum*; upper lamina 9 mm. long, spur 18 mm.; lower lamina 5 mm. long, claw 4 mm.; drawn from *Rock 9924* (US). B. *D. campylocentrum*; upper lamina 12 mm. long, spur 14 mm.; lower lamina 6.5 mm. long, claw 5 mm.; drawn from *Harry Smith 4138* (A). C. *D. eriostylum*; upper lamina 11 mm. long, spur 17 mm.; lower lamina 9 mm. long, claw 6 mm.; drawn from *Esquirol 141*, TYPE (E). D. *D. hamatum*; upper lamina 10 mm. long, spur 22 mm.; lower lamina 9 mm. long, claw 5 mm.; drawn from *Rock 22852* (UC) and upper lamina tip from TYPE (P). E. *D. polyanthum*; upper lamina 9 mm. long, spur 15 mm.; lower lamina 7 mm. long, claw 5 mm.; drawn from *Licent 7719* (BM). F. *D. potaninii*; upper lamina 12 mm. long, spur 20 mm.; lower lamina 7 mm. long, claw 5 mm.; drawn from *Farges 630*, ISOTYPE of *D. fargesii* (NY). G. *D. potaninii*; upper lamina 10 mm. long, spur 23 mm.; lower lamina 7 mm. long, claw 5 mm.; drawn from *E. H. Wilson 1999* (GH). H. *D. sinovitifolium*; upper lamina 9 mm. long, spur 23 mm.; lower lamina 7 mm. long, claw 5 mm.; drawn from *E. H. Wilson 3088*, ISOTYPE (P). I. *D. spirocentrum*; upper lamina 10

SPECIMENS SEEN. **Kansu** and **Szechwan:** at about 3000 to 3500 m., *H. Li 74095* (E); *H. Smith 4138* (A, BM); *Ching 849* (E, GH, NY, US); *Rock 13161* (GH, NY), *13111* (GH, NY), *13109* (GH, US).

237. **Delphinium eriostylum** Lévl. Bull. Herb. Boiss. II. **6:** 505. 1906.

FIG. 19, C.

Apparently tall robust perennial, the stem coarse, smooth, glabrous, remotely leafy; upper leaves 3–5-fid almost to base, with scattered stiff hairs on both surfaces but especially on veins beneath, the blades 5–12 cm. wide, each segment narrow cuneate-obovate, incised ca. halfway to midrib into lance-ovate lobules or teeth 3–10 mm. long, 1–5 mm. wide, acute to acuminate; inflorescence a few branched open panicle, each raceme 2- to 6-flowered; bracts stiff-hairy, lance-linear, 2–3 cm. long, 2–3 mm. wide, long-acuminate; pedicels stiff, 2–7 cm. long, arched-ascending to suberect, with few to rather many spreading glandular hairs; bracteoles linear-subulate, 7–15 mm. long, bristly, near the middle of the pedicel; sepals violet, subglabrous; upper sepal ovate, 14 mm. by 9 mm., obtuse, the strongly curved spur ca. 20 mm. long; lateral sepals round-ovate, 16–18 mm. by 10 mm., rounded-obtuse; lower sepals elliptic-obovate, 18–20 mm. by 8 mm., pointed; petals bluish, the upper laminae slightly oblique, 12 mm. long, 4 mm. wide, glabrous, bidentate, the spur ca. 16 mm. long; lower laminae perpendicular to the claws, 7 mm. by 3 mm., bifid to beyond middle into lance-oblong lobes ca. 4.5 mm. long, ciliate and somewhat bearded; stamens 6–7 mm. long, glabrous; anthers dark, linear-oblong, 1.5 mm. long; carpels 3, sparsely stiff-hairy.

TYPE: Kweichow, Ta-tsong, Kouy-hoa, *Esquirol 141* (E); seen.

Another specimen came from the same area, *2095* without collector's name (E), and one from Yunnan-sen district, Gan-chouen, *Cavalerie 4486* (E).

238. **Delphinium hamatum** Franchet, Pl. Delavay. 28. *pl. 7.* 1889.

FIG. 19, D.

> *Delphinium ceratophorum* var. *brevicorniculatum* W. T. Wang, Acta Bot. Sinica **10:** 157. 1962. Based on *T. T. Yü 9598* from Yunnan (A); seen.

Perennial from a large root system; stem ascending, to ca. 2 dm. long, mostly solitary, spreading-hairy, the hairs ca. 1 mm. long; leaves basal, the petioles purplish, slender, hairy, 3–12 cm. long, thin-vaginate at base; blades 3- or 5-partite, pentagonal, 1–7 cm. long, somewhat wider, the

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mm. long, spur 20 mm.; lower lamina 7.5 mm., claw 5.5 mm.; drawn from *Forrest 17187*, TYPE of *D. pediforme* (E). J. *D. spirocentrum*; upper lamina 9 mm. long, spur 16 mm.; lower lamina 7.5 mm. long, claw 6 mm.; drawn from *Handel-Mazzetti 4656*, ISOTYPE (E). K. *D. tongolense*; upper lamina 9 mm. long, spur 16 mm.; lower lamina 7 mm. long, claw 6 mm.; drawn from *Harry Smith 11594* (A). L. *D. tongolense*; upper lamina 8 mm. long, spur 17 mm.; lower lamina 5 mm. long, claw 5 mm.; drawn from *Soulié 396* (P).

lobes obovate-cuneate, strigulose above, more loosely pubescent beneath, ca. 1 cm. wide and with few coarse triangular teeth 1–6 mm. long; flowers 1 to few, racemose; lower bracts often foliose, the others lance-linear, 5–15 mm. long, acuminate; pedicels arcuate-erect, 1–3 cm. long; bracteoles 2, linear, to 1 mm. broad, near the flower; sepals purplish blue, strigulose without, the upper sepal ovate, 13–16 mm. long, 8–10 mm. wide, acutish, the spur 22–25 mm. long, 3.5 mm. wide at base, tapered gradually to the hamate apex; lateral sepals ovate-oblong, strigose on midvein, rounded at apex, 15–17 mm. by 8–10 mm.; lower sepals elliptic-ovate, 16–20 mm. long, 10–12 mm. wide, obtuse; petals pale blue, the upper laminae almost straight, 10 mm. long, glabrous or nearly so, entire to emarginate; the spur 22 mm. long; lower laminae bearded, 9 mm. by 8 mm., cleft to ca. 4 mm., the claw 5 mm. long; stamens 6–7 mm. long, slightly ciliate; anthers dark, 1.5 mm. long; follicles 3, short-hairy, oblong, 12–15 mm. long, the styles an additional 3 mm.; seeds brown, 2 mm. long, winged on angles.

TYPE: Yunnan, "in collibus calcareis ad Fang-yang-tchang supra Mo-so-yn, alt. 3200 m.," Oct. 14, 1887, *Delavay* (P), seen; isotype (K), seen. Additional sheets with somewhat different data as to elevation are (K, NY).

DISTRIBUTION. A species from Yunnan, largely toward Tibet.

COLLECTIONS SEEN. *Forrest 15555* (K); *Rock 23457* (NY), *22852* in part (NY, UC, US), *Delavay 1676* (K, P), *2676* (P); *T. T. Yü 9832* (A), *12702* (A), *15544* (A).

239. **Delphinium polyanthum** W. T. Wang, Acta Bot. Sinica 10: 145. 1962. FIG. 19, E.

Stem 1.5–2 m. tall, ca. 8 mm. in diameter, glabrous, branched, equally foliose; the middle cauline leaves with non-vaginate petioles slightly longer than the blades; the latter broadly pentagonal, 6.5 cm. long, 10 cm. wide, cordate at base, tripartite 6/7 of their length, the middle part entire below, 3-fid to the middle, the lobes further divided or toothed, the lateral parts unequally bifid to below the middle, loosely strigulose beneath, hirtellous on nerves above; racemes 15–20 cm. long, forming a terminal pyramidal panicle; peduncles 6–10 cm. long, glabrous, axes with white retrorsely appressed hairs above intermixed with yellow glandular hairs; pedicels divergent, 1.5–3 cm. long; bracteoles just above middle of pedicel, subulate, 1.5–4 mm. long, 0.3 mm. wide; sepals blue, elliptic, 10 mm. long, loosely puberulent; spur 18 mm. long; upper petal laminae yellowish, glabrous, emarginate; lower laminae bluish, yellow bearded below the middle, bifid into lance-triangular lobes, ciliate, the claw about as long as blade; stamens glabrous; carpels 3, glabrous, 11–20 mm. long in maturity; seeds obconic-triquetrous, 1.5 mm. long, scaly laminate.

TYPE: Yunnan, Teh-chin, Pai-ma-shan, 3500 m., Sept., 1935, *C. W. Wang 69805* (PE), not seen; photo. (E), seen.

Two herbarium sheets (Shansi, *Licent 7719* (BM) and W. Kansu, *Licent 4279* (BM) agree with the description and photograph of the type, but have glabrous pedicels.

240. **Delphinium potaninii** Huth, Bull. Herb. Boiss. **1**: *332. pl. 14.* June, 1893. FIG. 19, F, G.

Delphinium grandiflorum var. *potaninii* Brühl in Brühl & King, Ann. Bot. Gard. Calc. **5**: 98. 1896.

? *Delphinium potaninii* var. *latibracteolatum* W. T. Wang, Acta Bot. Sinica **10**: 147. 1962. Based on *F. T. Wang 22014* which I have not seen, but which has bracteoles 10–12 mm. long, 1–1.2 mm. wide.

Delphinium fargesii Franchet, Bull. Soc. Philom. Paris VIII. **5**: 164. (August?) 1893. Type from Szechwan, district Tchen-kéou-tin, *Farges 630* (P), seen; four sheets all with lower petal laminae deeply divided.

Delphinium bonvalotii Franchet, *loc. cit.* 165. (August?) 1893. Type, Szechwan, near Ta-tsien-lou, *Prince H. d'Orleans & Bonvalot* (P); seen. Lower petal lamina deeply lobed, gaping.

Perennial from a thick root, the stems several, erect, thick, leafy, subglabrous, tall; petioles glabrous to hairy, the lower 1 dm. or more long, scarcely dilated at the base, the upper shorter; lower leaf blades broadly rounded in outline, 8–15 cm. broad, subglabrous or with stiff hairs along the veins beneath, 5- or 7-parted into broad cuneate-obovate segments, these incisely lobed or toothed with sharp angles and acute lobes or teeth 8–30 mm. long; upper leaves reduced, 3- or 5-parted; inflorescence an open panicle, largely glabrous; lower bracts foliaceous, 3-parted into lanceolate lobes to ca. 3 cm. long, upper bracts entire and lanceolate to setaceous, then 3–6(–10) mm. long; pedicels arched or straight, more or less divaricate, slender, 1–5 cm. long; bracteoles setaceous to linear-lanceolate, 2–6 mm. or more long, near the middle of the pedicel; sepals bright blue or with some violet, more or less strigulose without; upper sepal ovate, 10–20 mm. long, 5–12 mm. wide, the spur 20–30 mm. long, 3–4.5 mm. wide at base, strongly curved, with a blunt tip; lateral sepals elliptic, 18–22 mm. long, 10–12 mm. wide, rounded at apex; lower sepals elliptic-rhombic, 14–24 mm. long, 8–9 mm. wide, rounded at tip; petals bluish, the upper laminae almost straight, 8–10 mm. long, entire to emarginate, glabrous; lower laminae hirsute at base, ciliate on margins, oblong to oblong-obovate, 6–8 mm. long, mostly divided into lance-oblong lobes 3–4 mm. long, claw ca. 5 mm. long; stamens glabrous, 6–7 mm. long; anthers dark, 1.3–1.6 mm. long; follicles 3, divergent, glabrous to pubescent, 10–13 mm. long, the styles an additional 2.5 mm.; seeds brown, ca. 1.3 mm. long, covered with minute scales.

TYPE: Kansu, China, *G. N. Potanin*, 1885 (B), not seen; isotype (K), seen.

RANGE. Apparently quite widely distributed in western China, at elevations of about 3000 to 4200 m.

EXAMPLES. **Szechwan:** *E. H. Wilson 1999* (BM, GH, US), *819* (GH, US), *1088* (BM), *3095* (A), *3097* (K), *4702* (K, P), *1169* (GH); *K. L. Chu 3246* (E); *Henry 8792* (GH, P); *Pratt 344* (K); *C. L. Sun 476* (US); *Rock 16743* (A, US), *23992* (UC), *16637* (US), *16694* (GH, NY, US), *24166* (GH, UC); *W. P. Fang 1480* (US); *Harry Smith 4072* (A); *T. K. Wang & T. S. Wen 581* (A); **W. Hupeh:** *Wilson 1523* (NY). **Yunnan:** *Ducloux 5153* (P).

241. **Delphinium pseudo-tongolense** W. T. Wang, Acta Bot. Sinica 10: 153. 1962.

Stem 6–10 dm. high, 5 mm. in diameter at base, glabrous, often branched, equally foliose; median cauline leaves with petioles 7–8 cm. long, not vaginate; the blades broadly pentagonal, ca. 7 cm. long, 11–12 cm. wide, cordate at base, 3-parted to 6–10 mm. above the base, the middle part rhombic-ovate, acuminate, 3-lobed to below the middle, the lobes with lobules acutely dentate; lateral parts bifid and with secondary or tertiary lobules loosely strigulose beneath, loosely hirtellous along veins on upper surface; racemes 5–18 cm. long, axillary and terminal, forming an open panicle; pedicels 1–3 cm. long, ascending; bracteoles 4.5–7 mm. long, near middle of pedicel, with spreading yellow glandular hairs and retrorsely appressed white ones; sepals bluish purple, oblong to oblong-obovate, 12–19 mm. long, puberulent; spur about as long as sepals, subulate, spirally decurved at middle; upper petal laminae blue or yellowish, glabrous, rounded or emarginate at apex; lower laminae blue, ovate, 2-lobed to middle, yellow bearded at base, long-ciliate, claw appendiculate, as long as limb; stamens glabrous; carpels 3, glabrous or puberulent above.

TYPE: Szechwan, Pao-Lsing, *T. P. Soong 38915* (PE), not seen; photo. (E), seen.

Said to be near *D. tongolense*, but with long-acuminate leaf parts, bracteoles at middle of pedicel, and spur spirally decurved.

242. **Delphinium sino-vitifolium** W. T. Wang, Acta Bot. Sinica **10**: 152. 1962. FIG. 19, H.

Delphinium vitifolium Finet & Gagnep. Bull. Soc. Bot. France **53**: 126. 1906, not Willd.

Stem slender with soft spreading hairs, 3.5–4 dm. high; cauline leaves few, pilose on both surfaces, slightly cordate, 3–5 cm. in diameter, 3-parted less than halfway into lobes broader than long, these lobes in turn divided into semi-ovate mucronate-acute lobules 3–5 mm. long, somewhat broader; petioles 3–5 cm. long, hirtellous; upper leaves smaller, 1–1.5 cm. long, sessile; raceme lax, few flowered, simple; lower bracts foliose, to 1.5 cm. long, the upper subfiliform, pilose, ca. 8 mm. long; pedicels hirtellous, slender, 3–4 cm. long; bracteoles setiform, pilose, 5–6 mm. long, removed as much as 1 cm. from the flower; sepals blue, pubescent, the upper ca. 10 mm. long with a spur 25 mm. long and hamate at apex; other sepals deltoid-ovate, ca. 12 mm. long; petals bluish, the upper laminae oblique, entire, rounded at apex, 9 mm. long, the spur 22–24 mm. long; lower laminae oblique, oblong-ovate, 7 mm. long, bearded yellow, white-ciliate, divided one third its length, claw hirtellous, appendiculate, 5–6 mm. long; anthers dark, elliptic; carpels 3, glabrous.

TYPE: Szechwan, 3200–4300 m., Sept., 1904, *Wilson 3088* (P, A); seen.

243. **Delphinium spirocentrum** Hand.-Mazz. Symb. Sinicae Pt. 7: 280. 1931. FIG. 19, I, J.

Delphinium spirocentrum var. *hirsutum* Chen, Bull. Fan Mem. Inst. Biol. Peping (n.s.) **1**: 169. 1948. Isotype, *T. T. Yü 7769* (A) from Yunnan; seen.

Delphinium spirocentrum var. *grandibracteolatum* W. T. Wang, Acta Bot. Sinica **10**: 153. 1962. Isotype, Yunnan, *T. T. Yü 9018* (A); seen.

Delphinium pediforme Comber, Notes Bot. Gard. Edinb. **18**: 237. 1934. Type, Yunnan, Mekong-Salwin divide, Salwin Valley, *Forrest 17187* (E), seen; istoype (P), seen.

Delphinium spirocentrum var. *pediforme* (Comber) W. T. Wang, Acta Bot. Sinica **10**: 152. 1962.

Stems usually more than one, simple, 1–9 dm. tall, rather slender, densely retrorse-villous, scattered leafy; lower petioles to ca. 3 dm. long, villous, more or less dilated at base, the upper cauline much shorter; leaves rounded-pentagonal in outline, 3–14 cm. in diameter, green and strigose above, paler and with longer stiffer hairs beneath, 5-fid to within 1 cm. of the base, the segments cuneate-obovate, rather shallowly pinnatifid into few lance-oblong teeth or lobules 2–5 mm. wide and rounded to obtuse at apex; racemes simple, rather few flowered, to ca. 2 dm. long; pedicels erect, 2–8 cm. long, with spreading or somewhat retrorse hairs; bracteoles linear, 8–10 mm. long, hairy, placed near the middle of the pedicel or above or below; sepals purplish blue, ovate, strigose without, the upper 15–18 mm. by 7–10 mm., obtuse, the spur sometimes coiled in an almost complete circle, ca. 2 cm. long, 5 mm. wide at base; lateral sepals oblong, 20 mm. by 8 mm.; lower sepals ca. 22 mm. long, 10 mm. wide, obtuse; petals blue, the upper laminae straight, 9–11 mm. long, entire to emarginate, the spur 16–20 mm. long; lower laminae elliptic-obovate, ciliate, bearded at base, 7–11 mm. long, shallowly to deeply bifid, the claw 5–6 mm. long, not appendaged; stamens 6–7 mm. long, glabrous; anthers blue, linear, 2 mm. long; follicles 3, hairy, 15–30 mm. long; seeds brown, 1.3 mm. long, squamate.

TYPE: Szechwan, west side of Mt. Piepun near Dschunglien, *Handel-Mazzetti 4656* (W), not seen; isotype (E), seen.

DISTRIBUTION. Occurring at elevations of 2800 to 4800 m., Szechwan and Yunnan.

EXAMPLES. **Szechwan:** *Handel-Mazzetti 7302* (GH, NY); *Rock 18015* (US), *16694* (GH, NY, US), *16637* (US), *24166* (GH, UC), *24589* (NY, UC), *16760* (P, US), *23979* (E, GH, NY), *16922* (NY, US), *16929* (GH, UC, US), *18294* (US), *13979* (GH, NY, UC), *16814* (F, US), *16398* (GH, US), *16694* (GH, NY, US); *Forrest 22184* (US); *Kingdon Ward 4375* (E). **Yunnan:** *Rock 24771a* (GH, K, NY, UC), *9706* (NY, UC, US), *23080* (K, NY, UC, US), *23101* (GH, UC), *22852* (BM); *Yü 7427* (A), *14577* (A, BM, E), *22461* (A, E), *23215* (A, E); *C. W. Wang 68543* (A), *68635* (A); *Kingdon Ward 4617* (E), *4604* (E), *4826* (E); *Schneider 3249* (GH, US).

244. **Delphinium tongolense** Franchet, Bull. Soc. Philom. Paris VIII. **5**: 166. 1893. FIG. 19, K, L.

Perennial from woody base; stems 1 or more, to 1 m. tall, glabrous or with long white or yellowish hairs, (some with enlarged base), few branched above, leafy almost to the summit; petioles slender, the lower 2–3 dm. long, not much widened at base, the upper shorter; blades palmately 3- or 5-lobed to middle or below, the lobes cuneate-obovate, coarsely rather few toothed or lobed, blade as a whole 5–10 cm. wide and long, mostly subglabrous; inflorescence largely paniculate, the branches few, lax, few to several flowered; lower bracts foliaceous, trifid, to 2.5 cm. long, the upper entire, linear or broader, 5–15 mm. long; pedicels slender, ascending, subglabrous to spreading-pubescent, 2–5 cm. long; bracteoles linear-setaceous, 4–7 mm. long, near the middle of the pedicel; flowers deep to pale blue; upper sepal ovate, 15–17 mm. long, 8–10 mm. wide, pubescent, obtuse, the spur 2.5 cm. long, 4 mm. wide at base, pointed; lateral sepals 13 mm. by 10 mm., rhombic-ovate, rounded at ends; lower sepals 15 mm. by 10 mm., more narrowed at base; petals bluish, the upper laminae oblique, 8 mm. long, entire to bidentate, the curved spur 18–20 mm. long; lower laminae bearded, 5–7 mm. long, with 2 divergent lance-oblong lobes 3.5–4 mm. long, claw broad, not appendaged, 5 mm. long; stamens 6–7 mm. long, glabrous; anthers dark, 1.6 mm. long; follicles 3, subglabrous, divergent, 1–2 cm. long, the styles an additional 2 mm.; seeds many, angular, covered with lamellose papillae.

TYPE: Western China, Szechwan, Tongolo, valley of Olong-chen, *R. P. Soulié 396* (P); seen. *Soulié 2383* is in a type cover at (K).

RANGE. Western China and adjacent Tibet at perhaps 3500 to 4500 m.

EXAMPLES. **Szechwan:** *E. H. Wilson 3089* (K, P); *Soulié 2383* (K, NY, P); *Stevens 454* (F); *McLaren's collectors 258* (E, UC), *206* (E). **Yunnan:** *Ducloux 4600* (P). **Sikang:** *H. Smith 11340* (A), *11339* (MO, NY), *11594* (A). **W. Tibet:** Batang, *Soulie 3890* (P), *3889* (P), *3888* (P), *3050* (P).

REPRESENTATIVE EXSICCATAE

(Unfortunately many important specimens, especially of early collections in Siberia, were not numbered. To cite Regel collections, for instance, is almost useless; often several made in the same year represent different species, so to say "*Regel* in 1891" is not definitive.)

Abolin *8193, D. confusum*

Aitchison *957, D. brunonianum; 1004, kohatense; 671, semibarbatum; 862, suave; 559, 575, uncinatum*

Alboff *194, 195, 196, 182, D. pyramidatum; 190, schmalhausenii; 15, speciosum*

Alexeenko *2620, D. crispulum*

Ali, Shaukat *53, 54, D. brunonianum*

Anderson, T. *345, D. viscosum*

Appleton in 1906, *D. dasyanthum; 3862, suave*

Arnold *104, 213, D. brunonianum; 12, kamaonense*

Artemjev *4266, D. duhmbergii*

Atkinson *24250A, D. roylei*

Aucher *79, D. tuberosum*

Bacon, Eliz. *73, D. suave*

Bailey, F. M. *100, D. vestitum*

Balansa *859, D. dasystachyum; 1352, formosum; 1353, longebracteatum; 728, peregrinum; 858, venulosum*

Balls, E. K. *496, 1975, D. formosum*; *1207, 2406, peregrinum*
Balls & Gourlay *1977, 1992, D. dasystachyum*; *1977a, longebracteatum*
Banerji *1231, D. vestitum*
Barbey *295, D. fissum* ssp. *anatolicum*
Beauvais *409, D. delavayi*; *1074, mosoynense*
Becker, Al. *29, D. turkmemum*; in 1873, *D. ochroleucum*
Biskam *2253, D. denudatum*
Bodinier & Ducloux *370, D. taliense*
Bohnhof *163, D. maackianum*
Boissier, June 1842, *D. cinereum*; in 1846, *ithaburense*; April 1846, *peregrinum*
Bor in 1941, *D. cashmerianum*
Borissowa *83, D. semibarbatum*
Bornmüller *972, D. albiflorum*; *6060, 6062, aquilegifolium*; *1529, 2674, 3093, venulosum*
Bourgeau *9, D. peregrinum*
Brandis *731, D. vestitum*
Brown, W. E. *804, D. nuristanicum*
Bullock *7, D. anthriscifolium* var. *calleryi*; *10125, anthriscifolium* var. *savatieri*
Burtt & Nairn *586, D. suave*
Bushnell *470, D. maackianum*

Callery *6, 51, D. anthriscifolium* var. *calleryi*
Calvert & Zohrab *1347, D. albiflorum*
Capus *50, 51, 53,* and June 12, 1886, *D. ochroleucum*
Carmichael *823, D. chefoense*
Cavalierie *2344, 2957, D. anthriscifolium*; *2169, 2822, anthriscifolium* var. *calleryi*; *2095, 4486, eriostylum*; *7871, georgei*
Cave, G. H. *6, D. caeruleum*; *177,* and in 1910, in 1917, in 1919, *D. viscosum*
Chaffanjon *804, D. biternatum*
Chand, T. R. *72A, 588, 406, 887, D. brunonianum*; *576, cashmerianum*; *881, densiflorum*; *3449, 7192, 31250, stapeliosum*; *1190, vestitum*
Chaney *136, 467, 1104, D. grandiflorum*
Chang & Jen *6099, D. glabricaule*
Chapman, F. S. *35, D. caeruleum*; *167, 201, gyalanum*
Chen, F. H. *341, D. maackianum*
Chiao *1758, D. hirticaule*
Chien *5877, D. anthriscifolium* var. *calleryi*
Ching, R. C. *1363, 8442, D. anthriscifolium* var. *calleryi*; *849, campylocentrum*; *21392, 21616, 30509, ceratophorum*; *21456, delavayi*; *21418, glabricaule*; *22022, 30535, hirticaule*; *30572, likiangense*; *922, 1070, pseudograndiflorum*; *1123, pulcherrimum*; *657, 6576, pylzowii*; *21372, tatsienense*; *861, trichophorum*; *534, tsoongii*
Chu, K. L. *3246, D. potaninii*; *3606, scaposum*
Chung *2602, anthriscifolium* var. *calleryi*
Clarke, C. B. *29095B, D. roylei*; *29506, pyramidale*; *16117, 6168, 16354, 16381, 38970, 40301, 44861, stapeliosum*
Collett, H. *964, D. burmaense*; *5404A, vestitum*
Colom *282, D. altissimum*
Conrath *1889, D. schmalhausenii*
Cooper, R. E. *760, D. caeruleum*; *5309, 5648, cashmerianum*; *2024, 2294, cooperi*; *4322, ludlowii*; *4791, muscosum*; *5253, vestitum*; *605, 1003, 2204, 4911, viscosum*
Cooper & Bulley *2008, 2556, D. altissimum*; *4114, 4223, scabriflorum*
Coventry *226, D. pyramidale*
Crookshank, Helen *324, 366, D. centeteroides*
Cunningham, R. *322, D. potaninii*; *327, souliei*; *352, trichophorum*

Davis, P. H. *30593, 31305, D. albiflorum*; *32562, buschianum* in part; *22801, 22593, 23061, 23325, 23349, 23954, 24370, carduchorum*; *23612, 23327, 32443, 32562, crispulum*; *31669, 31999, dasystachyum*; *39053, davisii*; *13140, 14703, fissum* ssp. *anatolicum*; *21122, 21211, formosum*; *38373, ilgazense*; *4608 & 4608a, 4894, ithaburense*; *31496, kurdicum*; *33853, 33907, ochroleu-*

cum; 4801, 9913, 13473, 14410, 15421, 31567, 38840, peregrinum; 32782, 32788, 32813, venulosum; 35701, virgatum

Delavay, Abbé *967, 1845, D. ceratophorum; 22, 74, 1846, 1847, 4109, delavayi; 1676, 2676, hamatum; 2484, likiangense; 8717, mosoyense; 993, 1844, 4220, pycnocentrum; 9, taliense; 967 bis, 6515, 6670, yunnanense*

Dhwoj, Lall *49, 0253, D. altissimum; 556, caeruleum; 0191, 0641, drepanocentrum; 0238, glaciale; 36a, 122, himalayae; 49, 267, incisum; 35, 225, nepalense; 234, pyramidale; 253, scabriflorum; 92, 128, 0258, vestitum*

Dickason *369, D. brunonianum; 9052, burmaense; 367, 368, 370, 371, 373, cashmerianum; 366, denudatum; 365, roylei; 335, pyramidale*

Dinsmore *1864, D. ithaburense*

d'Orléans, Prince, & Bonvalot 7–29–1890, *D. tatsienense*

Dorsett & Dorsett *696, 3367, D. grandiflorum*

Dorsett & Morse *7051, D. grandiflorum*

Douglas, W. O. *161, 236, D. aquilegifolium; 39, ithaburense*

Drummond, J. R. distributions *1313, 4341, 4346, 4348, D. brunonianum; 8328, denudatum; 14811, kohatense; 4345, 4349, 6285, vestitum*

Ducloux *597, D. ceratophorum; 5337, delavayi; 579, hirticaule; 3875, mosoynense; 5153, potaninii; 596, tatsienense; 4600, tongolense; 370, 2874, 5866, 7329, yunnanense*

Duthie, J. F. *745, 5301,* in 1896, *7–25–1899, 7–24–1899, 13370, 13751, 13921, D. brunonianum; 794, 3804, 5302, cashmerianum; 2677, 5303, densiflorum; 2675, 5299, kamaonense; 13490, 14123, pyramidale; 13440, 14091, roylei; 5304, 19119, vestitum*

Egorova, Tzelev, & Czerepanov *418, D. pallidiflorum*

Emme, L. *451, D. dasyanthum*

Esquirol *24, 122, D. anthriscifolium* var. *calleryi* & var. *savatieri* respectively; *141, eriostylum*

Eyerdam, W. *2, 7–27–28, 7–14–28, 7–15–28, 8–25–28, D. brachycentrum*

Faber, *725, D. anthriscifolium*

Falconer *66, D. brunonianum; 65, cashmerianum; 60, denudatum; 62, pyramidale; 61, roylei; 64, vestitum*

Fan & Li *98, D. anthriscifolium*

Fang, W. P. *758, D. anthriscifolium; 12258, anthriscifolium var. calleryi; 2944, delavayi; 9286, grandiflorum; 1083, 4037, orthocentrum; 2241, spirocentrum; 4038, sungpanense; 4276, tatsienense*

Farges *1146, 1440, 1441, D. anthriscifolium; 630 bis, 630 ter, hirticaule; 630, potaninii*

Farrer *159, D. georgei; 1156, 1867, micropetalum*

Farrer & Purdom *242, 243, D. albocaerulem; 237, beesianum; 578, 611, grandiflorum; 253, monanthum; 710, pylzowii; 798, 800, 803, trichophorum*

Faurie *26, D. maackianum*

Fedtschenko in 1901, *D. dasyanthum*

Feng, K. M. *2395, D. beesianum; 1982, 2001, bulleyanum; 2714, chefoense; 217, 1697, delavayi; 2742, 2272, georgei; 2207, mairei; 2514, mosoynense; 1836, 2115, pogonanthum; 2257, tatsienense; 2841, tenii; 1726, umbrosum; 89, yunnanense*

Field & Lazar *730, 850, D. peregrinum*

Fleming *5–23–51, D. uncinatum*

Forrest, G. *6694, 11276, 6364, 14857, 18961, 20204, 20572, 22967, 22577, D. beesianum; 2694, 6556, 11130, bulleyanum; 6403, 6568, 2763, 10967, ceratophorum; 3035, 6690, 11363, 15173, 15198, 16942, 22471, 22483, coleopodum; 2963, 2861, 2604, 6319, 28587, 2604, 6319, delavayi; 11353, georgei; 15555, hamatum; 6483, 6540, 2903, 11360, 11052, 11203, 16949, 15322, 15170, 16949, likiangense; 221, 27516, 27225, 25091, micropetalum; 20780, monanthum;*

2866, 6533, 15233, mosoynense; 6538, 10968, 11449, 15112, 16951, 23185, 22378, pseudograndiflorum; 14929, 17187, 19031, 30044, 22184, spirocentrum; 6494, 6538, tatsienense; 6683, 3030, 11305, 16923, 15194, 22347, 22603, 22966, trichophorum; 14665, 18962, 20060, 20979, tsarongense; 25052, umbrosum; 2977, 7216, 15536, yunnanense
Frödin *328, D. vanense*
Fu, K. N. *1146, D. acuminatissimum*
Furse *3654, 3785, D. albiflorum; 2627, aquilegifolium; 3061, cyphoplectrum; 3732, dasystachyum; 3404, macrostachyum*
Furse & Synge *329, 330, D. aquilegifolium; 784, laxiusculum*

Gaillardot *52, 367, D. peregrinum*
Garrett *452, D. siamense*
Giles 6–24–86, *D. kohatense*
Gill *151, D. brunonianum*
Gillett, J. B. *9501, 12473, D. micranthum; 11782, pallidiflorum*
Gillett & Rawi *7223, 7404, 11206, D. micranthum*
Gilliatt-Smith *2514, D. crispulum*
Giraldi *4819, 4820, 4823, 4825, 4826, D. giraldii*
Gontchazov 8–22–1928, *D. dasyanthum*
Gould, B. J. *1412, D. glaciale; 508, kingianum; 1300, viscosum; 1598, wardii*
Griffith *45, D. centeteroides; 43, kohatense; 42A, 461, 827, D. stapeliosum*
Grossheim, A. *305, D. crispulum; 37, ochroleucum*
Grossheim & Schischkin *333, D. flexuosum*
Guest, E. V. 7–28–33, *D. kurdicum*
Guest & Ludlow-Hewitt *2691, D. micranthum*
Gurvitsch in 1937, *D. laxiusculum*
Guthrie, J. in 1947, *D. gyalanum*

Haines, R. W. *416, D. kurdicum; 513, macrostachyum; 1320, micranthum; 1712, quercetorum*
Hanbury-Tracy *143, D. brunonianum; 195, pseudograndiflorum*
Handel-Mazzetti *5495, D. autumnale; 11802, anthriscifolium; 8128, beesianum; 4105, coleopodum; 9712, micropetalum; 5103, mosoynense; 4576, 7819, 7424, pogonanthum; 4656, 7302, spirocentrum; 5515, trichophorum; 7934, tsarongense; 7809, umbrosum*
Haradjian *552, 571, 2537, D. fissum* ssp. *anatolicum; 1525, 2158, peregrinum*
Harriss, S. A. *15837, D. suave*
Haussknecht, April 1868, *D. cyphoplectrum*; in 1865, *peregrinum*; June 1867, *quercetorum*; July 1868, *saniculifolium*
Hay *373, D. centeteroides*
Hazara, Burtt & Kazmi *1266, D. pyramidale*
Heideman 5–27–1932, *D. pallidiflorum*
Heideman & Aliev 7–2–1932, *D. szowitsianum*
Hemsley *7, D. anthriscifolium* var. *calleryi*
Henry, A. *1348, 1966, 5862, D. anthriscifolium; 7263, anthriscifolium* var. *calleryi; 200, anthriscifolium* var. *savatieri; 6952, 6952A, henryi; 9668, 9668A, pogonanthum; 8792, potaninii; 7448, trifoliolatum; 9272, 9272A, 13440, yunnanense*
Hingston *367, 408, D. gyalanum*
Hohenacker in 1834, in 1835, *D. laxiusculum*; in 1838, *ochroleucum*; in 1834, *puniceum*; July 1838, *szowitsianum*
Hooker, J. D. *2293, D. glaciale*
Horner, S. *152, 153, D. cyphoplectrum*
Hosie in 1904, *D. trichophorum*; in 1904, *tsarongense*
Hsia *3159, 2065, D. grandiflorum*
Huggins, P. *39, D. densiflorum*
Hultén *733, 638, D. brachycentrum*

Ikonnikov-Galitzky *365, 746, 3335, 3428, D. cheilanthum; 785, dissectum; 2915, elatum; 210, 314a, 802, grandiflorum; 82, triste*

Jacquemont *668, 2025, D. brunonia-*

num; 720, 1896, caeruleum; 671, 1005, cashmerianum; 721, 883, denudatum; 673/791, 791, 1171, roylei; 672, uncinatum; 2134, vestitum
Jafri & Akbar *2197, D. centeteroides*
Jaschke *2495, D. lacostei*

Kabir *14811, D. aquilegifolium*
Karelin & Kiriloff *1169, D. dasyanthum; 1164, duhmbergii; 1168, elatum*
Karjagin & Jsoev 8–25–1933, *D. foetidum*
Karjagin & Safiev *150, D. buschianum*
Karo, F. *188, D. cheilanthum; 207, grandiflorum*
Kass & Nuri *27607, D. quercetorum*
Keng 1311, *D. anthriscifolium* var. *calleryi; 880, anthriscifolium* var. *savatieri*
Kerr, A. F. G. *337, 4454, 6612, D. siamense*
Kingdon-Ward; see Ward
Kitamura 8–2–1955, *D. nuristanicum*
Knorrig, O. E. *368, D. knorringianum*
Koelz, W. *12719, D. afghanicum; 18257, aquilegifolium; 1000A, 1233, 2400d, 2407, 2508, 2804, 2835a, 3026, 5562, 6516, 6622a, 6703, 6841, 7006, 9551, 10112, brunonianum; A38, 1277, 850, 588, 1313, 2787, 2803a, 2973, 5803, 6026, 6927, 10028, 10041, cashmerianum; 21082, densiflorum; 1848, 3163, 4841, 4638, 4963, 8344, 8659, 8328, 21113, denudatum; 4757, 4921, 4922, koelzii; 18164, lanigerum; 12713, minjanense; 18015, pallidiflorum; 9313, pyramidale; 9261, roylei; 25579, 31250, stapeliosum; 18519, syncarpum; 13725, 13853, 14100, tetanoplectrum; 18110a, tuberosum; 3077, 21952, vestitum*
Kolenati *1590, D. ochroleucum*
Komarov, V. L. 6–26–93, *D. biternatum*; 7–18–1908, *3896, D. brachycentrum*; 6–26–92, *dasyanthum; 670, grandiflorum; 671, maackianum*
Korolkov *76, D. dasyanthum*
Korshinsky *80, D. karateginii*
Koslov, *240, D. grandiflorum*
Kotschy *239, 239b, D. aquilegifolium; 153, 393a, 400*, May 1842, *cyphoplectrum; 427, 503, kurdicum; 430, lanigerum; 754, longebracteatum; 410, 610, micranthum; 1*, 8–1–41, *peregrinum; 536, saniculifolium; 227, virgatum*
Krascheninnikov *87, D. dissectum*
Krause, K. *4109, D. peregrinum*
Kronenburg *166, D. pallidiflorum*
Kuan, K. C. *2290, D. tianshanicum*
Kuschakewicz 7–22–78, *D. dasyanthum*
Kusnezow *875, 885, D. elatum*

Lace, J. H. *3862, D. centeteroides; 164, 734, 1523, 1924, D. denudatum; 6012, lacei; 2094, lacostei; 467, 850, roylei; 3326, 3351, uncinatum*
Lacoste *11, D. molle*
Ladygin, Oct. 1900, *D. trichophorum*
Lamont, J. *1065, D. anthriscifolium*
Lance *18, D. brunonianum; 21, cashmerianum*
Ledebour *809, D. grandiflorum*
Legendre *1563, D. lancisepalum*
Lepcha *269, D. caeruleum; 865, micropetalum*
Li, C. F. *10707, D. grandiflorum*
Li, H. *74095, D. campylocentrum; 78175, lancisepalum; 78358, pseudocampylocentrum; 74016, pseudograndiflorum; 74723, souliei; 78699, trichophorum*
Li, K. F. *63169, D. trifoliolatum*
Li & Chu *7003, D. tianshanicum*
Licent, R. P. *1305, 1999, 7665, D. grandiflorum; 2760, 4544, henryi; 4279, 7719, polyanthum; 4686, pulcherrimum; 5655, siwanense*
Ling, K. *9143, D. grandiflorum*
Liou, K. M. *1405, D. grandiflorum; 5093, henryi*
Liou, T. N. & P. C. Tsoong *986, D. taipaicum*
Lipschitz *685, D. batalinii; 718, minjanense*
Liu, Y. *1433, 1968, 12689, D. grandiflorum*
Lipsky *1685, D. batalinii; 1783, duhmbergii;* 8–10–1896, *propinquum; 1887, semiclavatum; 3070,* 5–8–1912, *turkmemum*

Litchfield in 1890, *D. densiflorum*
Litwinow *490, 989, D. grandiflorum; 2026, 3013, maackianum; 443, 444, semibarbatum; 447, 448, turkmemum*
Loftus 5–3–1852, *D. cyphoplectrum*
Lomakin in 1895, *D. foetidum*
Lowndes, D. *1283, 1323, D. brunonianum; 1229, 1324, kamaonense; 1347, 1505, nepalense*
Ludlow, F. *433, 838, D. brunonianum; 332, candelabrum; 864, cashmerianum; 775, 781, kamaonense; 762, poltaratzkii; 48, psuedograndiflorum; 868, roylei*
Ludlow & Sherriff *1987, acuminatissimum; 523, 6899, D. albocaeruleum; 298, 3496, 3558, altissimum; 1995, 6912, 8504, 8930, 8561, 9010, 9925, brunonianum; 873, 887, 1016, 19686, bhutanicum; 779, 1968, 1977, 2400, 9751, 9952, 11067, caeruleum; 1881, 2814, 7914, cashmerianum; 523, candelabrum; 3519, 17065, 19578, cooperi; 7671, 8106, 9106, denudatum; 16786, 17128, 19724, glaciale; 9073, 9814, 11114, grandiflorum; 154, 528, 2421, 2461, 1942, 8781, 8789, 2777, 9893, 11108, gyalanum; 2424, hillcoatiae; 527, 855, kingianum; 894, 470, 368, 1008, 16972, 19485, 20978, 21303, ludlowii; 3537, muscosum; 17128, 19724, nepalense; 687, 499, 2595, pseudograndiflorum; 1958, 1977, pulcherrimum; 1534, pyramidale; 7560, 8213, 8238, 9376, roylei; 219, 3342, scabriflorum; 5833, sherriffii; 474, 2563, 2096, 2721, 864, 2515, 9958, 10069, 17151, 19702, 19770, 19787, 21057, viscosum*
Ludlow, Sherriff & Elliot *15683, D. pseudograndiflorum*
Ludlow, Sherriff & Hicks *17476, D. caeruleum; 16825, 17102, 19328, 19375, 19399, 19725, muscosum*
Ludlow, Sherriff & Taylor *6921, D. albocaeruleum; 6379, beesianum; 5329, 5329A, 5824, 5701, 6250, 4849, gyalanum; 5397, 6920, muliense; 5162, 6093, 13920, pseudograndiflorum; 6066, 6403, viscosum*
Ludlow, Stainton & Williams *15621, D. likiangense*
Lyon, Bowes *25, D. aquilegifolium; 1083, brunonianum*

Maack, R. *673, D. cheilanthum*
Macmillan, H. F. *7, 8, 9, D. tuberosum*
Maire, E. E. *2292, 3292, 6367, 7419, D. delavayi; 2128, D. georgei; 2669, mairei; 7437, mosoynense; 284/*1914, *pogonanthum; 208, 380, 720, 2675, tatsienense; 2127, 7437, tenii; 2962, trichophorum; 389, 1196, yunnanense*
Mamlev *211, D. elatum*
Manissadjian *675, D. fissum* ssp. *anatolicum; 26, peregrinum*
Martin & Bodinier *1789, D. yunnanense*
Matveeva, E. *555, D. laxiusculum*
Maydell, G. 8–8–1869, *D. brachycentrum*
McLarens collectors *159, D. bulleyanum; 171, beesianum; N–180, ceratophorum; N71, N132, N175, L131, delavayi; 165, mosoynense; N165, pycnocentrum; AC266, spirocentrum; AC295, souliei; AC193, AC201, AC275, B264, B213, V91, tatsienense; 206, 258, tongolense; AB79, F68, V88, yunnanense*
McNeill, *731, D. crispulum*
Melville, *43, D. burmaense*
Merton *3935, D. quercetorum; 3888, semibarbatum*
Merzbacher *723, D. duhmbergii; 1304, villosum*
Metcalf & Chang *797, D. anthriscifolium*
Metz *52, D. vestitum*
Meyer, C. A. *1727, D. caucasicum*
Meyer, F. N. *1057, D. grandiflorum; 626, semibarbatum; 552, turkmemum*
Meyer, F. S. *B4864, D. ithaburense; 99, virgatum*
Mikelson, A. *2279, D. biternatum*
Mozheeba *239, D. elatum*
Mussot (Moussot) *27, D. souliei; 28, 29, trichophorum*

Nasir, E. *28459, D. centeteroides*
Nath, M. *387, 437, D. vestitum*
Nevski, S. *790, D. ternatum*
Ngan, Han *92, D. grandiflorum*
Norton, J. *369, D. nortonii*

Ohwi, J. *10662, D. grandiflorum; 2808, maackianum*
Osmaston *75, D. roylei*

Parmanand, N. *588a, D. brunonianum; 1139a, vestitum*
Pavillon *1843, D. formosum*
Pavlov *336, D. dissectum*
Pei *2646, D. anthriscifolium* var. *calleryi*
Persnin *170, D. cinereum*
Pichler in 1882, *D. tuberosum*
Pinard in 1843, *D. cinereum*
Pinfold *164, D. denudatum; 329, pyramidale; 210, 224, roylei*
Polunin, O. *2599, 6250, D. brunonianum; 56/175, 56/597, 56/647, cashmerianum; 1440, 1247, densiflorum; 1905, 1790, 1949, glaciale; 555, 1413, 1489, 1778, himalayae; 872, 1576, kamaonense; 6208, lacostei; 56/699, pyramidale; 56/330, 56/602, roylei; 56/283, 56/803, vestitum*
Polunin, Sykes & Williams *3518, D. cooperi; 264, 2503, 4885, 5128, 5290, himalayae; 3533, nepalense; 2629, 5120, pyramidale; 386, 5025, 5441, vestitum; 1907, 3916, williamsii*
Popov *259, D. biternatum*
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Potanin in 1885, *D. orthocentrum, pylzowii* and *sutchuenense*
Prance & Ratcliffe *159, 265, D. peregrinum*
Pratt *462, D. pachycentrum; 344, potaninii*
Prokhanov *43, D. macropogon*
Przewalski in 1872, *D. albocaeruleum, pylzowii* and *sparsiflorum*; in 1873 and 1874, *przewalskii*; in 1880, *pylzowii* and *trichophorum*
Ptazycki *373, D. elatum*
Purdom *126, D. grandiflorum; 142, trichophorum*
Radde, G. *212, D. crispulum; 545, semibarbatum*
Rajkova *129, D. dasyanthum*
Ram Bahsli *14811, D. suave*
Ram Bahsh or Bakeh *8351, D. cashmerianum; 4342, 4344, roylei*
Rami, Hoshen & Nuri *29481, D. macrostachyum*
Ratcliffe *759, D. venulosum*
Rawi, *24731, D. micranthum; 12213, pallidiflorum; 22200, 22706, 23431, quercetorum*
Rawi & Serhang *20208, D. foetidum*
Read *746, D. grandiflorum*
Rechinger *3838, D. aquilegifolium; 1416, biternatum; 6093a, elbursense; 6191, gorganicum; 3364, saniculifolium; 1698, 4934, semibarbatum; 6083, ursinum*
Regel, A., June, 1883, *D. biternatum*; in 1878, in 1882, *dasyanthum; 286* and May, 1876, *longipedunculatum*; Aug. 1876 and 5–17–1880, *semibarbatum*
Ren *6290, D. ceratophorum*
Ribu & Rhomov *5234, D. glaciale*
Ridley *20, D. grandiflorum*
Robertson, W. A. *15, D. burmaense*
Rock, J. *13194, 14459, 14467, 14501, 14505, D. albocaeruleum; 5421, 7763, 10776, 10778, 10817, 11276, 13398, 13092, 14518, 14520, 14502, 14523, 14640, 17248, 18810, 20204, 22852, 24738, 24914?, beesianum; 6082, 6085, 5696, 6091, 9669, 9755, 9766, 9769, 9924, 10797, 16938, bulleyanum; 4746, 5006, 5669, 5696, 5888, 5774, 6948, 10737, 17321, 22852, 23080, 23992, ceratophorum; 6092, 6110, 7761, 7765, 10669, 10764, 10633, 10777, 11435, 11436, 11676, 24738, 24945, coleopodum; 4404, 4849, 5030, 5298, 5768, 5799, 5936, 6093, 6149, 6177, 9474, 9914, 5786, 5828, 10634, 11483, 18324, 18519, 24190, delavayi; 10539, georgei; 16830, 18121, glabricaule; 13361, grandiflorum; 16884, 22852* in part, *23457, hamatum; 6305, 17317, 22373, hirticaule; 13136, leptopogon; 5242, 6111, 6423, 9867, 10409, 10665, 10792, 11413, 11435, 15242,*

17332, 24914, 24920, 25330, likiangense; 18327, 23243, 24272, maximowiczii; 22373, 22401, 23086, 24190, micropetalum; 18317, mitzugense; 16916, muliense; 13024, 13185, monanthum; 13730, 17338, mosoynense; 16884, pachycentrum; 16743, 23992, potaninii; 5906, 6171, 6193, 10747, 14538, pseudograndiflorum; 14460, pulcherrimum; 16886, 18316, pumilum; 6135, 5787, 10670, 10813, 10657, 17319, 17338, pycnocentroides; 13023, 13041, 13086, 13088, 13093, 14504, 14625, 14482, 14483, 14513, 14641, pylzowii; 13191 sparsiflorum; 9755, 9766, 9669, 16760, 16345, 16767, 16814, 16797, 16398, 16637, 16694, 18015, 18294, 22852, 23080, 23101, 23979, 24166, 24190, 24771A, 24589, spirocentrum; 6292, 7770, 10686, 11485, 11545, 18485, 23243, tatsienense; 18205, 23457, tenii; 13154, 13193, 14547, tsoongii; 10779, 10860, 11696, 13740, 16824, 18237, 23090, 23444, 24938, trichophorum; 22267, wardii; 16930, wrightii; 6551, 6902, yunnanense
Roerich *60 I, 336 I, D. grandiflorum*
Russanov *119, D. inopinatum*

Sampson *10125, D. anthriscifolium*
Sanders, D. F. *8–22–39, D. nordhagenii*
Santapau *11551, 11552, 13868, 13869, D. malabaricum*
Sarchen & Bajkan *1169, D. dasyanthum*
Schelkownikow *65, D. foetidum*
Schindler *78, D. grandiflorum*
Schlagintweit *1711, 1985, 6306, 9004, D. brunonianum; 4824, 5171, 5484, 9007, cashmerianum; 9180, 9552, densiflorum; 3066, 5171, roylei*
Schmid, F. *1662, D. uncinatum*
Schneider, C. *2382, D. beesianum; 2245, 2983, 3459, ceratophorum; 2143, 2285, 3576, delavayi; 2928, 3251, 3774, likiangense; 2430, mairei; 2278, 3250, pseudograndiflorum; 2278, pycnocentroides; 3249, spirocentrum; 2121, 1510, tenii*
Schock *276, D. mosoynense*
Seringe *1489c, D. vestitum*
Sharma, H. N. *E295, D. brunonianum; E482, glaciale; 117, himalayae; E98, pyramidale; 55, vestitum; 54, 54/94, E140, viscosum*
Sherriff *7310, D. denudatum*
Siddiqui & Rahman *26868, D. suave; 26865, kohatense*
Sintenis *4883, D. albiflorum; 500, 850, 1891, biternatum; 4979, davisii; 7107, 7108, crispulum; 589, fissum* ssp. *anatolicum; 1590, formosum; 1185, kurdicum; 1266, macrostachyum; 473, 1207, peregrinum; 383, semibarbatum; 1672, 1672b, turkmemum; 4627, venulosum*
Skorobogdtko *302, D. biternatum*
Smith, H. *2985, 4243, 4326, 11712, 12619, 12515, 11939, 12421, D. beesianum; 4138, campylocentrum; 5741, chefoense; 173, 468, 1163, 4660, 6526, 7139, 8150, grandiflorum; 11248, lancisepalum; 7109, leptopogon; 3385, malacophyllum; 3132, monanthum; 3541, 4200, orthocentrum; 4072, 10316, potaninii; 3985, 13764, pseudograndiflorum; 2961, 3135, 3384, 4283, pylzowii; 11274, smithianum; 4048, 11732, 12056, souliei; 4397, 4660, 10798, 13764, tatsienense; 11339, 11340, 11594, tongolense; 11574, 11689, 4421, trichophorum; 11285, 11321, 11459, tsarongense*
Smith, W. W. *4128, D. viscosum*
Smith & Cave *1935, 2131, D. caeruleum*
Socalski *292, D. biternatum*
Sokolov *97, D. grandiflorum*
Soong, T. P. *38839, 38912, 38915, D. pseudotongolense*
Sorokin *1357, D. speciosum*
Soulié, R. P. *3040, 3041, 3042, 3042 bis, 3043, 3898, 3899, 3907, D. batangense; 3039, 3904, 3905, chrysotrichum; 1096, delavayi; 1098, micropetalum; 2387, 2389, mosoynense; 24, 2379, pachycentrum; 3903, 3911, 3914, pylzowii; 364, 399, 2388, souliei; 1097, spirocentrum; 25, 438, 525, 2027, 2381, 2382, 2481, 2489,*

3529, tatsienense; 3049, 3893, 3894, 3044, thibeticum; 396, 2383, 3889, 3890, 3880, 3050, tongolense; 23, 64, 359, 2029, 2384, 2386, 3038, 3909, trichophorum
Sovetkina & Czansova *4267, D. semibarbatum*
Stainton *2846, D. brunonianum; 1142, 1144, drepanocentrum; 1025, glaciale; 1708, nepalense; 2529, kohatense; 1162, stapeliosum; 1327, 1650, 1709, viscosum*
Stainton, Sykes & Williams *3707, D. densiflorum; 1871, 2026, 2200, 2233, 1930, 7216, 7351, 7742, 8035, 8142, kamaonense; 2278, 3769, 4602, 7773, nepalense; 7867, 8587, stapeliosum; 3724, 4401, 8485, 8586, 8585, 7729, 7733, 8007, vestitum; 4689, 7956, 8029, 8058, viscosum*
Stapf *2300, 2793, D. saniculifolium*
Steane *60, D. vestitum*
Steven *8711, D. ochroleucum*
Stevens, H. *457, D. delavayi; 88, 458, pseudograndiflorum; 89, 114, tatsienense; 454, tongolense*
Steward *2071, D. anthriscifolium* var. *calleryi*
Stewart, J. L. "K," *D. kohatense*
Stewart, H. M. 7–1–07, *D. gyalanum*
Stewart, R. R. *9819a, 9849, 20176, 20698, 22132, 22294, D. brunonianum; 62, 3485, 3759, 6325, 8413, 8785, 9400, 9881, 18137, 18369, 22179, cashmerianum; 2026 1/2, 6042, 12147, 17468, 17534, 19440, denudatum; 10936, kohatense; 3082, 5268, 8079, 5714, 9225, 18316, 18357, 21882, 28781, 29167, pyramidale; 5694, 6530, 7272, 8102a, 10546, 19239, 19586, 19693, roylei; 579, suave; 7002, 12688, 27322, uncinatum*
Stewart & Rahman *25229, D. aquilegifolium; 25125, tenuipes*
Stocks *994, D. uncinatum*
Stötzner *26, D. grandiflorum*
Strachey & Winterbottom *8, D. brunonianum; 10, 11, 13, caeruleum; 6, cashmerianum; 3, denudatum; 4, densiflorum; 2, pyramidale; 1, 7, vestitum*
Stukow *1358, D. grandiflorum*
Sun, C. L. *1765, D. anthriscifolium* var. *calleryi; 476, potaninii*
Swann *R8, D. brunonianum*
Swigh *11, D. denudatum*
Szowitz *168, D. laxiusculum; 439, szowitsianum*

Tang *13795, D. anthriscifolium*
Ten, S. *69, 579, D. delavayi; 1292, lilacinum; 581, tenii; 134, yunnanense*
Teng *153, D. anthriscifolium* var. *savatieri; 90112, anthriscifolium* var. *calleryi*
Timins *203, D. pyramidale*
Tolmatchew, *174, D. elatum*
Toppin *769, D. vestitum*
Tsai, H. T. *53738, 59749, D. delavayi; 57754, hirticaule; 57615, pogonanthum; 51974, 56240, tenii; 52675, umbrosum*
Tsiang, Y. *8571, D. anthriscifolium*
Tü, T. H. *4366, D. saxatile*
Turczanowicz *929, D. triste*
Tyson, J. B. *95, D. kamaonense*

Uvarov *29, D. peregrinum; 98, venulosum*

Vnorrili *43, D. longipedunculatum*

Wallich *1832, D. brunonianum; 4717, incisum; 4716, pyramidale; 4715, 4715A & B, D. vestitum*
Walton, H. J. *106,* and July, 1904, *D. gyalanum;* July, 1904, *pseudograndiflorum*
Wang, C. W. *20450, D. anthriscifolium* var. *calleryi; 65706, ceratophoroides; 71376, delavayi; 69547, hamatum; 71576, mairei; 69805, polyanthum; 64594, 68543, 69805, 68635, 68390, 68590, spirocentrum; 66226, tatsienense; 68051, 69397, 64707, 69117, 64733, 69174, tenii; 64959, tsarongense; 69052, umbrosum*
Wang, F. T. *21767, D. laxicymosum*
Wang, H. *41742, D. pseudograndiflorum*
Wang, T. P. *3073, D. grandiflorum*
Wang & Wen *581, D. potaninii*
Ward, F. Kingdon- *6123, 12244, 12317,*

12224, D. albocaeruleum; 14015, altissimum; 4856, beesianum; 10900, brunonianum; 995, 4811, 4846, bulleyanum; 3351, 9819, 10115, 13170, 14308, 18121, 22505, burmaense; 10854, 12317a, 12367, cashmerianum; 5969, 12031, gyalanum; 12370, hillcoatiae; 22749, lacei; 12190, 12240, muliense; 10881, 10621, 12077, 12402, pseudograndiflorum; 4375, 4604, 4617, 4826, spirocentrum; 4677, 4932, 4956, trichophorum; 5390, tsarongense; 12303, 12337, 14329, viscosum

Watt, G. *612, D. denudatum*

Webster & Naser *6100, 6192, 6560, D. brunonianum; 6524, cashmerianum*

Wen, T. S. *568, D. mosoynense*

Wigram, O. *99, D. altissimum; 118, himalayae; 112, viscosum*

Wilson, E. H. *95, D. anthriscifolium; 4690, davidii; 3090, delavayi; 1088, 1099, 3093, orthocentrum; 1169, 1523, 2142, 1088, 819, 1999, 3095, 3097, 4702, potaninii; 3088, sinovitifolium; 3092, 3092a, 4689, souliei; 4691, 3094?, tanguticum; 3096, tatsienense; 3089, tongolense; 2004, 2044, 3107, 4688, trichophorum; 2496, trifoliolatum*

Winkler, C. *7230, D. winklerianum*

Winterbottom *348, D. denudatum*

Wollaston *18, D. caeruleum*

Woronow, G. *195, D. laxiusculum; 990, ochroleucum*

Wu, S. K. *2662, D. pumilum*

Wunderlich *1863, D. puniceum*

Yang, K. H. *58311, D. anthriscifolium; 65383, henryi; 58941, pseudocampylocentrum*

Yaroshenka & Ubanonow 7–23–1945, *D. szowitsianum*

Yü, T. T. *12827, D. aconitioides; 13140, 13649, beesianum; 15544, bulleyanum; 12809, chenii; 12548, 13824, 13543, 22461, delavayi; 14008, dolichocentroides; 14490, georgei; 9598, 9832, 12702, hamatum; 14022, hirticaule; 13101, hui; 9670, mairei; 10504, maximowiczii; 20369, 20639, 20783, 22320, micropetalum; 1598, mitzugense; 6989, muliense; 13129, oxycentrum; 13270, 14367, pogonanthum; 13481, pseudograndiflorum; 9330, pulcherrimum; 14413, pumilum; 7427, 14577, 20685, 22461, 23215, spirocentrum; 12941, 14527, tatsienense; 1400, 9885, 10432, 13336, tenii; 14642, trichophorum; 979, umbrosum; 7797, wrightii; 12490, 10547, 13852, 14613, yuanum*

Zimmerman *192, D. chefoense; 561, hirticaule.*

INDEX TO NAMES

This is an alphabetical list of names that have been proposed for the Asian species of *Delphinium*. Subspecific and varietal epithets are indented under the appropriate specific epithet. The numbers refer to the species number in this paper. Names printed in *italics* are names of taxa reduced to synonymy here. Species referred to *Consolida* have been omitted.

ADDENDUM

Chienia honanensis W. T. Wang. Dr. Lothar Benzing of the Institut für Allgemeine Botanik at Mainz, West Germany, has very kindly called my attention to, and sent me a xeroxed copy of an article in *Acta Phytotaxonomica Sinica* **9**: 104–107. *pls. VI, VII.* 1964, in which W. T. Wang proposed a new genus *Chienia*, closely related to *Consolida* and *Delphinium*. As the Royal Botanic Garden at Edinburgh had received photographs, and even isotypes, of many of Wang's earlier species of *Delphinium*, I asked Dr. Peter Davis whether they had any material of the *Chienia*, but word has just come that he and Mr. Lauener have none.

Wang's excellent illustration of *Chienia honanensis* W. T. Wang and the detailed Latin descriptions of the genus and species certainly suggest *Delphinium grandiflorum* L. in habit, vesture, leaf dissection, flower color, and size. The plant comes from Honan, China, which is far enough north to be in the range of the *Delphinium*, from which it differs in the shorter spur on the upper sepal and the lack of spurs on the upper petals (staminodia of Wang), so that the upper and lower petals are quite alike and clawed.

In the course of examining perhaps 6000 specimens of the *Consolida-Delphinium* complex I have met a number of cases of spurlessness. For example, in the discussion of *Consolida rugulosa* (Boiss.) Schröd. it was pointed out (Jour. Arnold Arb. **48:** 188, 189. 1967) that *C. paradoxa* (Bunge) Nevski [*Delphinium paradoxum* Bunge] was apparently a spurless form of *C. rugulosa.* In *Delphinium anthriscifolium* Hance a spurless collection was seen, *H. B. Morse* (NY). In *D. macrocentron* Oliver, *Bally 1205* (K) has spurless petals. I remember seeing a sheet of another species in which spurred and spurless flowers occurred on the same plant, but unfortunately I have misplaced my record of it.

Without seeing material of the proposed *Chienia honanensis*, I am inclined to suspect that Wang, whose comprehensive treatment of the Chinese species of *Delphinium* (Acta Bot. Sinica **10:** 59–89, 137–165, 164–284. 1962) has given him a much better knowledge of those species than I have, has dealt with an abnormal plant of *Delphinium grandiflorum* L.

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MORPHOLOGY AND ANATOMY OF CROOMIA PAUCIFLORA (STEMONACEAE)

P. B. TOMLINSON [1]
AND
E. S. AYENSU

THE STEMONACEAE (Roxburghiaceae) comprises a small and taxonomically isolated family of monocotyledons with its main distribution in the Far East. *Stemona* ranges from the Himalayas to southern Australia and *Stichoneuron* is found in Indonesia. The remaining genus *Croomia* (commemorating the pioneer Florida botanist H. B. Croom), has a widely disjunct range with two species in Japan and one (*C. pauciflora* Torr.) in the southeastern United States. This family therefore provides a further example of distribution demonstrating the ancient floristic affinity between eastern North America and eastern Asia to which Asa Gray drew attention.

There is little agreement amongst taxonomists as to where in a natural sequence the Stemonaceae should be situated. Burkill (1960) provides a useful survey of the taxonomic history of the family. Its wide and discontinuous distribution has led to the assumption that it is ancient (Hutchinson, 1959) but there is much evidence that the taxon is not very homogeneous. Any information likely to shed light on the systematics of the family is therefore of value, especially in view of its possible relationship with the economically important Dioscoreaceae. Recently one of us (P. B. T.) had the opportunity to collect *Croomia pauciflora* in northern Florida and to investigate its morphology and anatomy with ample fresh material at hand. The other (E. S. A.) has investigated the vegetative anatomy of the three genera and the total contribution permits a discussion of their systematic affinities. Only limited herbarium material of *Stichoneuron* and *Stemona* has been available for microscopic investigation, and observations on these two genera are still very tentative. The vegetative anatomy of *Croomia pauciflora* was investigated previously by Holm (1905) with some of the information repeated in a later paper (Holm, 1927), but it is quite clear that many fundamental morphological features have hitherto remained undescribed. They are presented in this paper, together with a detailed re-examination of anatomy. In addition the anatomy of the flower has been studied in order to compare it with that of *Stemona* about which there is a good deal more information.

In the United States *Croomia* grows on richly wooded bluffs along the Apalachicola River from Florida into Alabama (Harper, 1942). Plants form small, very localized populations in dense shade on steep, well-drained

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[1] Research on the systematic anatomy of monocotyledons supported by N.S.F. Grant GB-5762-X.

slopes amongst loose litter. According to Harper they remain green all summer. Populations seem to persist and spread largely by rhizomes which are, however, shallow and easily dug up. We have not seen any seedlings. Harper spoke of plants being "more or less connected by a network of rootstocks." This is substantiated by the abrupt boundary to the populations and the high density of leafy shoots. Rhizome morphology described below accounts for this method of vegetative survival but also suggests that *Croomia* would be vulnerable to any disturbance of its habitat.

MATERIAL AND METHODS

Living plants came from Torreya State Park, Bristol, Florida. We are indebted to Dr. S. McDaniels and Dr. A. F. Clewell of Florida State University for the arrangements made so that specimens could be collected. Plants were examined largely in a fresh condition. Microscopic details were studied in unstained freehand sections cut with a razor blade, supplemented by observations on preparations made by routine clearing, staining, and maceration methods. Details of the vascular system were examined in serial sections of paraffin-embedded material stained in safranin and Delafield's haematoxylin. The vascular anatomy of open flowers and mature flower buds was studied in serial paraffin sections and in whole flowers cleared and stained in safranin. A number of foliage leaves were cleared and stained in Heidenhain's haematoxylin.

Material of *Stichoneuron* and *Stemona* from the Herbarium, Royal Botanic Gardens, Kew, as follows, was supplied through the generosity of Dr. C. R. Metcalfe, Keeper of the Jodrell Laboratory: *Stemona curtisii* Hook. f. (*Haniff & Nur 4368*); *S. kerrii* Craib (*Kerr 707*); *Stichoneuron caudatum* Ridley (*Corner 28716 & 37056*).

VEGETATIVE MORPHOLOGY

GROWTH HABIT (FIGS. 35–39). Growth of shoots is sympodial with a remarkably precise and constant arrangement of parts on each unit of the sympodium. Each of these units consists of an underground rhizomatous portion terminating in an erect leafy shoot which bears the flowers (FIG. 35). At the time of flowering, in March to April, the renewal shoot has already been initiated (FIG. 37) for the next unit which will culminate in the following year's erect shoot. Leafy shoots are, therefore, annual but the slender rhizomatous part of the sympodium is long persistent and marked by the scars of each erect shoot. These scars therefore represent the limit of each annual growth increment. Long rhizomes with many scars can be dug up easily.

Each unit of the sympodium begins with a series of scale leaves. Their position and number are so constant from year to year that they may be identified by letters for convenience (FIGS. 35, 37). Leaves are arranged distichously (FIG. 38). The plane of distichy is horizontal although this is interrupted once in a very significant way. The following sequence is standard for each renewal shoot. The first leaf (A) is a scale leaf at the end of a long internode; it subtends no axillary bud. Leaf B is a scale leaf opposite leaf A and also at the end of a long internode. It subtends a conspicuous bud which is, however, strongly inhibited (*dormant bud,* FIG. 39). Leaf C is a scale leaf at the end of a short internode and inserted on the dorsal (lower) side of the rhizome and therefore perpendicular to the plane of distichy of leaves A and B. Leaf C subtends the bud which grows out, without inhibition, as the renewal shoot (*renewal bud*). Beyond leaf C the axis turns erect (FIG. 37). Three (sometimes only two) overlapping scale leaves (D, E or F) separated by short internodes are inserted at the base of the erect shoot. These re-establish the earlier distichy so that D is always on the same side of the shoot as B. The last scale leaf (E or F) is often somewhat remote from the other two and its apex is usually above ground. The extent to which the internode below the last scale leaf is elongated and whether two or three scale leaves occur beyond leaf C may be determined by the depth to which the rhizome is buried. These 2 or 3 ultimate scale leaves subtend no conspicuous buds although microscopical examination of sections through their nodes sometimes reveals vestigial buds with little or no vascular connection to the main vascular system. These may be described as *non-functional* buds since they never seem to expand and are in sharp contrast to the conspicuous *functional* buds at nodes B and C which have a strong connection to the main vascular system of the rhizome.

Beyond the last scale leaf (E or F) is the long internode, up to 30 cm. tall, which supports the leafy crown. This internode is white below ground but exposed parts are red below and green above. The exposed apex of the distal scale is also red. Foliage leaves from a terminal, irregular, obliquely ascending series spreading backwards more or less in one plane and apparently continuing the distichy of the scale leaves although they are irregularly spaced and often subopposite (FIG. 36). The axis of the whole sympodium is apparently terminated by a leaf or pseudo-pair of leaves. Vigorous shoots bear as many as nine leaves, from five to seven are the most common numbers. Small shoots may have as few as two or three foliage leaves but we have seen no shoot with one leaf. Flowering branches are in the axils of leaves. In non-flowering shoots there may be vestigial axillary buds.

From the above description it is evident that branching is very restricted. Each sympodial unit bears only two functional buds (FIG. 38), one (renewal bud) is necessary to maintain the sympodium, leaving only one (dormant bud) to effect multiplication by branching. At the time of anthesis the renewal bud has usually commenced growth, piercing the back of its subtending scale leaf (FIG. 37). At this stage the primordia of the first two scale leaves of next year's increment are already present but they so firmly enclose the bud that its apex appears to be naked and leafless. Examination of herbarium specimens collected in the fall suggest that the rhizome overwinters with a full complement of leaves initiated.

In contrast, the dormant bud is strongly inhibited because many rhizomes remain undivided even after several years' growth. However, divided rhizomes, in which the dormant bud has grown out to initiate a new sympodium, are quite common. Normally this branch axis repeats the arrangement of parts shown on the parent axis and produces a vigorous but flowerless leafy shoot in the first year. Commonly, however, the lateral shoot is not vigorous and the first two internodes remain unextended so that a short, depauperate leafy shoot with few (2–3) foliage leaves is erected close to the parent axis. Although it is reasonable to assume that damage to a vigorous renewal shoot will release inhibition of dormant buds, most branched rhizomes appear undamaged. Therefore, it is not easy to account for the outgrowth of dormant buds which otherwise are strongly suppressed.

Roots are restricted to the nodes at which leaves B and C are inserted, from three to five growing out adventitiously on the lower side of the rhizome (FIGS. 35, 37). Roots are somewhat fleshy and produce a fine system of first-order branches but without conspicuous root-hairs.

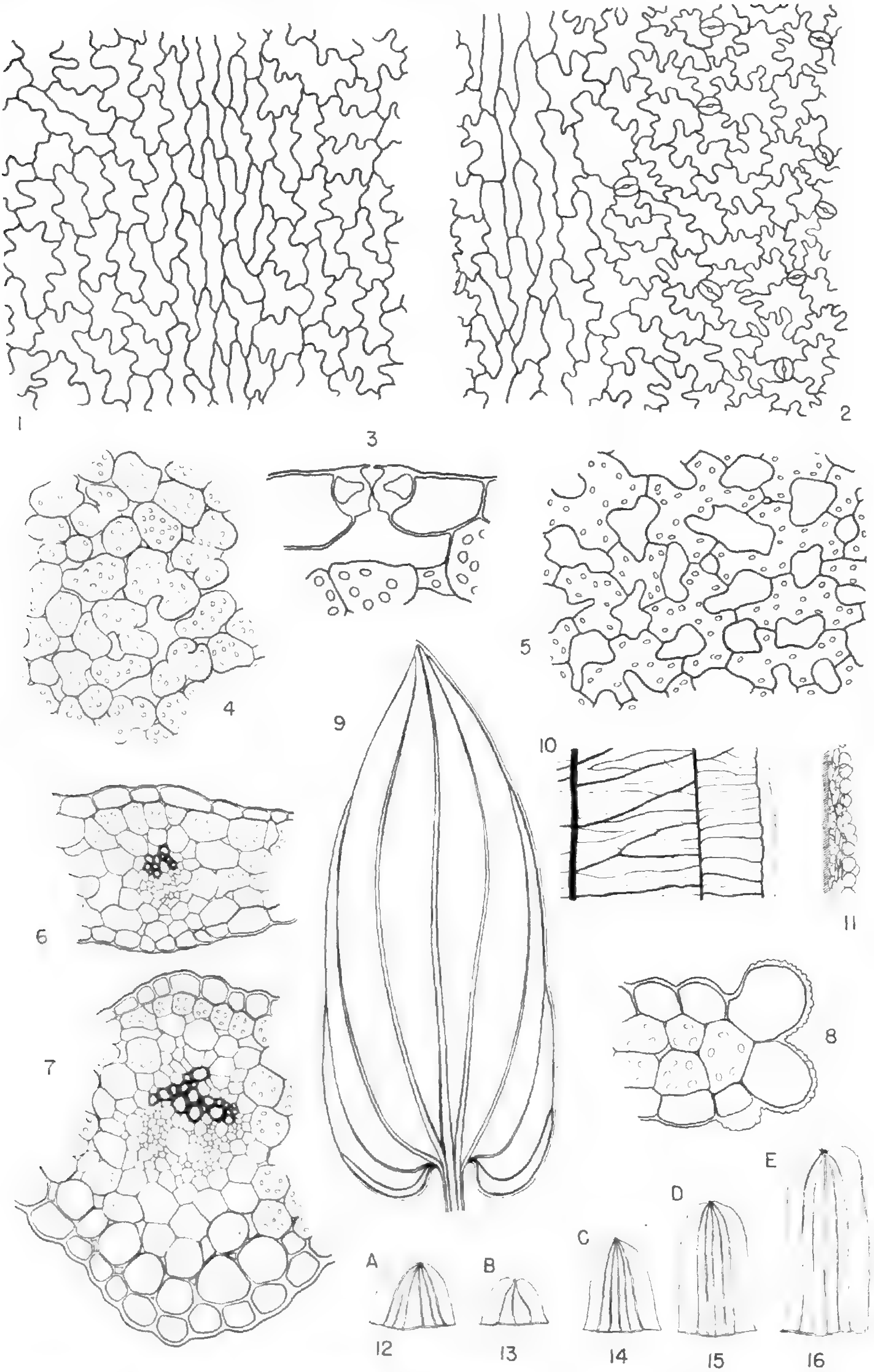
LEAVES. Scale leaves (FIGS. 12–16) borne on underground parts are readily distinguishable from foliage leaves borne on aërial parts. In many monocotyledons the morphological nature of the scale leaf, which is equivalent to the leaf base of a foliage leaf, is clear from a series of transitional leaves. In *Croomia,* without transitional leaves, this obvious relationship is lost. The two types of leaf seem to be very dissimilar developmentally because the foliage leaf has no sheathing base.

Scale leaves are open, opposite margins scarcely overwrapping. Leaves A and B are usually shortest with fewest (usually 3–4) veins (e.g. FIG. 13) whereas distal scales are longest and almost invariably have five veins (e.g. FIGS. 14–16). A regular progression in size along the rhizome is not always maintained, however (e.g. FIGS. 12–16), perhaps because growth of the renewal shoot is not continuous. Veins are parallel, converge and unite at the apex but are unconnected by transverse veins. A conspicuous mid-vein is not developed.

Foliage leaves (FIGS. 35, 36; 9) are petiolate but without a sheathing, encircling insertion. The blade has five major veins, prominent abaxially, the veins entering the blade from the petiole independently of each other. The outermost vein on each side gives off a marginal and two submarginal veins into the cordate base of the lamina. The veins unite in turn with the marginal commissure which itself joins the median vein at the apex (FIG. 9). Longitudinal veins are connected by an irregular series of transverse veins. Many minor transverse veins end blindly (FIG. 10), an unusual feature for a monocotyledon, not found in *Stichoneuron* and very rare in *Stemona.*

VEGETATIVE ANATOMY

LAMINA OF FOLIAGE LEAVES. Dorsiventral. **Hairs** absent. **Cuticle** thin on both surfaces. **Epidermis** moderately shallow, more or less uniformly thin walled, outer wall scarcely thickened. Adaxial epidermis (FIG. 1)



FIGS. 1–16, *Croomia pauciflora*. Leaf anatomy. FIGS. 1 and 2. Surface view of epidermis, × 100. FIG. 1. Adaxial view. FIG. 2. Abaxial view. FIG. 3. Transverse section of stoma, × 470, from abaxial epidermis of lamina. FIGS. 4 and 5. Mesophyll in paradermal view from cleared whole mount of lamina, ×

uniform in surface view, cells more or less isodiametric with markedly sinuous anticlinal walls; costal cells elongated, narrow and with less obviously sinuous but somewhat thicker walls than intercostal cells, the costal cells most distinct above and below large veins. Abaxial similar to adaxial epidermis except for numerous stomata (FIG. 2). **Stomata** anomocytic, 27–36 μ long, the stomatal pore apparently orientated at random. Each guard cell with a wide lumen, somewhat thickened towards the pore below the two more or less equal ledges (FIG. 3). Guard cells including numerous small chloroplasts. Marginal epidermal cells papillose, the outer wall distinctly striate (FIGS. 8, 11).

Mesophyll uniformly chlorenchymatous, 3–5-layered; mostly 3-layered at margin and becoming several-layered towards midrib and main veins. Mesophyll cells much lobed; adaxial layer (FIG. 4) relatively compact, but cells not anticlinally extended to form a distinct palisade; abaxial layer (FIG. 5) loose, much lobed, the intermediate mesophyll layers intermediate in extent of lobing; differences between successive mesophyll layers most evident in paradermal view (FIGS. 4 and 5). Chloroplasts appearing somewhat denser in adaxial as compared with abaxial mesophyll layers. **Veins** (vascular bundles) all alike apart from range in size, from small blind-ending veins to midrib (e.g. FIGS. 6 and 7); all separated from each epidermis by at least one layer of chlorenchyma. Largest veins (FIG. 7) resembling vascular bundles of petiole and with inconspicuously collenchymatous subepidermal layers below; small veins with reduced vascular tissues (FIG. 6). Veins inconspicuously sheathed by a single layer of elongated chlorenchymatous cells, without thick-walled sheathing layers except for cells below phloem with slightly thickened walls.

PETIOLE (FIGS. 17 and 18). **Epidermis** without sinuous walls, resembling that of aërial stem, with somewhat thicker walls than epidermal cells of lamina. **Cuticle** conspicuously striate. **Stomata** common. Outermost layer of chlorenchymatous ground parenchyma somewhat collenchymatous but **collenchyma** most conspicuous in abaxial hypodermal layer and in petiole margin. **Vascular bundles** collateral, usually 5 throughout greater part of petiole (FIG. 17), but 7 according to Holm; each vascular bundle (FIG. 18) with many narrow adaxial tracheal elements, the narrowest, adaxial (protoxylem) elements often partly occluded. Phloem with irregularly arranged, narrow sieve tubes. Bundle sheath cells usually distinctly collenchymatous.

SCALE LEAF. **Epidermal cells** thin walled, more or less rectangular

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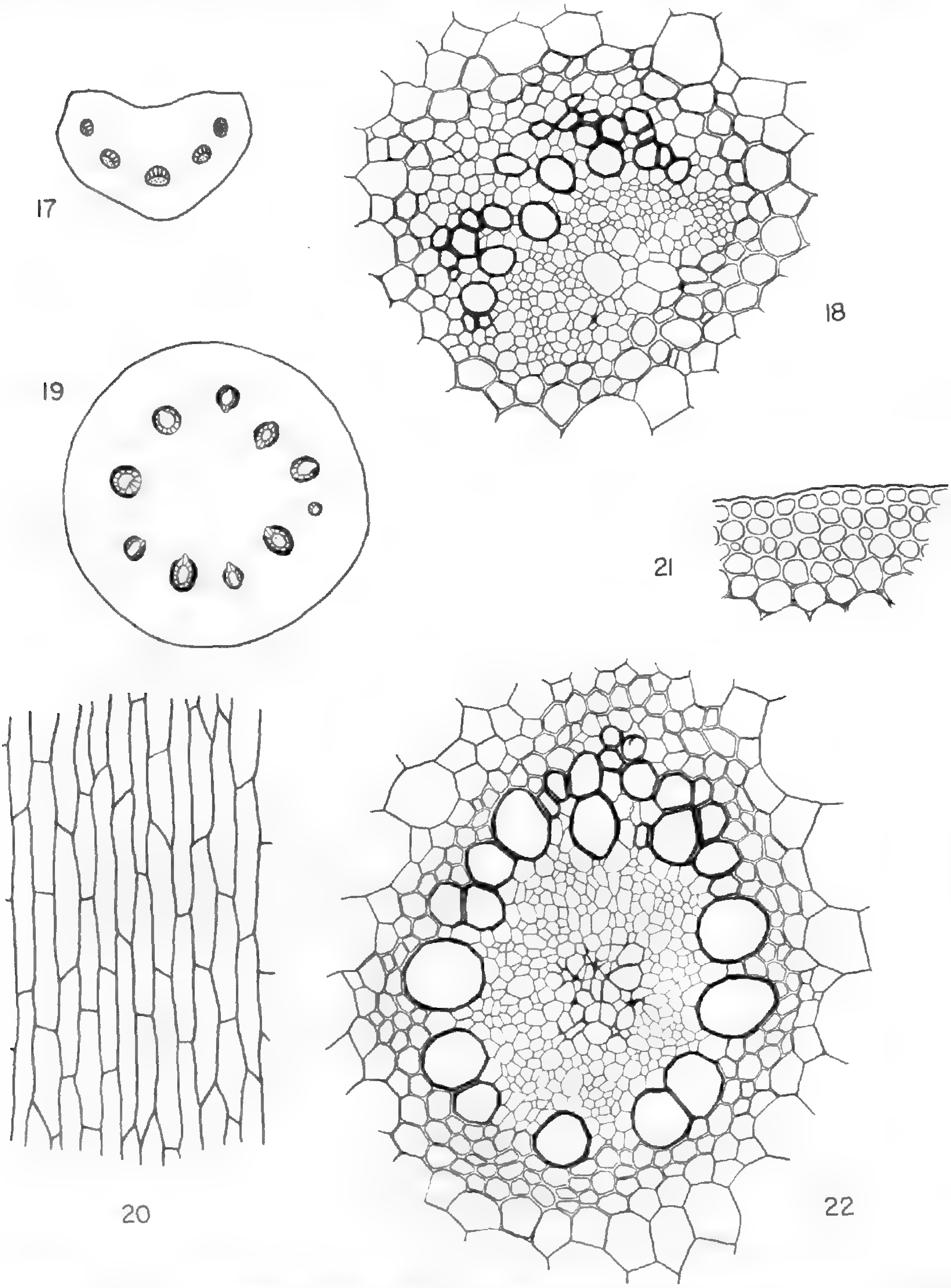
180. FIG. 4. Adaxial layer. FIG. 5. Abaxial layer. FIG. 6. Transverse section of minor vein of lamina, × 180. FIG. 7. Transverse section of midrib, × 180. FIG. 8. Transverse section of margin of lamina, × 290. FIG. 9. Outline of lamina to show distribution of major longitudinal veins, × 1. FIG. 10. Details of venation drawn from cleared whole mount of a leaf, midrib to left, × 3. FIG. 11. Details of leaf margin from same preparation to show papillae, × 30. FIGS. 12–16. Series of scales from rhizome, letters corresponding to nodes shown in FIG. 35; scales laid flat, × 1.

in surface view. **Mesophyll** of uniform colorless parenchyma. **Veins** resembling major longitudinal veins of foliage leaf.

AËRIAL STEM (FIGS. 19–22). Stem more or less circular in transverse section, including up to 13 but usually 10 vascular bundles arranged in a

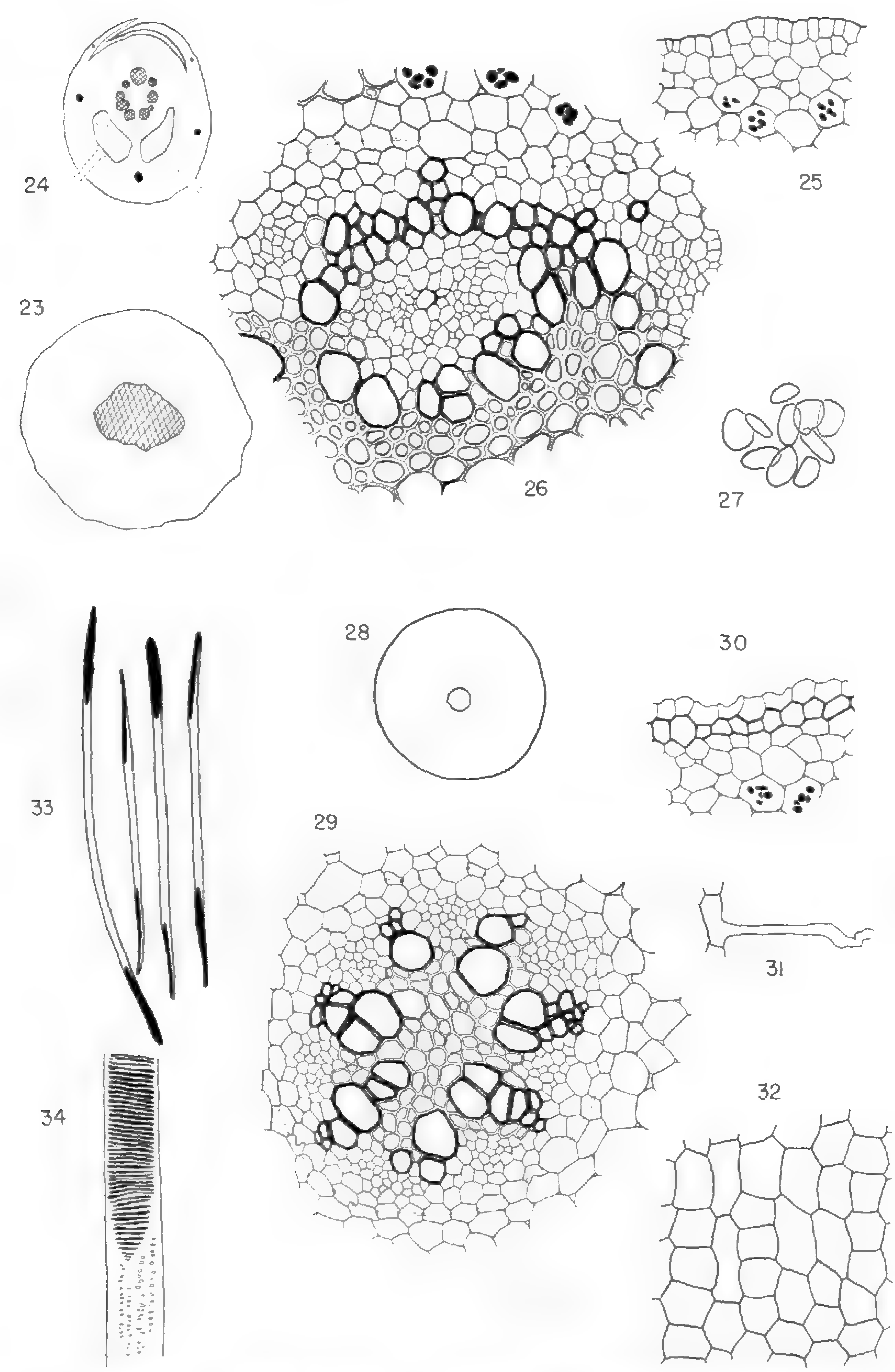


FIGS. 17–22, *Croomia pauciflora*. Anatomy of petiole and aërial stem. FIGS. 17 and 18. Petiole. FIG. 17. Transverse section, × 10. FIG. 18. Transverse section of single collateral vascular bundle from petiole, × 180. FIGS. 19–22. Aërial stem. FIG. 19. Transverse section, × 10. FIG. 20. Epidermis, surface view, × 100. FIG. 21. Surface layers of stem in transverse section, × 100. FIG. 22. Transverse section of single amphivasal vascular bundle, × 180.

circle (FIG. 19), the number of bundles increasing distally towards the insertion of foliage leaves. **Stomata** absent. **Cuticle** thin. **Epidermis** somewhat thick walled; epidermal cells longitudinally extended, more or less rectangular in surface view but commonly with oblique end walls (FIG. 20), normally colorless but basal cells with red (presumably anthocyanin-containing) vacuoles. **Cortex** with outermost 2–3 layers small celled and distinctly collenchymatous (FIG. 21), the collenchyma most pronounced distally; ground parenchyma otherwise uniformly large celled, thin walled, and colorless except for chloroplasts in outermost cells distally. Medullary ground parenchyma cells widest and with some tendency to collapse in a lysigenous manner. Each of largest **vascular bundles** (FIG. 22) amphivasal, including a continuous cylinder of tracheal elements, uniseriate except in region of narrow, often obliterated protoxylem elements on the inner side. Narrower vascular bundles collateral, the xylem discontinuous on the outer side and without conspicuous protoxylem. Phloem with inconspicuous sieve tubes surrounded by xylem and in turn surrounding a central strand of somewhat inflated cells (FIG. 22) with apparent wall thickenings which may represent obliterated protophloem. Vascular bundles sheathed by 2–3 layers of narrow, slightly thick-walled fibers or prosenchymatous cells, the sheath in large bundles usually incomplete next to protoxylem.

RHIZOME (FIGS. 23–26). **Epidermis** uniform, thin walled and closely resembling that of aërial stem. **Cortex** wide, uniformly parenchymatous and with abundant starch except for somewhat narrower but scarcely collenchymatous peripheral cells (FIG. 25). **Stele** angular in outline (FIGS. 23 and 24), delimited from cortex by a more or less continuous but indistinct endodermis of cells with suberized walls but without obvious Casparian thickenings (FIG. 26). Endodermis separated from vascular tissues by an indistinct 1–3-layered pericycle. Stele including an irregular cylinder of 9–10 indistinct and anastomosing vascular bundles forming a more or less continuous cylinder except for 2 somewhat more isolated and opposed lateral bundles. Additional small isolated phloem strands common next to pericycle. Larger vascular bundles more or less amphivasal (FIG. 26). Vascular cylinder enclosing a more or less continuous but irregular cylinder of fibers which often penetrate deeply between the vascular bundles. Sclerenchyma delimited internally by a further suberized layer resembling the peripheral endodermis, the two layers sometimes continuous via gaps in the vascular system. Medulla of thin-walled, starch-filled tissue resembling cortical ground tissue.

ROOT (FIGS. 28–32). **Epidermis** persistent but often collapsing somewhat; cells in surface view more or less rectangular, somewhat longitudinally extended (FIG. 32). Root-hairs uncommon, arising as outgrowths of otherwise unmodified cells (FIG. 31). Exodermis a compact layer of narrow, suberized, but scarcely thick-walled cells (FIG. 30). **Cortex** very wide, of uniformly starch-filled parenchyma with well-developed intercel-



FIGS. 23–34, *Croomia pauciflora.* Anatomy of rhizome and root. FIGS. 23–27. Rhizome. FIG. 23. Transverse section, × 10, stele cross-hatched. FIG. 24. Diagram to show insertion of vascular tissues of lateral organs on rhizome. Leaf

lular space system; innermost cells somewhat wider than outermost. **Endodermis** inconspicuously differentiated from innermost cortical layer but small celled, thin walled and with conspicuous Casparian strips (Fig. 29). **Pericycle** uniseriate, thin walled, inconspicuous but usually distinguished from tissues within by its larger cells. **Stele** narrow (Fig. 28), polyarch with few (usually 6–7) xylem poles, the xylem arms irregular. Tracheal elements, together with central, thick-walled medulla, forming a fairly regular stellate core, the narrow, thin-walled phloem strands occupying the angles between the protoxylem poles (Fig. 29). Lateral roots are diarch with a more conspicuous endodermis according to Holm (1905).

Conducting, storage and secretory elements. **Vessels** apparently restricted to metaxylem of roots (Figs. 33 and 34); elements average 2 mm. long and 33 μ wide, each with long scalariform perforation plates on very oblique end walls up to 300 μ long, the thickening bars between the perforations (Fig. 34) scarcely thinner than those on very similar imperforated end walls of tracheids in other organs; lateral walls with scalariform pitting in areas of contact between adjacent vessels, otherwise walls with diffuse, narrow pits. Tracheal elements in rhizome often much longer than those in root; end walls scalariformly pitted but imperforate. Tracheids in aërial stem and leaves without definite end walls and with annular or spiral, rarely scalariform-reticulate wall thickenings, the thickening usually wound in one gyre. **Sieve tubes** in leaf, aërial stem and rhizome mostly with simple sieve plates on transverse to oblique but often rather indistinct end walls; sieve plates in sieve tubes of root compound, on oblique end walls.

Starch grains abundant in ground parenchyma of rhizome (Fig. 27) and root; grains up to 18 μ wide, ellipsoidal, flattened; hilum inconspicuous but not obviously excentric. Crystalline or other secretory products not observed.

COURSE OF VASCULAR BUNDLES

Early authors had included *Croomia* in the Berberidaceae because the morphology of its embryo was uncertain and the rhizome had been regarded as having a closed cylinder of wood. This was corrected by Gray

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traces to subtending scale leaf C, solid black. Vascular masses of branch trace, stippled. Vascular bundles of rhizome stele cross-hatched. Traces to two roots attached directly to bud trace outlined with dotted lines. Fig. 25. Transverse section of surface layers, × 100. Fig. 26. Transverse section of periphery of stele to show one large amphivasal bundle, × 180. Fig. 27. Starch grains, × 400. Figs. 28–34. Root. Fig. 28. Transverse section, × 10. Fig. 29. Transverse section of stele, × 180. Fig. 30. Transverse section of surface layers, × 100. Fig. 31. Longitudinal section of root hair, × 100. Fig. 32. Epidermis from branch root, surface view, × 100. Fig. 33. Isolated vessel elements, × 25, extent of perforation indicated by solid black. Fig. 34. Details of vessel element, × 180, lower limit of a perforation plate.

(1859). The vascular bundles which constitute the vascular system of the rhizome are certainly not obviously discrete but they are best revealed by tracing the changes in anatomy at nodes B and C where scale leaves, roots, and functional buds are inserted. The basic pattern is indicated diagrammatically in FIG. 24 which is constructed from serial sections through node C. The vascular system of the rhizome consists of an irregular series of larger strands alternating with smaller strands which are the traces to the scale leaves. These traces appear well below their exsertion and pass gradually into the scale leaving a distinct "gap" in the main rhizome system. Two are usually conspicuous in a lateral position as indicated in the description of the rhizome. The bud trace system is a series of numerous isolated xylem and phloem strands which are aggregated into two large masses, each mass attached to a main rhizome strand. The middle trace of the subtending scale leaf passes between these two masses of bud trace tissue. Root traces may be attached directly to the branch system, others directly to large strands on the upper side of the rhizome. Beyond this complex nodal system there is a rapid change to the ring of discrete vascular bundles found in the erect stem, these bundles initially giving off traces to scales D, E and F. At the distal end of the aërial stem traces to foliage leaves and branches diverge shortly below the leafy shoot. There are no complicated nodal anastomoses such as have been described for *Stemona* by Lachner-Sandoval (1892).

REPRODUCTIVE MORPHOLOGY

GENERAL MORPHOLOGY (FIGS. 40–46). Flowers (FIGS. 40–44) are borne in long-stalked, few (1–3)-flowered cincinni (FIG. 46) in the axils of foliage leaves on vigorous shoots. Each flower is terminal on an axis bearing a single scale leaf (bracteole) which subtends the next flower-bearing axis. Each bracteole appears to be at right angles to the preceding one. Each pedicel has a distinct joint beyond the bracteole, representing a line of abscission. There are 4 green tepals in 2 pairs at right angles, the outer incompletely enclosing the inner (FIGS. 40–44). All tepals are somewhat reflexed in the open flower but in bud the apex of each, especially the inner pair, is distinctly hooded. The four stamens, each opposite a tepal, constitute a single whorl. Their bases are widened and united. In *Stemona* there have been attempts to interpret the stamens as forming two series so that they would correspond to the tepals, e.g. by Swamy (1964) who describes the stamen traces in *Stemona tuberosa* as diverging in pairs at different heights; but in this species Baillon (1860) showed the stamen primordia to arise simultaneously, as did Lachner-Sandoval (1892) in *Stemona javanica*. Each stamen (FIGS. 40–43) has a short fleshy filament, enlarged above, with two lateral 2-lobed thecae inserted somewhat obliquely and with latrorse dehiscence. Pollen grains are more or less spherical and with a finely reticulate surface (FIG. 45). The ovary is globular, unilocular, and appears to be unicarpellate. It is grooved on one side only (the presumed ventral side (FIG. 42)). The placentation is unusual with

2–5 (usually 4) ovules all pendulous from an *apical* placenta below the short and inconspicuously 2-lobed stigma. However, the bitegmic ovules are irregularly anatropous so that the micropyle is directed upwards. The funiculus varies in length so that the ovules hang at varying heights in the loculus. A conspicuous feature of the funiculus is the mat of short, uniseriate hairs which later develop into the filamentous aril described and illustrated by Gray (1859). There are no nectaries but the epidermis on the inner surface of the tepals and of the filament and exposed part of the connective is papillose, the enlarged cells being densely cytoplasmic and filled with anthocyanin (FIG. 42).

VASCULAR ANATOMY (Figs. 47, 48). The vascular system of the flower is very simple (FIG. 47). Each tepal has five vascular bundles, a median and two pairs of laterals. All tepal bundles end blindly in a distal direction and never converge or anastomose although they may produce short, blind-ending branches. Each stamen has a single vascular bundle and the carpel has two. The vascular system of the flower arises from an irregular ring of narrow vascular strands, which may be regarded as a very reduced version of the system in the aërial axis. The way in which vascular strands initially diverge is not very uniform. The tepal and stamen traces arise first, the remaining central bundles aggregating to form the 2 bundles which irrigate the carpel. Tepal traces are small and collateral, each pair of laterals diverging from a common bundle; the median usually originates independently but sometimes diverges from the common bundle of one of its lateral pairs. The stamen trace most commonly diverges from the median trace to the corresponding tepal, less commonly it originates directly from the pedicel system, independently of the tepal traces. It may, however, diverge from the common bundle which produces 2 lateral tepal traces. The stamen trace is irregularly collateral with an admixture of phloem and xylem elements, most pronounced in the connective where the bundle is enlarged. There is no indication of the stamen appendage which is such a conspicuous feature of the flower of *Stemona*.

There is no difficulty in interpreting the vascular system of the ovary (FIG. 48) according to the classical theory of carpel morphology and its modern counterpart, which interprets the carpel as a conduplicate structure. One strand (the smaller) can be regarded as the dorsal bundle. It runs independently up one wall of the ovary into the stigma where it divides into 2 short procambial strands. In the opposite wall is the ventral bundle, beneath the distinct ventral groove. It bifurcates at the apex of the ovary, the two bundles constituting the vascular supply to the apical placenta. Each ovule is supplied by a branch from one half of this placental supply. The ovule trace ends in the funiculus, there being no vascular supply to the integuments, at least at the time of anthesis. There is no anatomical indication that either the dorsal or the ventral carpel bundle is a dual structure; in fact xylem and phloem are rather diffuse. The general configuration of this ovary recalls that of *Sarcandra* and other Chloranthaceae described by Swamy and Bailey (1950), except that in *Sarcandra* the ovary has one ovule and the dorsal and ventral traces are most commonly double.

DISCUSSION

GROWTH HABIT. Our analysis of *Croomia* demonstrates that each unit of the sympodium has only two functional buds (the renewal bud and the dormant bud), the position of which is quite fixed. The rotation of one scale so that the renewal bud it subtends finds a position most favorable for continued growth is noteworthy. Of the two buds, one maintains the sympodium leaving only one to propagate the rhizome by branching. Even so, this is strongly inhibited and thereby the potential for vegetative propagation is reduced. It must be admitted that minute buds can be demonstrated, by microscopical methods, in the axils of other scale leaves. Their feeble vascular connection with the main vascular system of the rhizome, compared with that which connects functional buds to the main rhizome system, suggests that these obscure buds are vestigial. If propagation by seed is not vigorous the survival potential of *Croomia* must be low. This may well account for the relict status of the genus as indicated by its restricted and markedly disjunct distribution.

FLOWER. The morphology of the ovary calls for discussion since there seems to be lack of agreement in interpreting its structure in the related *Stemona* (cf. Baillon (1860) and Lachner-Sandoval (1892) on the one hand with Swamy (1964) on the other). It might be unwise to compare the ovary of *Croomia*, which has apical placentation, with *Stemona* which has basal placentation, but there are some notable anatomical similarities. It is unfortunate that *Stichoneuron* (with apical placentation) has to be excluded from this discussion but we have no comparable information about this genus.

Both Swamy and Baillon studied *Stemona tuberosa* Lour., Baillon using the name *Roxburghia gloriosoides* by which it was earlier known (Burkill, 1960). Lachner-Sandoval studied mainly *Stemona javanica* (as *Roxburghia javanica*), which has much smaller flowers, but he also investigated *Stemona tuberosa* (referred to as *Roxburghia gloriosa*) and does not comment on any major differences. The two early authors interpreted the carpel of *Stemona* as unicarpellate largely on developmental evidence. It originates as a single crescent-shaped protuberance opposite the first-formed tepal. This cushion of tissue grows in such a manner as to enclose the basal placenta. Swamy unfortunately had no access to this earlier information so his analysis based simply on the anatomy of the mature ovary is entirely original. He interpreted the ovary of *Stemona tuberosa* as bicarpellate because the ovules (up to 10) are in 2 rows. There are two identical vascular bundles in the ovary wall, one opposite each of the outer tepals. These Swamy regards as the dorsal bundles of 2 carpels, the ventral bundles being represented by the vascular supply direct to the basal ovules. In *Stemona javanica* according to Lachner-Sandoval, the two bundles in the ovary wall are dissimilar, one bundle being double. This difference is most obvious in the dehiscing capsule, the line of dehiscence passing through the single bundle but between the double one. *Croomia* corresponds to *Stemona* in having 2 ovary bundles, one opposite each outer tepal. However, there is no indication of a bicarpellate condition since there is no reason to interpret these bundles other than as a dorsal and a ventral. Also the way in which the ovary is closed in the stigmatic region suggests a manner of development comparable to that described for *Stemona* by Baillon, although this speculation has not yet been verified. However, the great difficulty in comparing the ovaries of these two genera is the marked difference in placentation and consequently in placental vascular supply. In the absence of extensive comparative and developmental studies we must confess that the interpretation of the ovary of the Stemonaceae still remains open.

TABLE 1. **Comparison of the three genera of Stemonaceae**

	CROOMIA	STEMONA	STICHONEURON
HABIT			
General	erect herb	scandent	low shrub
Leaf arrangement	distichous	distichous, spiral or whorled	distichous
Longitudinal veins of lamina	diverging from base	diverging from base	some diverging from midvein
Free vein-endings in lamina	present	rarely present	absent
Rhizome	extensive	not extensive ?	not extensive ?
ANATOMY			
Hairs	absent	absent	uniseriate, thick-walled
Cauline and common bundles in stem internode	not distinct	distinct	distinct
Crystals	no raphides	raphides and styloids	raphides
Vessels in stem	absent	present	present ?
Sieve tubes in stem	sieve plates simple	sieve plates compound	sieve plates simple ?
REPRODUCTIVE PARTS			
Cincinni	few-flowered	few, many-flowered or flowers solitary	many-flowered (if a cincinnus)
Stamens	not appendaged	appendaged	not appendaged
Pollen	sculptured	smooth	sculptured ?
Ovary	unicarpellate	disputed	?
Placentation	apical	basal	apical
Aril	filamentous	vesicular	?

TAXONOMY. These morphological problems are compounded because in dealing with the three genera of the Stemonaceae it is not evident that they form a natural assemblage. Similarities between the genera are few but differences are many. The following features are common to them and diagnose the Stemonaceae. Flowers are somewhat perigynous and have: — two pairs of sepaloid tepals, the outer pair at right angles to the inner; four stamens in a single whorl, one stamen opposite each tepal; a unilocular ovary with a short stigma. The ovules are anatropous, few to several, each with two integuments. The seeds are endospermous, ribbed and conspicuously arillate. The fruit is a 2-valved capsule. Leaves have a narrow insertion (not broadly encircling the stem) and a fairly characteristic cordate base. Stomata are anomocytic. The epidermis of the lamina has sinuous anticlinal walls. Some of the vascular bundles in the axis are amphivasal.

More detailed examination reveals marked differences which are set out, insofar as they are available, in TABLE 1. Even with this limited evidence it is clear that we are not dealing with a homogeneous assemblage. At this stage it would be presumptuous, therefore, to make any statements about the phylogenetic position of the Stemonaceae if it is suspected that they are an artificial group. A prior requisite to a correct understanding of their taxonomic status is the accumulation of a great deal more factual knowledge not only about them, but about their putative relatives.

SUMMARY

Shoots in *Croomia* are made up of units which branch sympodially. Each unit consists of a long-persistent rhizomatous portion and an annual erect, leafy shoot. The number of organs and their sequence, at least on the underground parts of the axis, is fixed within narrow limits. Only two functional vegetative buds are developed on the rhizome, a renewal bud which grows out immediately and a dormant bud which provides the only method of branching for the rhizome, although it is initially strongly inhibited. The anatomy of the vegetative organs and the flower is described. The simple vasculature of the ovary suggests that it is a single carpel despite its peculiar apical placentation. A summary of anatomical and morphological evidence suggests that *Croomia*, *Stemona*, and *Stichoneuron* constitute a rather heterogeneous assemblage.

ACKNOWLEDGMENTS

We are indebted to Miss Priscilla Fawcett, Botanical Illustrator at Fairchild Tropical Garden for the preparation of the morphological illustrations which make Plates I and II. Miss Mary Gregory, Bibliographer at the Jodrell Laboratory, Royal Botanic Gardens, Kew, was kind enough to supply us with bibliographic information about the Stemonaceae. Miss Anne Bellenger is thanked for the series of preparations on which the analysis of vascular systems is based.

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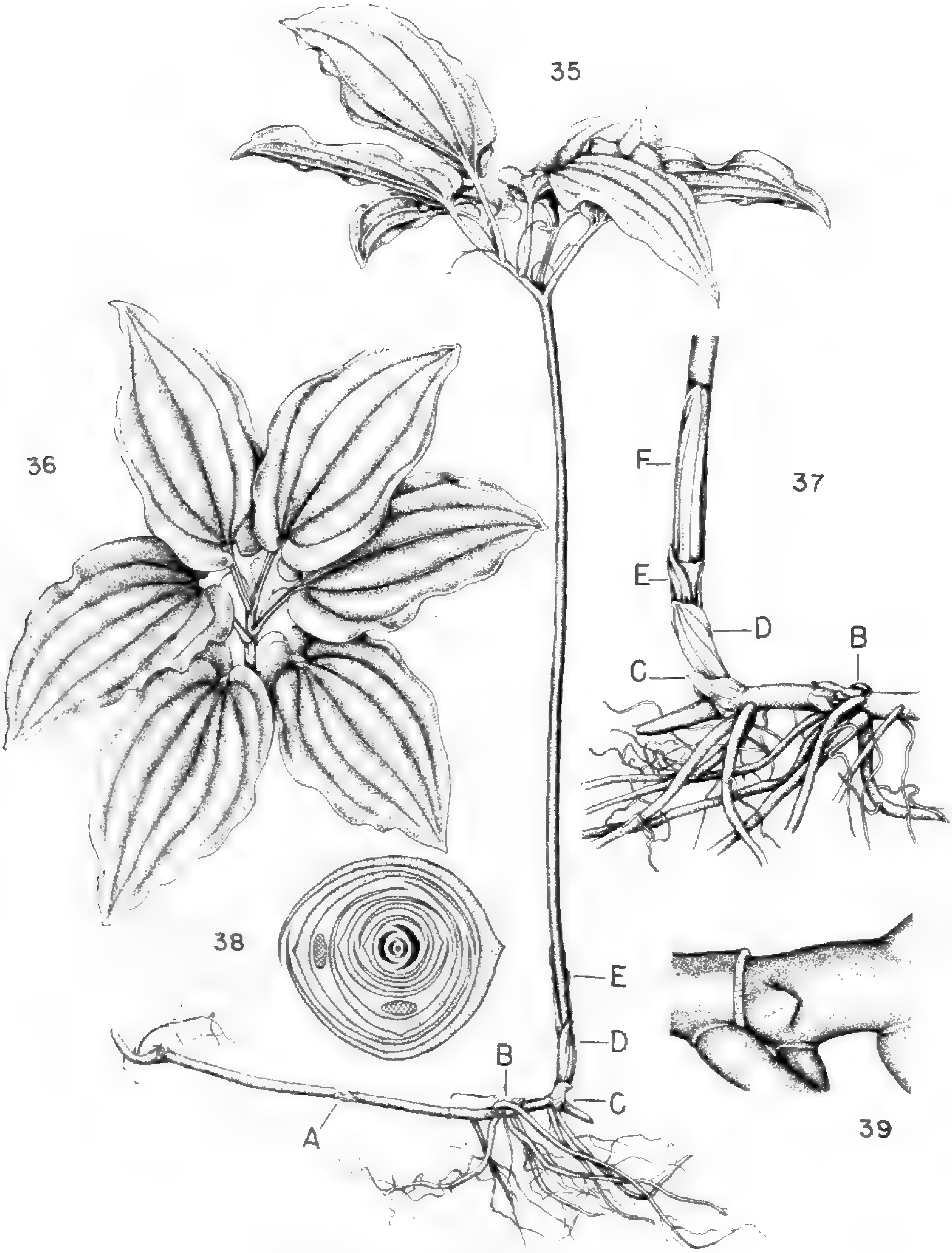
EXPLANATION OF PLATES

PLATE I

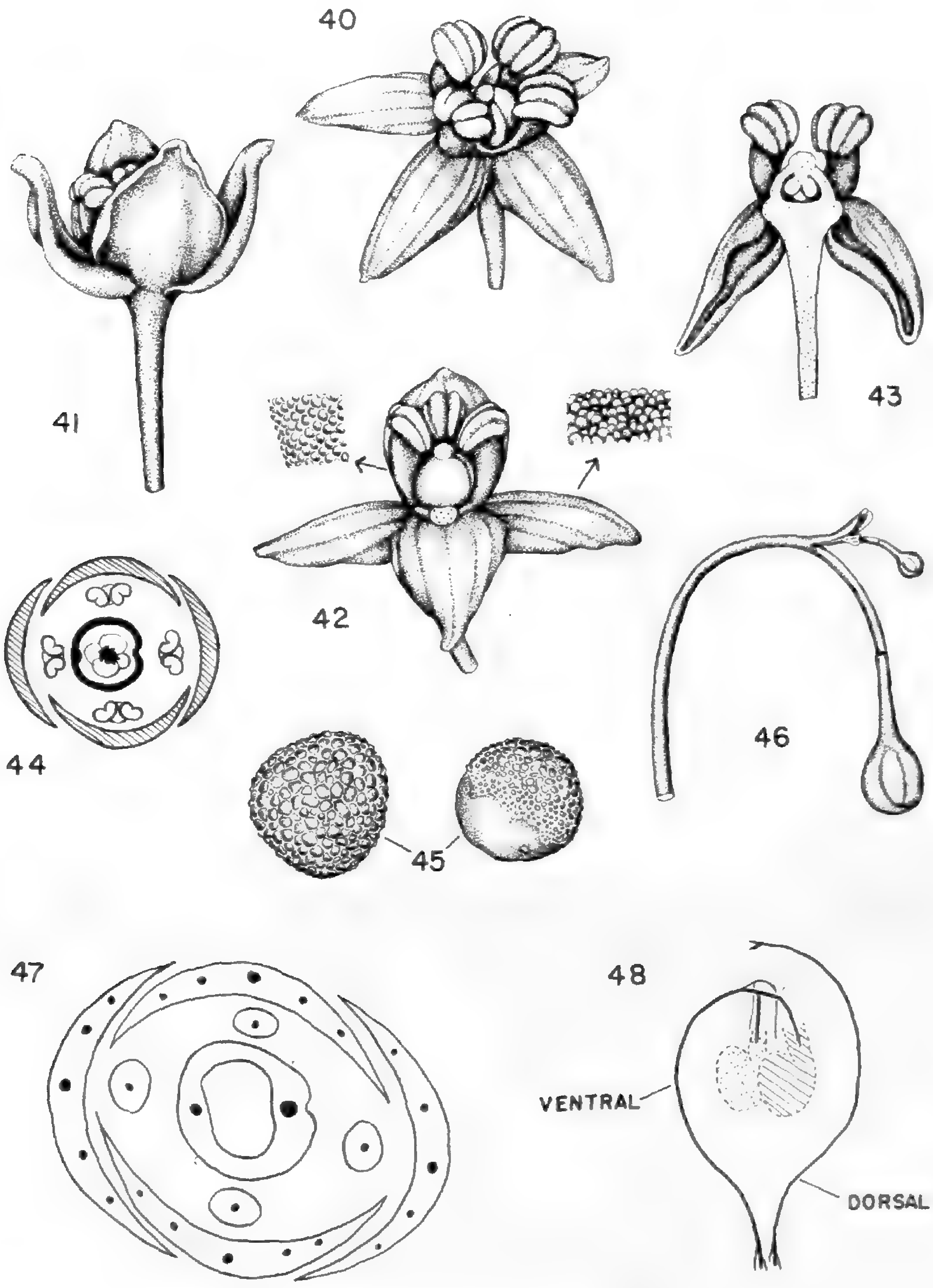
FIGS. 35–39, *Croomia pauciflora*, vegetative habit. FIG. 35. General habit of a plant in early April, × 1/2. Scar of previous year's erect shoot on rhizome to left. FIG. 36. Leafy shoot from above, × 1/2. FIG. 37. Details of base of erect shoot showing scales and renewal shoot, × 1. FIG. 38. Diagram of growth unit in transverse section; scale leaves, stippled; foliage leaves, solid black; functional buds, cross-hatched. FIG. 39. Details of node B with scale-leaf removed to show dormant bud, × 3. Letters A–F indicate successive nodes on early part of growth unit.

PLATE II

FIGS. 40–48, *Croomia pauciflora*, flowers. FIGS. 40–43. Open flowers in different aspects, × 4. FIG. 40. Obliquely from above. FIG. 41. Lateral view. FIG. 42. Same, with one stamen cut off to show ovary. Insets: surface of filament (left), and adaxial surface of tepal (right), to show papillose epidermis. FIG. 43. Median section at 45° to dorsiventral plane of ovary. FIG. 44. Floral diagram. FIG. 45. Pollen grains, × 300. FIG. 46. 2-flowered cincinnus, × 2. FIGS. 47 and 48. Diagrams of vascular system of flowers. FIG. 47. Transverse section of flower constructed from several sections at different levels. Vascular bundles in solid black. FIG. 48. Ovary as seen in cleared flower, only 2 ovules shown.



TOMLINSON & AYENSU, CROOMIA



Tomlinson & Ayensu, Croomia

HERISSANTIA, BOGENHARDIA, AND GAYOIDES (MALVACEAE)

GEORGE K. BRIZICKY

IN 1903, J. K. Small raised the section ["subgenus"] *Gayoides* A. Gray of *Abutilon* Mill. to the rank of genus, with *Gayoides crispum* (L.) Small (*Abutilon crispum* (L.) Medic., *Sida crispa* L.) as the type (Fl. Southeast. U.S. 764, 1335). Subsequently, *Gayoides* has been adopted and used by many authors for this segregate of *Abutilon*. In 1954, Kearney checked the availability of two older names, *Herissantia* Medic. and *Bogenhardia* Reichenb., for this genus. He found (Leafl. West. Bot. 7: 119, 120. 1954) *Herissantia* (Medicus, Philosophische Botanik 1: 90. 1789) to be a ***nomen nudum***, but *Bogenhardia* (Reichenbach, Repertorium Herbarii 1: 200. 1841; 2: 48. 1841) to be validly published and hence much earlier than *Gayoides*. Consequently, Kearney transferred *Gayoides crispum* into *Bogenhardia* as *B. crispa* (L.) Kearney.

There is, however, an earlier work by Medicus, "Kurzer Umriss einer systematischen Beschreibung der mannigfaltigen Umhüllungen der Saamen" (Vorles. Churpfälz. Phys.-Oekon. Ges. 4(1): 244. 1788), in which *Herissantia* was published with the following description: "224. HERISSANTIA (Sida crispa. Cavanil. Dissertatio prima, num. 65). Dem äussern Ansehen nach sieht die Saamenkapsel gänzlich jener von Abutilon gleich, unterscheidet sich aber von derselben merkwürdig dadurch, dass bei gänzlicher Zeitigung keine einzelne Saamenkapseln da sind, sondern alle Schaalen bis unten gänzlich geöffnet, und nur wo sie in der Mitte gemeinschaftlich zusammenstossen, miteindander verwachsen sind." Although the description is rather brief and only refers to the fruit, it indicates the main character distinguishing *Herissantia* from *Abutilon* and certainly merits recognition as a formal generic description no less than Endlicher's diagnosis (Gen. Pl. 986. 1840) of the subdivision *Gayoides* of *Bastardia* HBK. on which Reichenbach's *Bogenhardia* was based. Moreover, an additional Latin diagnosis of *Herissantia* is found interpolated in Medicus's system of or key to the fruit types (*loc. cit.* 369), namely: "G. [*Capsulae*] *plures, receptaculo communi affixae, suntque* . . . a. 3. *multivalves* 224. Herissantia." Thus, *Herissantia* appears to be a validly published name which is to be taken up in place of the later *Bogenhardia* (1841). Since this neotropical genus of at most three species (see H. Monteiro, Anais Soc. Bot. Brasil 5: 438–444. 1956) is economically unimportant, there is no reason at all to propose for conservation either *Gayoides* or *Bogenhardia*. For convenience I present below the correct name for this segregate of *Abutilon*, with its synonyms, the type species common to all, and the necessary new combinations.

Herissantia Medic. Vorles. Churpfälz. Phys.-Oekon. Ges. 4(1): 244. 1788.

Bastardia HBK. b. *Gayoides* Endl. Gen. Pl. 986. 1840.
Bogenhardia Reichenb. Repert. Herb. 1: 200. 1841; 2: 48. 1841, *nom. illeg.*
Abutilon sect. *Gayoides* (Endl.) A. Gray, Gen. Pl. U.S. 2: 65. 1849.
Gayoides Small, Fl. Southeast. U.S. 764, 1335. 1903, *nom. illeg.*
Pseudobastardia Hassler, Bull. Soc. Bot. Genève II. 1: 209. 1909, *nom. illeg.*

TYPE SPECIES: ✓**Herissantia crispa** (L.) Brizicky, comb. nov. (*Sida crispa* L. Sp. Pl. 2: 685. 1753; *Abutilon cryspum* (L.) Medic. Künstl. Geschl. Malven-Fam. 29. 1787; *Gayoides crispum* (L.) Small, Fl. Southeast. U.S. 764. 1903; *Bogenhardia crispa* (L.) Kearney, Leafl. West. Bot. 7: 120. 1954).

The correct names for two Brazilian species recognized by Monteiro (*loc. cit.*) are the following:

Herissantia tiubae (K. Schum.) Brizicky, comb. nov. (*Abutilon tiubae* K. Schum. *in* Mart. Fl. Brasil. 12(3): 381. 1891; *Bogenhardia tiubae* H. Monteiro, Anais Soc. Bot. Brasil 5: 440. 1956).

Herissantia nemoralis (St.-Hil. *et al.*) Brizicky, comb. nov. (*Bastardia nemoralis* St.-Hil. *et al.*, Fl. Brasil. Merid. 1: 195. 1827; *Bogenhardia nemoralis* (A. Juss.) H. Monteiro, *loc. cit.* 442.

Derivation of the generic name was not indicated by Medicus. There is little doubt, however, that the name commemorates Louis Antoine Prospère Hérissant, 1745–1769, a French physician, naturalist, and poet, the author of the *Bibliothèque physique de la France ou Liste de tous les ouvrages, tant imprimés que manuscrits, qui traitent de l'Histoire naturelle de ce Royaume; avec des notes critiques & historiques* (8°. 496 pp. Paris), published posthumously in 1771. Besides this rather well-known bibliographic work, Hérissant's other, apparently very rare, publication, *Jardin des curieux, ou catalogue raisonné des plantes les plus belles et les plus rare avec leur culture* (12°. Paris) appeared in the same year. (Cf.: A. Haller, Bibliot. Bot. 2: 611. 1772; G. R. Boehmer, Bibliot. Script. Hist. Nat. Oekon. 3(1) [III, a]: 719. 1787.)

JAMAICAN AND OTHER SPECIES OF BUMELIA (SAPOTACEAE)

WILLIAM T. STEARN

THE GENUS *Bumelia*, with which *Dipholis* is here united, comprises about forty species, all American, of which nine occur in Jamaica. They have been the subject of a careful, detailed, very useful revision by Cronquist in the *Journal of the Arnold Arboretum* **26**: 435–471. 1945, which provides keys, descriptions, and synonymy, the last very extensive owing to insufficient allowance by many authors for variation within species.

The following notes arising out of a study of the Sapotaceae for the *Flora of Jamaica* supplement Cronquist's work.

In Jamaica these trees are often known under the name of "Bullet," formerly "Bully-tree," the ripe fruits of some species recalling to the early colonists those of the European bullace (*Prunus insititia*).

THE IDENTITY OF MAUROCENIA AMERICANA

In 1754, Philip Miller maintained the genus *Maurocenia* (in his *Gardeners Dictionary Abridged*, 4th ed.) as distinct from *Cassine*, with which Linnaeus had united it, observing that "in this he is mistaken," and thus gave the name *Maurocenia* valid post-1753 publication. In 1768 (in the 8th edition of the *Gardeners Dictionary*), Miller included four species in the genus. The first, *Maurocenia frangula* Miller (*Cassine maurocenia* L., 1753), the lectotype of the genus, belongs to the Celastraceae. This and Miller's two other species, *M. phillyrea* Miller (i.e., *Cassine peragua* L. sensu stricto, syn. *C. capensis* L.) and *M. cerasus* Miller (possibly an *Euclea*) were all from South Africa. His fourth species, *M. americana*, however, came from Jamaica and, although not hitherto placed, it is evidently not congeneric with the African members of the genus. Miller's account is as follows:

> 4. MAUROCENIA (*Americana*) foliis obverse ovatis emarginatis, floribus solitariis alaribus. *Maurocenia with obverse oval leaves which are indented at the edges, and flowers growing singly from the sides of the branches.* Frangula folio subrotundo rigido subtus ferrugineo. Houst. MSS. *Berry-bearing Alder with a rounded stiff leaf, which is of an iron colour on the under side.*
>
> The fourth sort was discovered by the late Dr. Houstoun, growing naturally at the Palisadoes in Jamaica, from whence he sent the seeds to Europe; this rises with a woody stalk from fifteen to twenty feet high, covered with a rough brown bark, and divides into many branches, which are garnished with stiff leaves, placed alternately; they are about an inch and a half long, and a little more in breadth, indented at the top, with a stiff reflexed border, of a gray colour on their upper side, but of a rusty iron colour on their under, standing upon short foot-stalks. The flowers come out singly along the side of the

FIG. 1. Type specimen of *Maurocenia americana* Miller (*Bumelia americana* (Miller) Stearn) in herb. British Museum (Nat. Hist.).

branches; they have small white petals which end in acute points, and five slender stamina, which spread open, and are terminated by obtuse summits. In the center is situated a roundish germen, supporting a long bifid stigma, which is permanent. The germen afterwards turns to a round berry, with one or two cells, each having one oblong seed.

The Palisadoes is a coastal strip of land enclosing Kingston Harbour with Port Royal at its tip. Houstoun's specimen (FIG. 1) from the Palisadoes is in Miller's herbarium, now incorporated in the general herbarium of the British Museum (Natural History), London; it lacks flowers but undoubtedly belongs to *Bumelia retusa* Swartz, the lectotype of the genus *Bumelia* (Sapotaceae), which is common on the coasts of the Bahamas, Jamaica, and Cuba. This varies much in the size, shape, pubescence, and veining of the leaves. The leaves of Houstoun's specimen agree essentially with those of *B. retusa* from southern Jamaica, e.g., *Proctor 17427* from Little Goat Island, St. Catherine, as well as from elsewhere, e.g., *Stearn 314* from St. Ann, *Proctor & Stearn 11762* from Trelawny. Although the fruits are usually solitary in the axils, the flowers are rarely so and are usually in sessile axillary fascicles of 2 to 15. In consequence of the identity of Miller's species with Swartz's, Miller's epithet must be transferred to *Bumelia* and replace Swartz's.

Bumelia americana (Miller) Stearn, comb. nov.

Maurocenia americana Miller, Gard. Dict. ed. 8, art. Maurocenia no. 4. 1768. *Bumelia retusa* Swartz, Prodr. 49. 1788; Fl. Ind. Occ. 1: 490. 1797. Cronquist, Jour. Arnold Arb. 26: 460. 1945.

For further synonymy, see Cronquist, *loc. cit.*

THE JAMAICAN SPECIES OF BUMELIA

After stating that *Bumelia* Swartz (1788) and *Dipholis* A. DC. (1884), showed "no real diversity in structure or habit" and that the presence of albumen in *Dipholis* and its absence in *Bumelia* have no practical importance owing to the rarity of fruiting specimens, Hartog in 1879 (Jour. Bot. (London) 17: 356) accordingly proposed to abolish *Dipholis* even as a section of *Bumelia*. Nevertheless most other authors have continued to maintain them, by attributing scanty or no albumen and fleshy cotyledons to *Bumelia* and abundant albumen and thin cotyledons to *Dipholis*. Aubréville (Adansonia, Mém. 1: 78. 1965), for example, keys them out as:

Graine sans albumen	*Bumelia*
Graine avec albumen	*Dipholis*

The seeds are, however, unknown for many species of this group, and it is thus uncertain whether such species really possess the seed characters of the genera in which they have been placed. Despite certain tendencies noted by Cronquist (Jour. Arnold Arb. 26: 445. 1945), e.g. "plant commonly spiny or thorny" in *Bumelia* and "plant unarmed" in *Dipholis*, "ovary usually hairy, occasionally glabrous" in *Bumelia* and "ovary nearly always glabrous" in *Dipholis*, the "fruit commonly . . . rounded . . . at the apex" in *Bumelia* and the "fruit commonly abruptly tapering to the style" in *Dipholis*, there are no constant correlations between these characters and those of the seed. Hence it is difficult and arbitrary to recognize two groups. Baehni in his first memoir on the Sapotaceae (Candollea 7: 434. 1938) referred *Dipholis* to *Bumelia*. In his posthumous survey of the genera (Boissiera 11: 133–136. 1965) he concluded that "en somme leur séparation aurait plutôt comme base une croyance, un mythe," the amount of albumen and thickness of the cotyledons being a relative and not absolute distinction. No good purpose is served in trying to keep them separate.

The Jamaican species of *Bumelia*, including those formerly placed in *Dipholis*, are as follows:

1\. Calyx ca. 2–2.5(–3) mm. long. Flowers usually many (3–15) in a cluster.
  2\. Petiole 15–32 mm. long. Leaf-blades often more than 8 cm. long and 4 cm. broad; lateral veins clearly evident. Fruits large (12–15 mm. in diameter), subglobose. .... *B. nigra.*
  2\. Petiole 2–15 mm. long. Leaf-blades rarely up to 8 cm. long and 4 cm. broad; lateral veins inconspicuous. Fruits smaller (4–10 mm. in diameter).
    3\. Leaf-blades acute or shortly acuminate, mostly narrowly elliptic. Fruits ca. 5 mm. long. .... *B. salicifolia.*
    3\. Leaf-blades obtuse or rounded, sometimes emarginate at apex, mostly almost orbicular, rotund or broadly elliptic, varying to obovate or oblanceolate. Fruits ca. 8–10 mm. long.
      4\. Young branchlets, pedicels, and sepals glabrous. Leaves green beneath when young. Fruits oblong-ellipsoid, ca. 4–5 mm. in diameter. .... *B. rotundifolia.*
      4\. Young branchlets, pedicels, and sepals minutely hairy. Leaves brown-tomentose beneath when young. Fruits subglobose to broadly ellipsoid, ca. 10 mm. in diameter. .... *B. americana.*

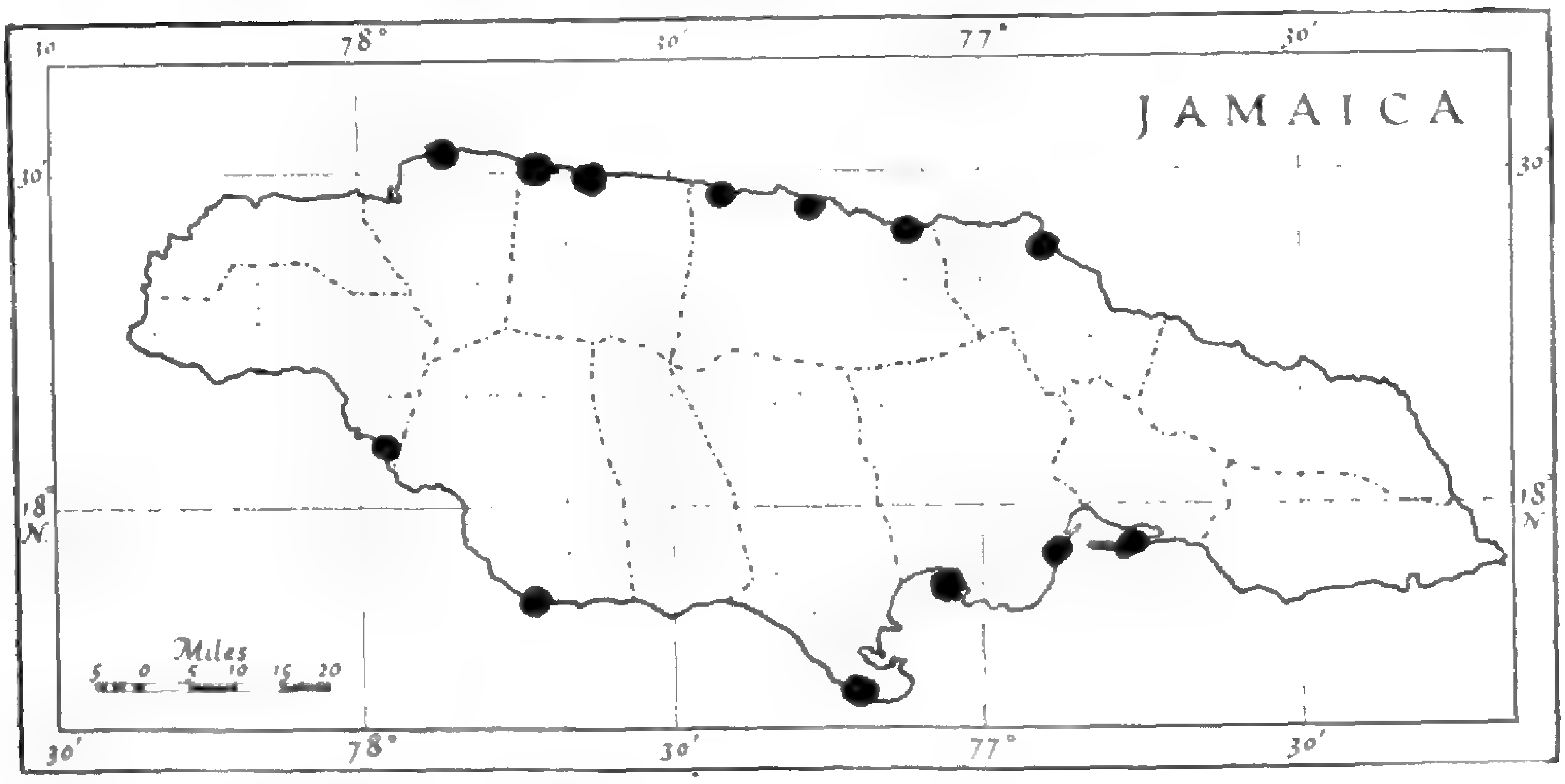
1\. Calyx (3–)3.5–4 mm. long. Flowers usually few (1–8) in a cluster.
  5\. Sepals 8–9, the outer as well as the inner brown-tomentose. Pedicels persistently hairy. Central Jamaica. .... *B. octosepala.*
  5\. Sepals 5–8, the outer 2 glabrous or sparsely hairy, the inner tomentose or sericeous. Pedicels glabrous or sparingly hairy.
    6\. Leaf-blades not more than 5 cm. broad.
      7\. Leaves without raised network of veins beneath. Blue Mountains. .... *B. montana.*
      7\. Leaves with raised network of veins beneath. Santa Cruz Mountains. .... *B.* sp. nov. I.
    6\. Leaf-blades some or all more than 5 cm. broad, with raised network of veins beneath immediately visible under a lens.
      8\. Petiole 1–10 mm. long. Leaf-blades obovate or broadly obovate. Eastern Jamaica. .... *B. bullata.*
      8\. Petiole 10–20 mm. long. Leaf-blades elliptic-oblong. Western Jamaica. .... *B.* sp. nov. II.

Bumelia americana (Miller) Stearn, comb. nov. See above.

B. americana subsp. **americana** FIG. 1; FIG. 2, G–K; FIG. 3, I.

Bumelia retusa subsp. *typica* Cronquist, Jour. Arnold Arb. **26**: 460. 1945.

Bahamas, Cuba, Jamaica, Navassa. See MAP 1.



MAP 1. Distribution of *Bumelia americana* in Jamaica.

B. americana subsp. **neglecta** (Cronquist) Stearn, comb. nov.

Bumelia retusa subsp. *neglecta* Cronquist, Jour. Arnold Arb. **26**: 461. 1945.

Mexico, British Honduras.

Bumelia bullata (Howard & Proctor) Stearn, comb. nov.

Dipholis bullata Howard & Proctor, Jour. Arnold Arb. **39**: 103. 1958.

Jamaica: Parish of Portland.

Bumelia montana Swartz, Prodr. 49. 1788; Fl. Ind. Occ. 1: 493. *t. 8, fig. e–n.* 1797. FIG. 3, A–D, J.

Dipholis montana (Swartz) Griseb. Fl. Brit. W. Indian Is. 401. 1861. Pierre & Urban in Urban, Symb. Antill. **5**: 135. 1904. Cronquist, Jour. Arnold Arb. **26**: 442. 1945.

Jamaica: Parishes of St. Andrew, Portland, St. Thomas.

Bumelia nigra Swartz, Prodr. 49. 1788; Fl. Ind. Occ. 1: 487. *t. 8, fig. a–d.* 1797. FIG. 3, F–H.

Dipholis nigra (Swartz) Griseb. Fl. Brit. W. Indian Is. 400. 1861. Pierre & Urban in Urban, Symb. Antill. **5**: 137. 1904. Cronquist, Jour. Arnold Arb. **26**: 439. 1945.

Jamaica: Parishes of Westmoreland, Trelawny, St. Elizabeth, Manchester, Clarendon, St. Ann, St. Andrew.

Bumelia octosepala (Urban) Stearn, comb. nov. FIG. 3, E.

Dipholis octosepala Urban, Symb. Antill. **7**: 324. 1912. Cronquist, Jour. Arnold Arb. **26**: 442. 1945.

Jamaica: Parishes of Trelawny, Clarendon, St. Ann, St. Catherine.

Bumelia rotundifolia Swartz, Prodr. 50. 1788; Fl. Ind. Occ. 1: 495.

1797. Pierre & Urban in Urban, Symb. Antill. **5**: 143. 1904. Cronquist, Jour. Arnold Arb. **26**: 459, 1945. FIG. 2, A–F.

Jamaica: Parishes of Hanover, Trelawny, Manchester, St. Ann, Clarendon, St. Catherine, St. Andrew.

Bumelia salicifolia (L.) Swartz, Prodr. 50. 1788; Fl. Ind. Occ. **1**: 491. 1797.

Achras salicifolia L. Sp. Pl. ed. 2. **1**: 470. 1762.
Dipholis salicifolia (L.) A. DC. in DC. Prodr. **8**: 188. 1844. Sargent, Silva N. Am. **5**: 179. *t. 250.* 1893. Pierre & Urban in Urban, Symb. Antill. **5**: 138. 1904. Cronquist, Jour. Arnold Arb. **26**: 440. 1945.

Florida, Bahamas, Jamaica (Parishes of Westmoreland, St. James, St. Elizabeth, Trelawney, Clarendon, St. Ann, St. Catherine, St. Mary, St. Andrew), Cuba, Hispaniola, Puerto Rico, Virgin Islands, Guadaloupe, Barbados, Central America.

Bumelia, sp. nov. I.

Jamaica: Parish of St. Elizabeth; Santa Cruz Mountains, Malvern, 2,200′, ix. 1907, *Harris 9742*; same locality, 2,100′, ix. 1907, *Harris 9803*.

This is closely related to *Bumelia montana* of the Blue Mountains, eastern Jamaica, but seems distinct in the more evident veining of the leaves and slightly smaller calyx. Complete flowers and fruits are unknown.

Bumelia, sp. nov. II.

Jamaica: Parish of Hanover; interior summit slopes of Dolphin Head, limestone ridge forest, 1,100′ – 1,700′, iv. 1955, *Proctor 10039*.

This species is notable for its large leaves with elliptic blades 5–18 cm. long, 2.5–8 cm. broad. Complete flowers and fruits are unknown.

OTHER SPECIES

The following species distinguished by Cronquist or by Standley and Williams under *Dipholis* do not occur in Jamaica.

Bumelia bellonis (Urban) Stearn, comb. nov.

Dipholis bellonis Urban, Symb. Antill. **5**: 137. 1904. Cronquist, Jour. Arnold Arb. **26**: 440. 1945.

Puerto Rico.

Bumelia cubensis Griseb. Cat. Pl. Cub. 164. 1866.

Dipholis cubensis (Griseb.) Pierre in Urban, Symb. Antill. **5**: 140. 1904. Cronquist, Jour. Arnold Arb. **26**: 443. 1945.

Cuba.

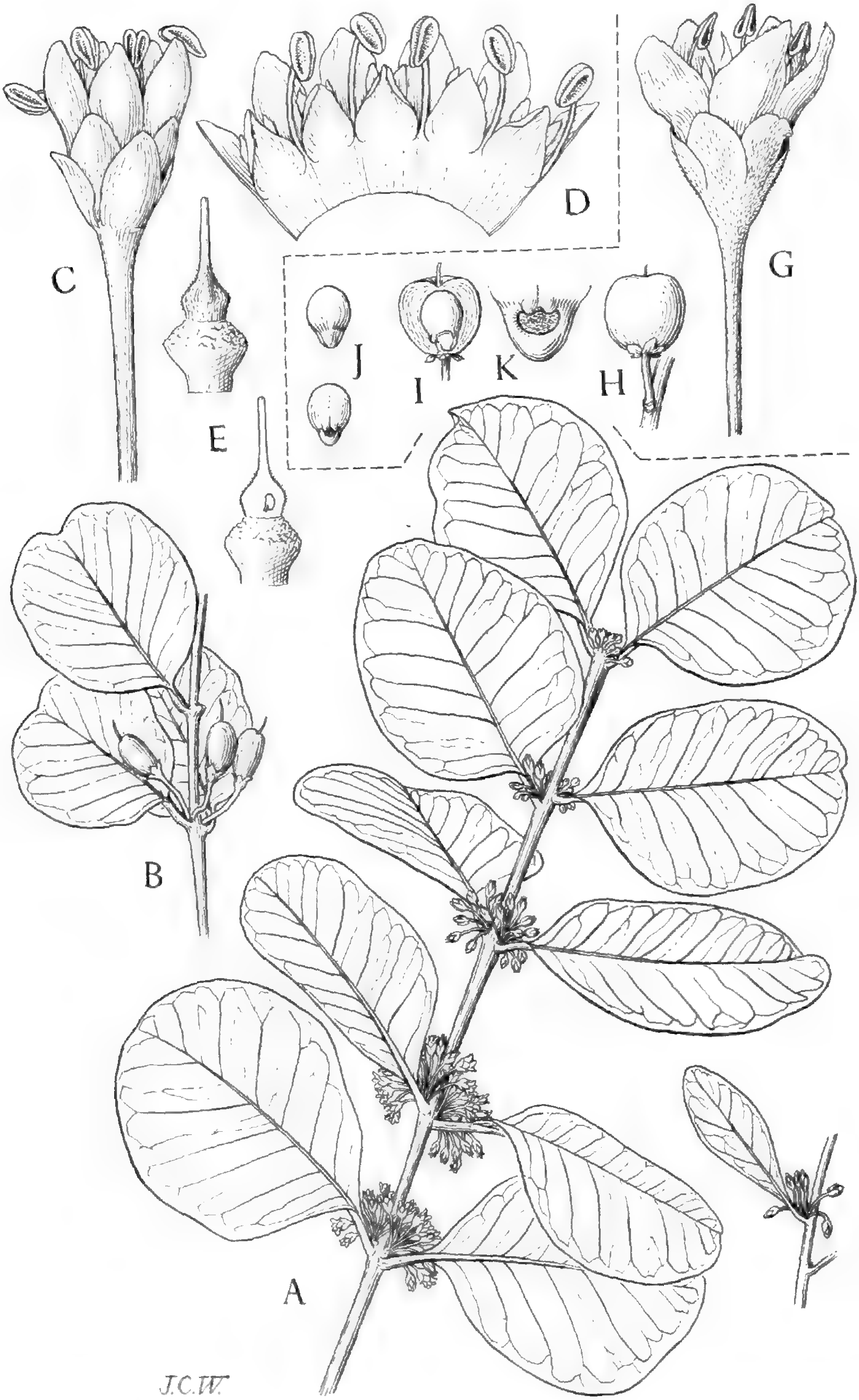


FIG. 2. A–F, *Bumelia rotundifolia*. A, flowering shoot (*Norman 158*) × 3/5; B, fruiting shoot (*Webster & Wilson 4928*), × 3/5; C, flower (*Norman 158*), × 6; D, dissected corolla (*Norman 158*), × 6; E, gynoecium (*Norman 158*),

Bumelia durifolia (Standley) Stearn, comb. nov.

Dipholis durifolia Standley, Carnegie Inst. Wash. Misc. Publ. **461** (Bot. Maya Area 4): 78. 1935. Cronquist, Jour. Arnold Arb. **26**: 441. 1945.

British Honduras.

Bumelia ferruginea (Ekman & O. C. Schmidt) Stearn, comb. nov.

Dipholis ferruginea Ekman & O. C. Schmidt, Fedde, Repert. Sp. Nov. **32**: 94. 1933. Cronquist, Jour. Arnold Arb. **26**: 444. 1945.

Hispaniola: Dominican Republic.

Bumelia jubilla (Urban) Stearn, comb. nov.

Dipholis jubilla Ekman ex Urban, Symb. Antill. **9**: 415. 1925. Cronquist, Jour. Arnold Arb. **26**: 439. 1945.

Cuba.

Bumelia matudae (C. Lundell) Stearn, comb. nov.

Sideroxylon matudae C. Lundell, Phytologia **1**: 221. 1937 (as *matudai*).
Sideroxylon steyermarkii Standley, Field Mus. Publ. Bot. **22**: 368. 1940.
Dipholis matudae (C. Lundell) C. Lundell, Contr. Univ. Michigan Herb. **7**: 43. 1942 (as *matudai*); Standley & L. O. Williams in Fieldiana, Bot. **24**: 220. 1967 (as *matudae*).

Mexico, Guatemala.

Cronquist included this in *Bumelia minutiflora*, from which it differs, according to Standley and Williams, in having much larger and differently veined leaves. The genitive of Matuda being *matudae*, like *balansae* from Balansa (cf. Int. Code Bot. Nomencl. 1966, Art. 73, Rec. 73C), Lundell's original spelling *matudai* is to be treated as an orthographic error.

Bumelia minutiflora (Pittier) Baehni, Boissiera **11**: 135. 1965.

Dipholis minutiflora Pittier, Contr. U.S. Natl. Herb. **13**: 464. 1912. Cronquist, Jour. Arnold Arb. **26**: 438. 1945.

Mexico, Guatemala, Honduras, Costa Rica, Panama.

Bumelia sp.

Dipholis parvifolia Standley, Field Mus. Publ. Bot. **18**: 909. 1938. Cronquist, Jour. Arnold Arb. **26**: 442. 1945.

Transfer of Standley's epithet *parvifolia* to *Bumelia* is precluded by

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× 6; [F] unlettered figure in lower right corner, leaf and inflorescence (*Harris 11040*, isotype of *B. peckhamensis*), × 3/5. G–K, *Bumelia americana*. G, flower (*Stearn 314*), × 6; H, fruit (*Proctor 2197*), × 1; I, fruit in longitudinal section (*Proctor 2197*), × 1; J, seed (*Proctor 2197*), × 1; K, scar of seed (*Proctor 2197*), × 3. Drawing by Joanna C. Webb, from specimens in British Museum (Natural History), London.

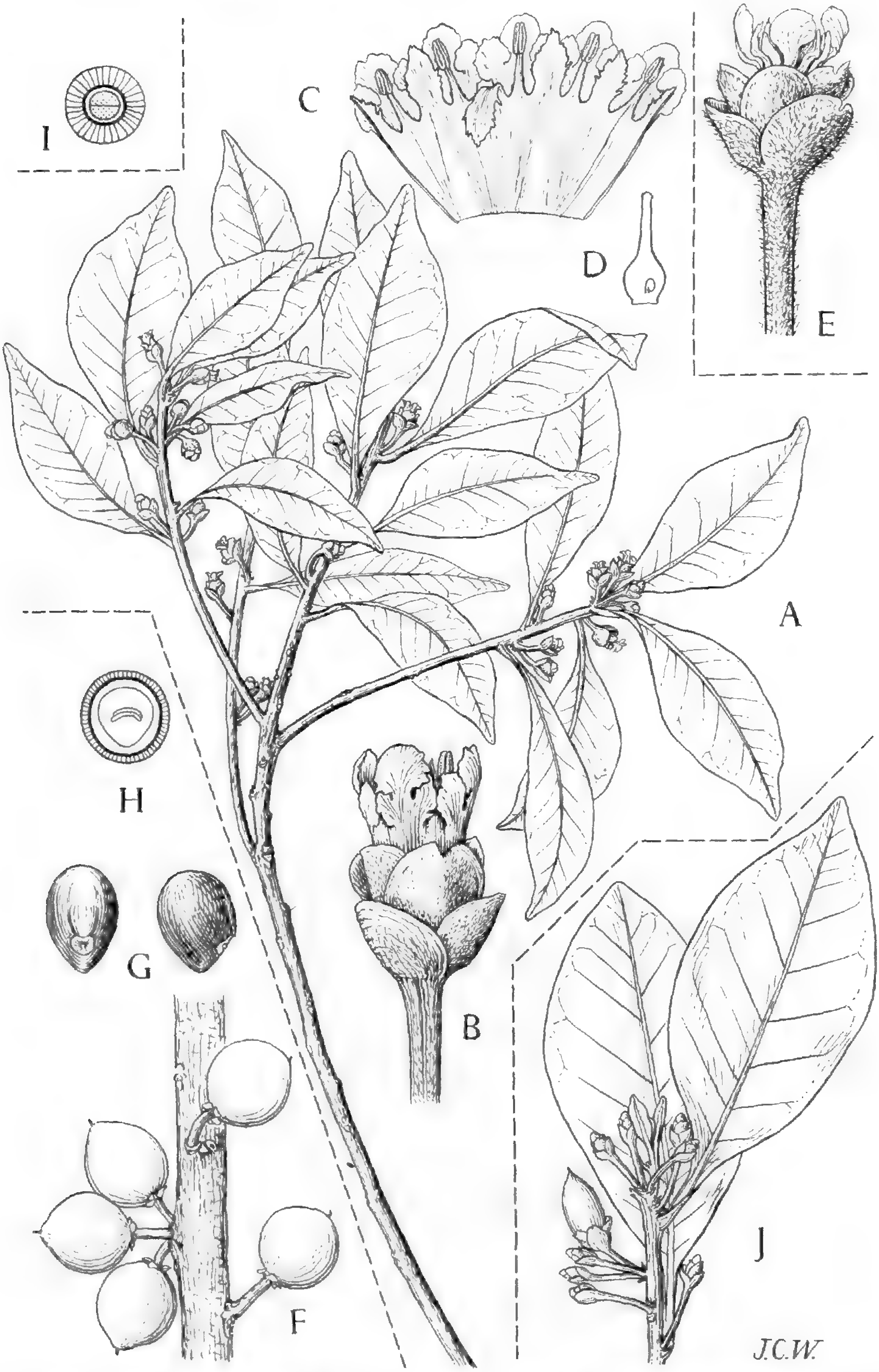

FIG. 3. A–D, J, *Bumelia montana*. A, flowering shoot (*Proctor 9538*), × 3/5; B, flower (*Proctor 9538*), × 4; C, dissected corolla (*Proctor 9538*), × 4; D, gynoecium in section (*Proctor 9538*); J, fruiting shoot (*Harris 10118*),

Bumelia parvifolia A. DC. in DC. Prodr. **8**: 190. 1844. Since this species was described by Standley from specimens without flowers, it would seem prudent to await more complete material from the type-locality, Los Ayotes, prov. Guanacaste, Costa Rica, before providing it with a new name.

Bumelia repens (Urban & Ekman) Stearn, comb. nov.

Dipholis repens Urban & Ekman, Ark. Bot. 22A. **17**: 70. 1929. Cronquist, Jour. Arnold Arb. **26**: 444. 1945.

Hispaniola: Dominican Republic.

Bumelia sericea (Cronquist) Stearn, comb. nov.

Dipholis sericea Cronquist, Jour. Arnold Arb. **26**: 444. 1945.

Hispaniola: Dominican Republic.

Bumelia stevensonii (Standley) Stearn, comb. nov.

Dipholis stevensonii Standley, Trop. Woods **11**: 21. 1927. Cronquist, Jour. Arnold Arb. **26**: 438. 1945.

British Honduras.

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BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON, S.W. 7, ENGLAND

× 2/3. E, *Bumelia octosepala*, flower (*Proctor 5421*), × 4. F–H, *Bumelia nigra*. F, fruits (*Proctor 20591*), × 3/5; G, seed (*Proctor 20591*), × 1; H, fruit in transverse section showing cotyledons embedded in abundant endosperm and scanty pulp, × 3/5. I, *Bumelia americana*, fruit in transverse section showing fleshy cotyledons, without endosperm, and abundant pulp, × 1. Drawing by Joanna C. Webb, from specimens in British Museum (Natural History), London.

VOLUME 49 NUMBER 3

JOURNAL
OF THE
ARNOLD ARBORETUM
HARVARD UNIVERSITY

JULY, 1968

PUBLISHED BY
THE ARNOLD ARBORETUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS

THE JOURNAL OF THE ARNOLD ARBORETUM

Published quarterly by the Arnold Arboretum of Harvard University.

Subscription price $10.00 per year.

Volumes I–XX, reprinted, and back issues of volumes XXI–XLV are available from the KRAUS REPRINT CORPORATION, 16 EAST 46TH STREET, NEW YORK, N.Y. 10017.

Subscriptions and remittances should be addressed to MISS DULCIE A. POWELL, ARNOLD ARBORETUM, 22 DIVINITY AVENUE, CAMBRIDGE, MASSACHUSETTS 02138.

CONTENTS OF NO. 3

Volume 49, No. 2, including pages 167–290,
was issued April 22, 1968

Second-class postage paid at Boston, Massachusetts

JOURNAL
OF THE
ARNOLD ARBORETUM

VOL. 49 JULY 1968 NUMBER 3

ANATOMY OF THE PALM RHAPIS EXCELSA, V. INFLORESCENCE

P. B. TOMLINSON [1] AND M. H. ZIMMERMANN

PREVIOUS ARTICLES IN THIS SERIES on the anatomy of *Rhapis* have described the construction of aërial and underground (rhizomatous) axes and something of the developmental principles underlying this construction (Zimmermann & Tomlinson, 1965, 1967a; Tomlinson & Zimmermann, 1966a & b). The vascular system thus revealed has also demonstrated a continuous pathway for long-distance transport. Further, the organization of newly developed vascular strands in the apex shows how new leaves are continuously attached to the axial system.

For further appreciation of vascular continuity an understanding of the method of attachment of lateral organs to the main axis has been sought. The present article describes the attachment of the inflorescence axis to the aërial stem and something of the attachment of lateral branches of various orders to the main inflorescence axis. A description of the attachment of flowers to rachilla is reserved for a future article dealing with floral anatomy.

To complete a full understanding of the vascular pathways throughout *Rhapis* the attachment of roots and vegetative branches (rhizomatous suckers) still remains to be described. This will be done in another paper of this series whereupon a general discussion of developmental principles involved in branch-axis union in monocotyledons will be permitted. It is remarkable how little this aspect of monocotyledonous anatomy has attracted the recent attention of botanists despite its obvious and fundamental physiological significance. To the question "Is there, in palms, any vascular connection between the lateral inflorescence and the foliage leaf which subtends it?" there has hitherto been no answer, although it is of obvious significance to tropical agronomists. This present article gives some indication of a satisfactory answer.

The only previous work on this topic is by the indefatigable von Mohl (1824) who illustrated various kinds of union without showing anatomical detail. Micheels (1892) has described the anatomy of the ultimate, fruit-

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[1] Research on the anatomy of palms by P. B. Tomlinson is supported by National Science Foundation Grant GB-2991 and its continuation GB-5762-X.

bearing axis of the inflorescence in 32 species from 19 genera of palms with a discussion restricted to the mechanical significance of the tissues he observed. Otherwise the anatomy of the inflorescence axis in palms seems never to have been examined.

The general features of flowering in palms is a subject scarcely considered in botanical textbooks. Palm inflorescences are seemingly complex organs and they are not normally available in herbaria, except as fragments. Constructional principles, however, are straightforward even though the multiplicity and size of branches tends to obscure this. The recent account by Tomlinson and Moore (1968) of inflorescence in *Nannorrhops* has indicated some of the essential features of the reproductive axis in palms and it is against this background of understanding that the inflorescence in *Rhapis* is described.

MATERIAL AND METHODS

Microscopic analyses of vascular systems are based on the cinematographic methods which have been described in detail in previous articles (Zimmermann & Tomlinson, 1965, 1966, 1967b). Inflorescence insertion was studied in several continuous series of sections cut through nodes bearing fully developed inflorescences. For the branching of the inflorescence itself, serial sections along its main axis were studied together with a similar series along one first-order branch.

INFLORESCENCE MORPHOLOGY

Development of lateral inflorescences in the reproductive phase is irregular in *Rhapis*. Potentially there is an inflorescence bud in the axil of each leaf. Each node is therefore capable of bearing a lateral inflorescence but many abort. Those which do develop seem to expand quite randomly, but mostly in the summer months and in order of their age. Aborted inflorescences at intervening nodes are present as small, scale-like flaps of tissue in the leaf axils. The vascular system of "satellite" bundles associated with aborted inflorescences was described in the first paper of this series (Zimmermann & Tomlinson, 1965). The presence of a vestigial vascular supply to aborted inflorescences is of considerable developmental significance and we will discuss this in a later article.

An inflorescence normally bears either wholly male or wholly female flowers but inflorescences with both female and perfect flowers are not uncommon. The two kinds of inflorescence which bear female flowers are superficially indistinguishable and may for convenience be referred to as "female" inflorescences. Male can be distinguished readily from female inflorescences by their more numerous, densely crowded, smaller flowers on more slender and more elaborately branched axes (cf. TABLE 1 and FIGS. 11 & 12). It is not known if an erect aërial shoot continues to bear inflorescences of one kind.

Comparative study of inflorescences in Coryphoid palms shows that

FIG. I

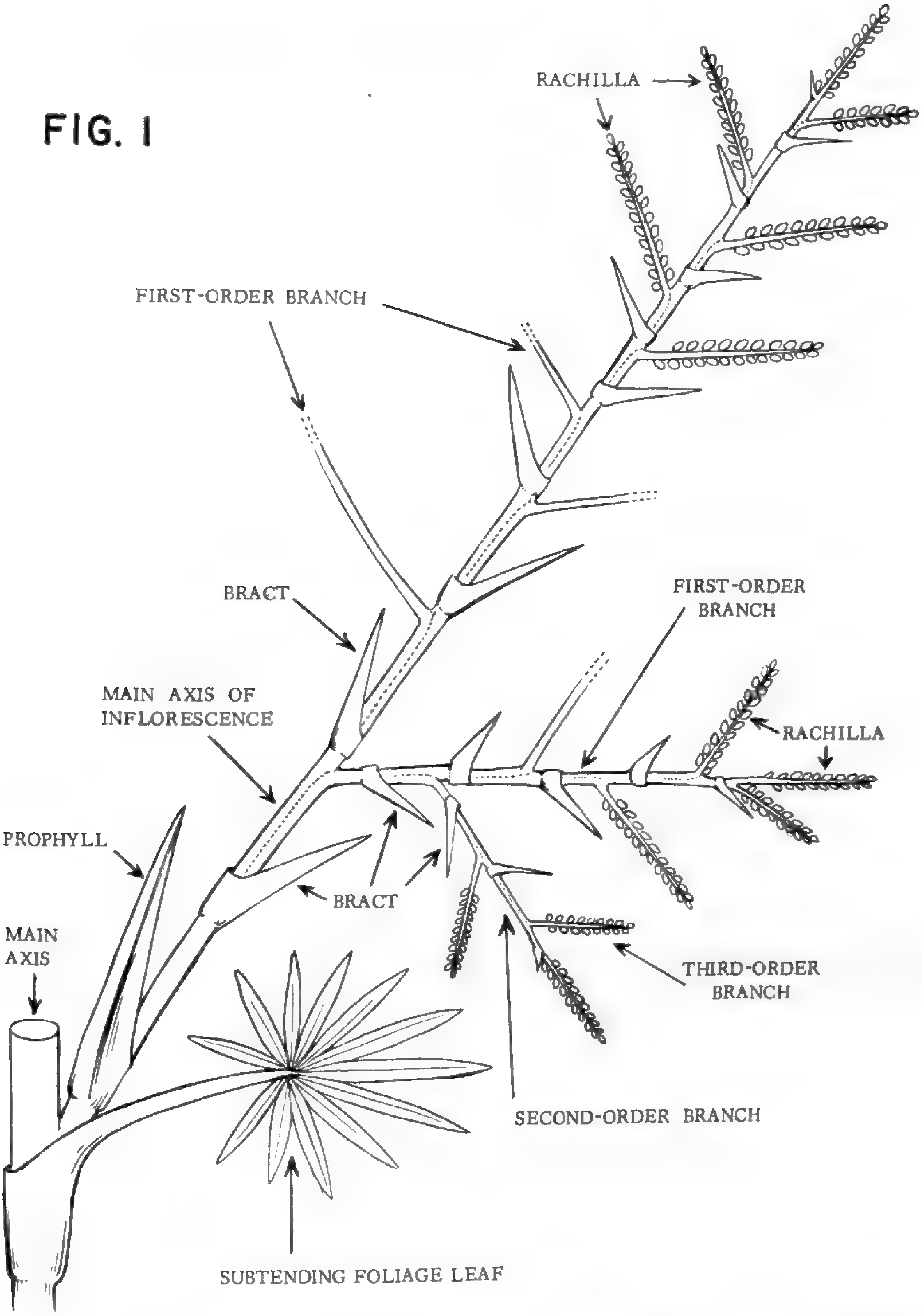
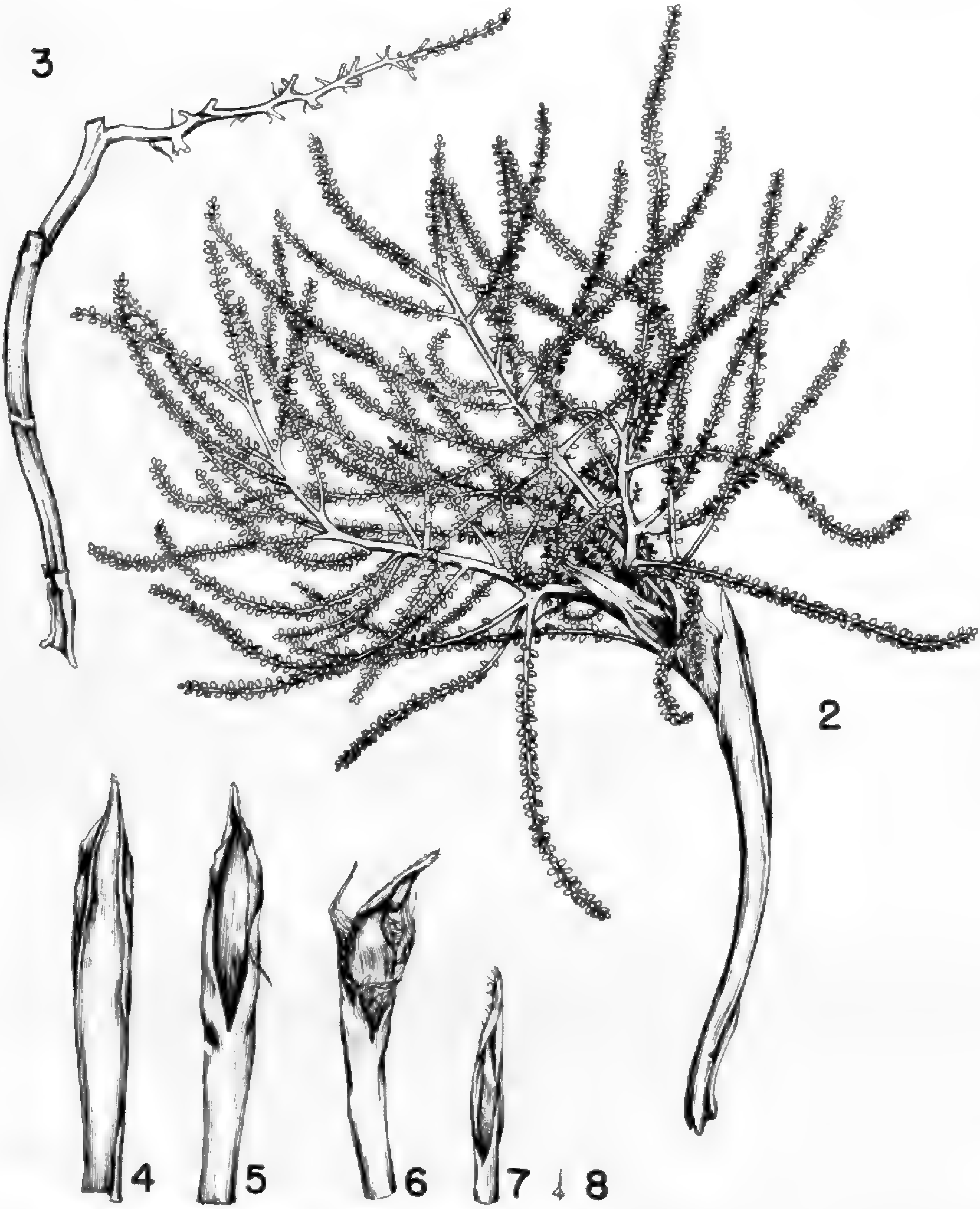


Fig. 1. Diagram of construction of *Rhapis* inflorescence. Branches ending in discontinuous lines are not completed. Adnation between branch and parent axis is shown with dotted lines.

Rhapis has a relatively specialized type of inflorescence (Fig. 2). Nevertheless the general principles of inflorescence construction in palms, as revealed by the detailed analysis of *Nannorrhops* by Tomlinson and Moore (1968), are clearly demonstrated in *Rhapis* (Fig. 1). Apart from the



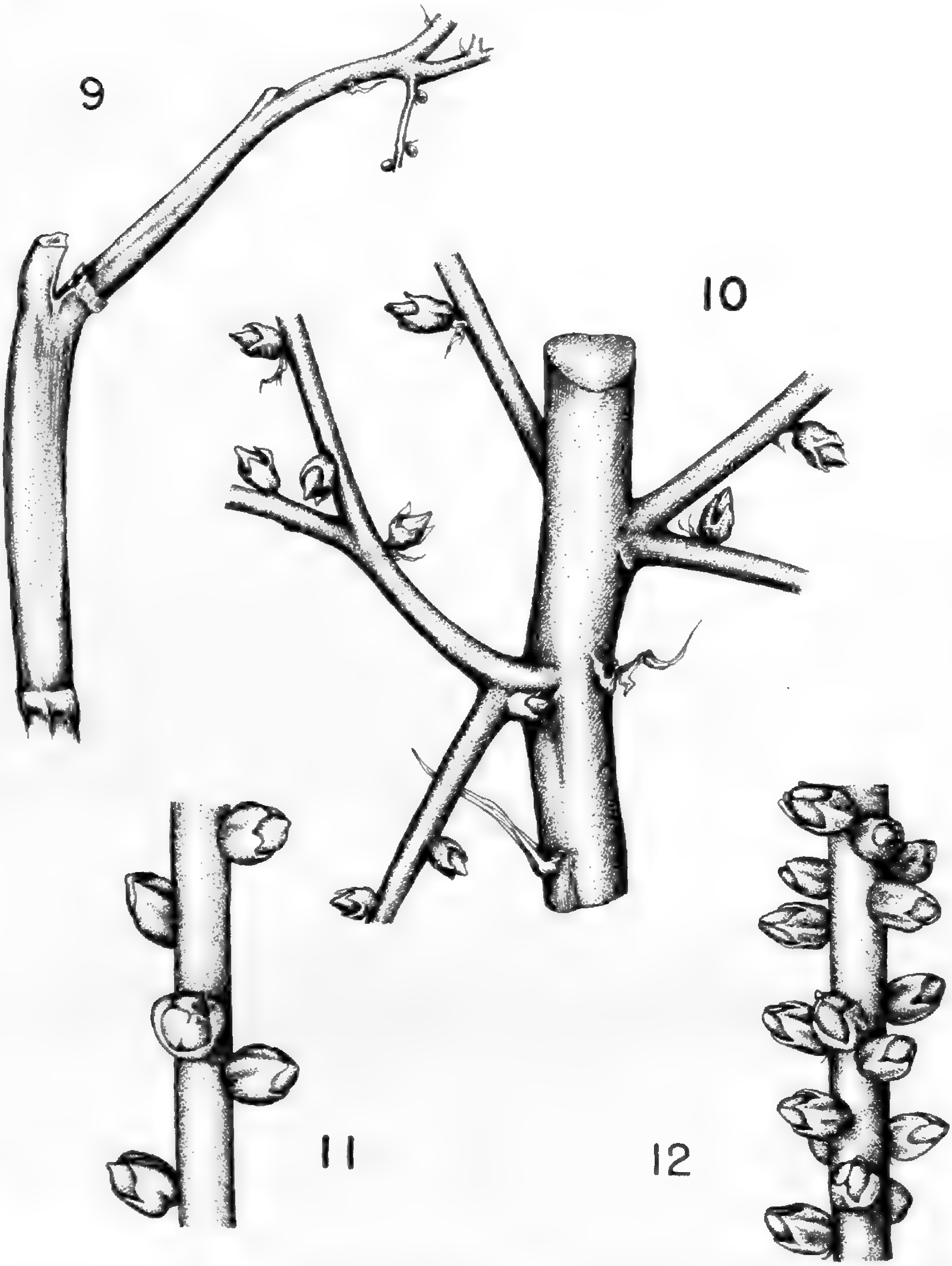
Figs. 2–8. Inflorescence morphology of *Rhapis excelsa*, × 1/3. Fig. 2. Male inflorescence. Fig. 3. Another inflorescence stripped of bracts and branches to show extent of main inflorescence axis. Figs. 4–8. Series of bracts from base of an inflorescence. Fig. 4. Prophyll (first bract), from dorsal side. Fig. 5. Same, from ventral side. Fig. 6. Second bract. Fig. 7. Third bract. Fig. 8. Abruptly reduced fourth bract.

pronounced segregation of the sexes, *Rhapis* obviously differs from *Nannorrhops* in that flowering does not terminate vegetative growth (shoots are pleonanthic rather than hapaxanthic). Each lateral "inflorescence" of *Rhapis* is strictly a partial inflorescence, equivalent to one first-order branch unit in *Nannorrhops* but with fewer degrees of branching. A further important difference is that ultimate branch units in *Nannorrhops* are condensed few-flowered cincinni whereas in *Rhapis* branching is racemose throughout the inflorescence, the flowers being borne singly (FIGS. 11 & 12). Otherwise *Rhapis* retains the paniculate construction of *Nannorrhops* with the consistent one-to-one relation between bract and branch which is its essential feature, although adnation of branch to parent axis tends to obscure this. The distal reduction in bract size is abrupt in *Rhapis* rather than gradual as in *Nannorrhops*.

The morphology of the *Rhapis* inflorescence is shown diagrammatically in FIG. 1, with aspect and essential features in FIGS. 2–12. Further quantitative information is presented in TABLE 1 which also shows differences between male and female inflorescences. The inflorescence base has a broad attachment encircling more than one half of the circumference of the node (FIG. 15). Until final expansion it is wholly enclosed within the tubular sheath of the subtending leaf and further protected by the three to five basal bracts (FIGS. 4–7). These are papery but fairly rigid, although they tend to show a fibrous breakdown with age (e.g. FIG. 6). This is understandable in comparative terms, because bracts are equivalent to the sheath of a foliage leaf which characteristically shreds into its constituent fibers with age. *Rhapis* has the *Cocos*-type of leaf base, according to their classification by Tomlinson (1962). This morphological equivalence between bract and leaf base, so striking in *Nannorrhops* (Tomlinson & Moore, 1968), is not apparent in *Rhapis* because it lacks transitional forms.

The first bract (FIGS. 4, 5) is a 2-keeled prophyll in the adaxial (adossierte) position normal for the first leaf on a branch in monocotyledons. However, the branching of the inflorescence axis itself does not continue this rule because there is no bract in the prophyllar position on subsequent branch orders. The first bract is situated above a short (sub-prophyllar) internode. Unlike all subsequent bracts it subtends no branch. It encloses the whole of the developing inflorescence until just before final expansion. The main axis continues with a succession of bracts separated by long internodes, each bract subtending a branch. Two or three of the lowest bracts are well-developed, tubular, and approach or even exceed the prophyll in size (FIGS. 6, 7). They are clearly of some initial protective value but later are torn irregularly at the mouth as the inflorescence expands. Beyond the last of these conspicuous bracts there is an abrupt decrease in the size of bracts (cf. FIGS. 7 & 8) and length of internodes (FIG. 3) so that distally bracts are narrow scale-like structures and branches are more crowded. Although these distal bracts are vestigial and somewhat dissociated from their branch, careful search will always reveal the bract corresponding to each branch. Flowers in turn are each directly subtended by a minute bract, only conspicuous below the lowermost flowers of the rachilla (FIG. 10).

Branches of up to three orders occur (ax_{1-3} (FIG. 1) disregarding the flower as an ultimate order of branch), although third-order branches are few and found only on the proximal part of the inflorescence. Third-order branches are more numerous on male than female inflorescences (TABLE 1). The lowest first-order branch is often so well developed as to equal the



FIGS. 9–12. Details of inflorescence in *Rhapis excelsa*. FIG. 9. Main axis, × 2/3, with bracts removed to show extent of adnation between axis and corresponding branch. FIG. 10. Detail of distal part of main axis, × 2, showing scale-like bracts subtending branches and flowers, adnate branches and basally inserted second-order branches. FIGS. 11 and 12. Rachillae, × 3. FIG. 11. Rachilla with female flowers. FIG. 12. Rachilla with male flowers.

whole of the remainder of the inflorescence, as in FIG. 2. Adnation between branch and parent axis in all but the smallest axes obscures the bract-branch relation. The lowest first-order branches, for example, are adnate to the main axis throughout the whole of the internode above, diverging shortly below the insertion of the next bract (FIG. 9). This may introduce seeming irregularities where a morphologically lower branch diverges above the next (morphologically higher) branch inserted on the opposite side. In this way a branch may diverge beyond the first flower on a rachilla. In addition a branch may be inserted so close to the base of its parent axis that two unequal axes seem to diverge at one level (FIG. 10). Bracts in a prophyllar (adaxial) position do not occur at the base of branches.

Bracts and corresponding branches are arranged in no obvious, regular phyllotactic order. Probably any primordial order is early lost because of the requirements of close packing within the protective envelope of leaf base and lower bracts. The lowest bracts are apparently inserted distichously at right angles to the plane of insertion of the prophyll, and subsequent branches seem to prefer this plane, possibly for the simple reason that it is the one in which there is most room for expansion. The irregularity is further emphasized by the variable spacing of branches along a parent axis and in spacing and arrangement of flowers along and around the rachillae (FIGS. 11, 12). "Rachilla" is a convenient term for the flower-bearing ends of axes of all branch orders (cf. Tomlinson & Moore, 1968).

INFLORESCENCE ATTACHMENT

In the first article of this series, in which we described the vascular system of the mature aërial axis in its vegetative phase, it was shown how each of the larger bundles of the trace system to every leaf was associated with a cluster of derivative bundles appearing like a "halo" around the leaf trace in transverse section. Although all of these derivative bundles diverged successively from the leaf trace in the same way, and all were anatomically identical, three kinds could be distinguished in each leaf trace complex, according to their ultimate behavior. The first, and usually the largest, was the continuing vertical bundle; a number of subsequent ones functioned as short bridges linking with nearby peripheral vertical bundles; others (termed by us "satellites" because of their longer association with the leaf trace) were traces to the vestigial inflorescence commonly found in the lower parts of the stem before it has fully entered the reproductive phase of growth. Despite these vestigial inflorescences these nodes may be described as "sterile." Examination of higher "fertile" nodes (with fully developed inflorescence branches) shows that the satellites are more pronounced and can be referred to more accurately as "inflorescence traces." However, a second kind of vascular connection between inflorescence and main axis, not found in association with aborted inflorescences, now becomes evident. We can distinguish the first kind of inflorescence trace by following the vascular system at a node from below upwards, the second by following it from above downwards. This is essentially the way in which the two kinds of traces were recognized in our analytical films since there is otherwise no obvious anatomical way of

FIG. 13

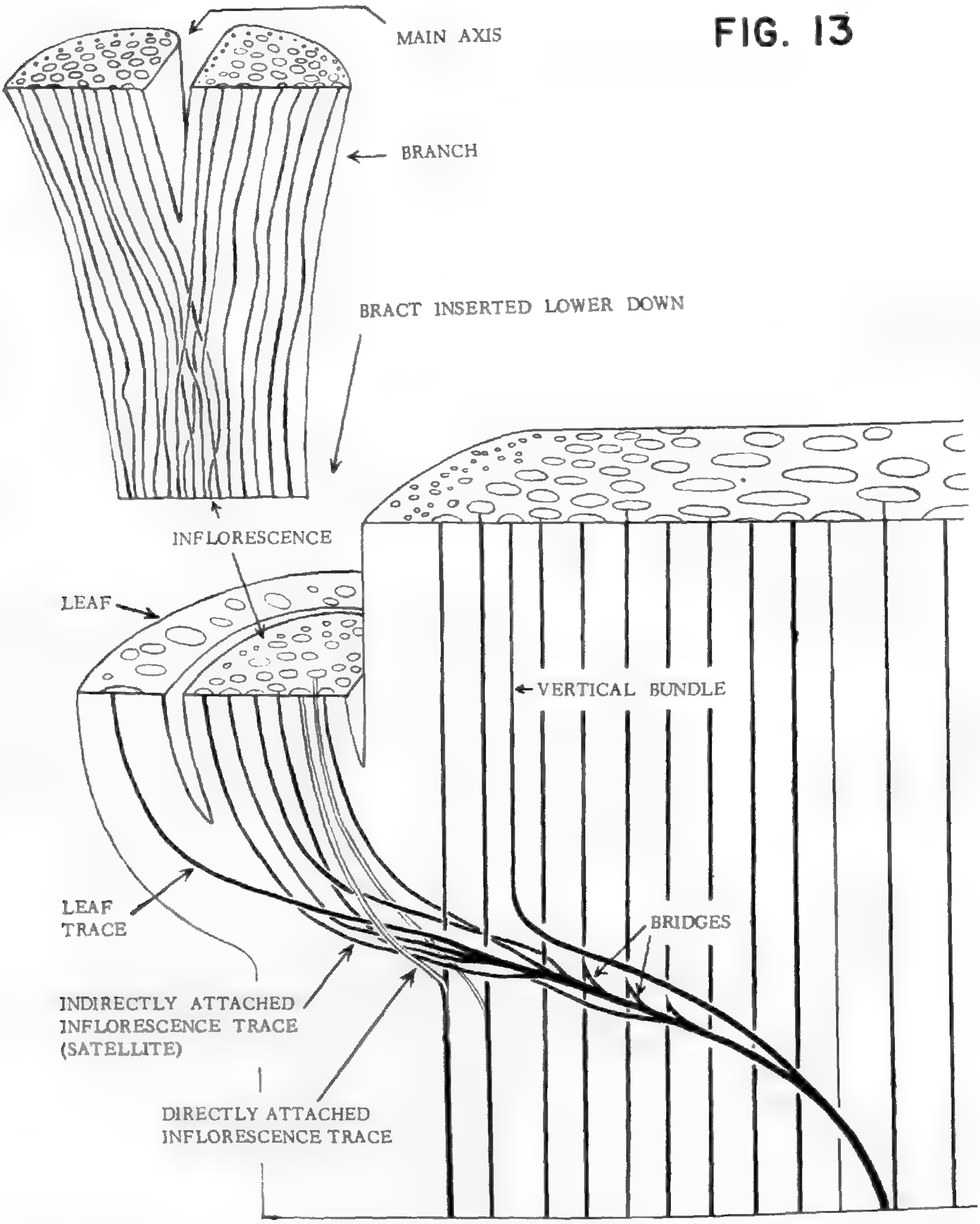


FIG. 13. Diagram illustrating vascular connection between inflorescence and main axis (below); method of attachment of inflorescence branch to inflorescence axis (above). Bundles in longitudinal view are represented by solid lines for clarity except for directly attached inflorescence traces (double lines). In the upper figure the bract which subtends the branch is inserted at a much lower level (cf. FIG. 9).

differentiating them in single sections. The difference between these two bundles is shown diagrammatically in the lower diagram of FIG. 13.

Following a major leaf trace up, derivative bundles first begin to split off at about three internodes below the node at which the trace makes its exit from the stem. The first is almost invariably the large vertical bundle which remains associated with the leaf trace complex until it turns upwards near the periphery of the central cylinder. The production of derivative bundles then continues from each side of the leaf trace but on a much larger scale than is characteristic of traces to a sterile node (FIG. 14). Several of these make bridging union with nearby vertical bundles, but most (up to 15) remain to form a semicircle on the inner face of the leaf trace (FIGS. 14, 19, 20). The xylem of all these derivative bundles is continuous with the metaxylem of the leaf trace in such a way that only protoxylem remains in the leaf trace beyond the level of departure of the last derivative bundle. At the node (FIGS. 15, 21) the leaf trace passes fairly abruptly into the leaf base whereas the inflorescence traces, often anastomosing amongst themselves in an irregular manner, pass into the base of the inflorescence axis. The majority of inflorescence traces are derived directly from leaf traces in this way.

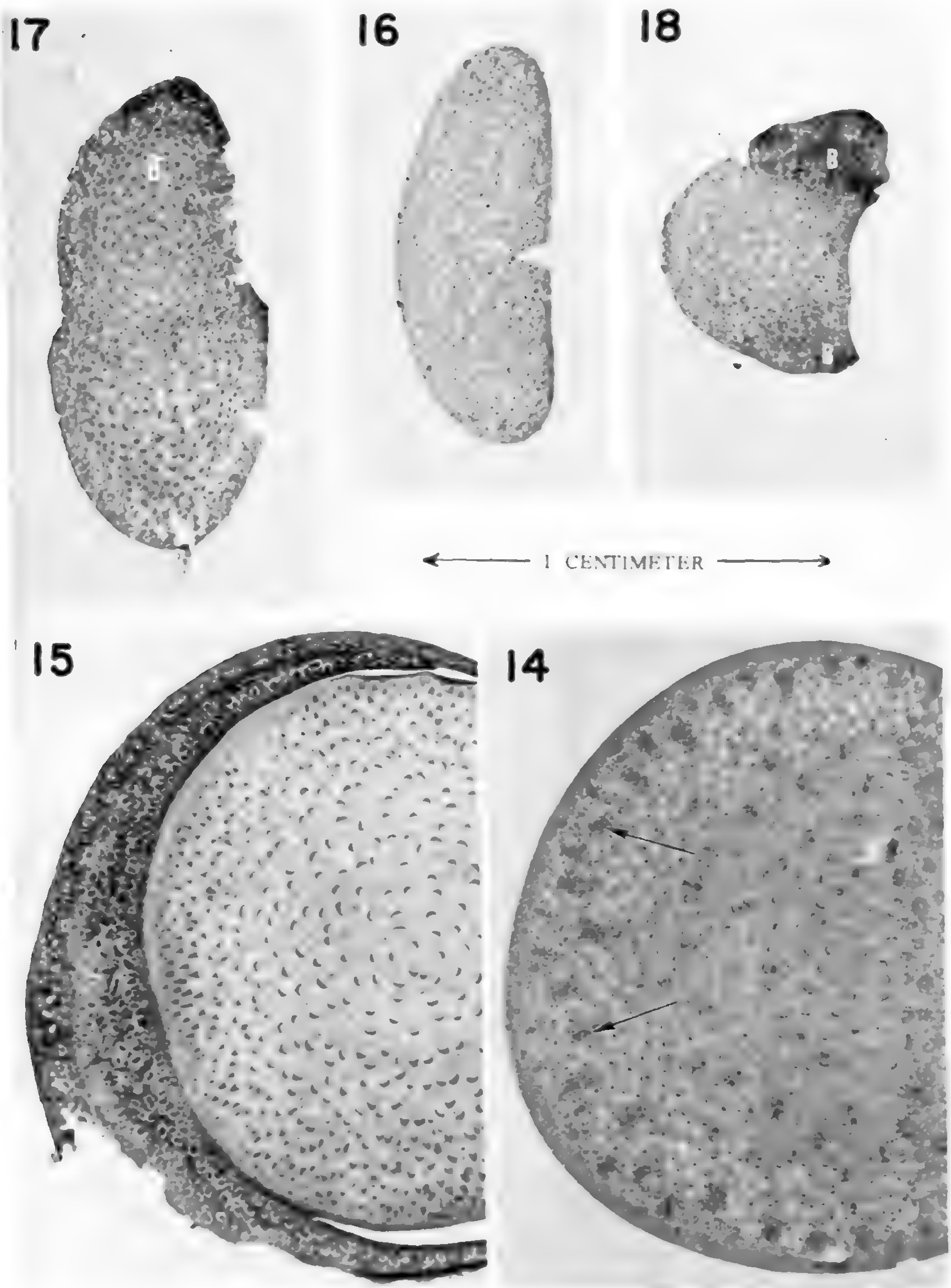
If the vascular bundles in the irregularly anastomosing system in the base of the inflorescence axis are followed downwards, it is evident that many attach directly to vertical bundles at the periphery of the central cylinder (FIG. 13, directly attached inflorescence traces). These directly attached bundles cannot be distinguished from satellites in a single transverse section. They form an indistinct series on the adaxial (inner) side of the inflorescence base although many penetrate much deeper. Both types of bundle are alike in possessing a few narrow metaxylem elements and a single phloem strand, the whole bundle surrounded by a narrow sheath of thin-walled fibers (FIGS. 19–21).

The physiological significance of this method of attachment of inflorescence to main axis is obvious. The inflorescence not only taps the main vascular system via the directly attached bundles but is also in *direct vascular contact with the subtending leaf* via the satellite bundles and dorsal leaf traces.

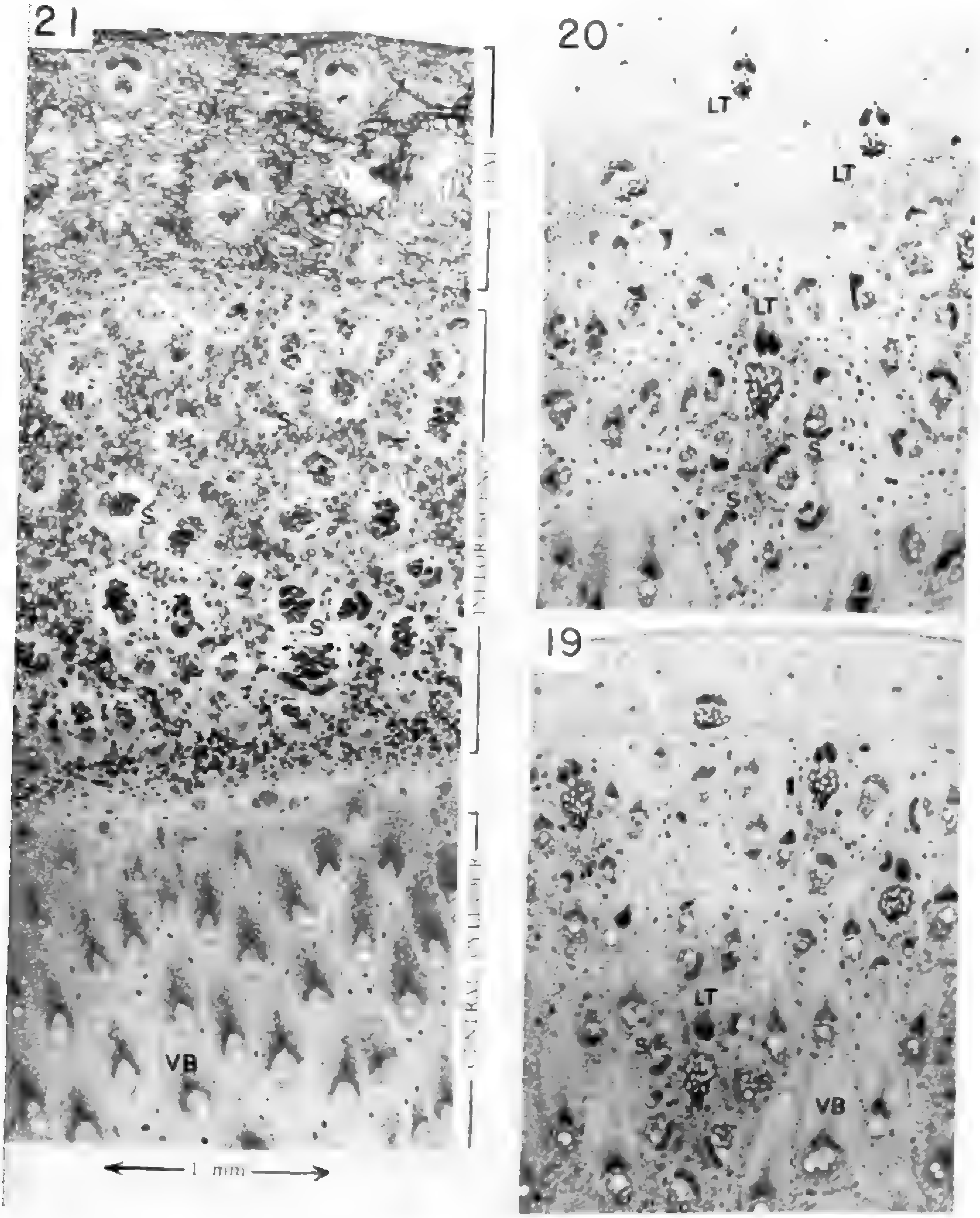
ANATOMY OF INFLORESCENCE AXIS

Shortly above its level of insertion (i.e. within the sub-prophyllar internode) the arrangement of vascular bundles typical of the inflorescence axis is established. Irregular anastomoses between inflorescence traces are thus restricted to the very base of the axis. Morphologically the inflorescence axis is equivalent to the main stem but there are many quantitative differences. The following description of general anatomy refers to a level about halfway up the second internode of the main axis (FIG. 16).

Outline elliptical in transverse section as a result of flattening against main stem. **Scales** numerous especially on adaxial surface; each scale more or less peltate and consisting of a flattened series of thin-walled cells arising from a group of sclerotic epidermal cells. **Epidermis** smooth or at most slightly papillose with a distinct cuticle; epidermal cells longitudinally extended, irregularly rectangular in surface view, with non-sinuous walls. **Stomata** infrequent. **Cortex** narrow, the outermost layer of ground tissue thick-walled and lignified. Cortex including numerous strands of thin-walled fibers, the larger strands including a narrow phloem strand and usually one (rarely more) narrow and inconspicuous



FIGS. 14–18. Inflorescence anatomy in *Rhapis excelsa*. FIGS. 14 and 15. Transverse section of aërial stem. FIG. 14. Shortly below node, leaf traces and associated satellites conspicuous (arrows). FIG. 15. Shortly above node, inflorescence base almost free of stem (cf. FIG. 21). FIGS. 16–18. Transverse section of inflorescence axis. FIG. 16. Halfway between base and apex of second internode. FIG. 17. At level of departure of first branch. FIG. 18. Distally, showing trace systems to two branches. B — branch.



Figs. 19–21. Details of inflorescence insertion on main stem in *Rhapis excelsa*, in transverse section. Fig. 19. Well below node, leaf traces with very conspicuous inflorescence traces (satellites). Fig. 20. Shortly below node (3.25 mm. above Fig. 19). Inflorescence traces becoming free of leaf traces. Fig. 21. At node (5.7 mm. above Fig. 19). All inflorescence traces free of leaf traces and in base of inflorescence. LT — leaf trace; S — satellite; VB — vertical bundle.

tracheal element. **Central cylinder** not separated from cortex by any limiting layer but by crowded peripheral bundles; central vascular bundles somewhat less crowded, wider, and uniformly scattered. Central vascular bundles very uniform, each with protoxylem and one or more conspicuous wide metaxylem elements; phloem usually divided into two lateral strands by a median sclerotic isthmus. Fibrous sheathing tissues not well developed. Peripheral narrower than central bundles, without protoxylem, the phloem undivided; fibrous sheath usually continuous but not well developed. **Ground parenchyma** uniform, compact in cortex but with well-developed intercellular spaces in central cylinder. **Stegmata** abundant next to all bundles. **Vessel** elements of metaxylem usually with more numerous thickening bars than corresponding elements in aërial stem.

In general, the inflorescence axis differs from the aërial axis in the smaller vascular bundles which do not show a marked peripheral crowding or pronounced mechanical development of sheathing fibers.

COURSE OF BUNDLES IN INFLORESCENCE

Bract attachment. Bracts are supplied in essentially the same way as foliage leaves with which they are homologous, differences being largely quantitative and related to the reduced size of the bract. Structural (and very probably developmental) principles which govern the distribution of traces to leaves also govern the distribution of traces to bracts. Each bract is supplied by relatively few traces which diverge from the central cylinder, but many more bract traces are continuous with the cortical system. The lowest 3–5 well-developed bracts are most like foliage leaves. The few traces originating from the very center of the central cylinder correspond to major leaf traces of foliage leaves. The somewhat more numerous ones diverging from intermediate and peripheral levels of the central cylinder correspond to intermediate and minor bundles of foliage leaves. Traces derived from the cortex, on the other hand, are very numerous and correspond to cortical bundles of foliage leaves. Bract traces originating in the central cylinder do not have the "double curve" of von Mohl which is such a pronounced feature of the trace to foliage leaves. Followed downwards from the bract node, they show no tendency to approach the periphery nor is there any helical curve in the center of the axis. In these respects bract traces are similar to scale traces in the rhizome (cf. Tomlinson & Zimmermann, 1966a). In the nodal region the outgoing bract trace also behaves like a scale-leaf trace in that it gives off a continuing vertical bundle near the center, followed by one or more short bridge bundles which link with nearby vertical bundles. As in the rhizome *bract traces have no associated satellites*; this is related to the very different method of branch supply described below.

Corresponding to the decline in length of bracts distally along the inflorescence axis there is a distal decline in number of bract traces (both those derived from the central cylinder, as well as cortical traces). The number of centrally derived traces is reduced much more drastically than the number of cortical traces. Quite clearly distal, scale-like bracts are connected to the axial system via cortical bundles alone or at the most with very few central traces.

Branch attachment. Each branch is morphologically fused with the main axis but there is no anatomical indication of this in the adnate part of the internode. At the level of divergence of the branch a portion of the axis is then simply "pinched off," the vascular system of the main axis being correspondingly diminished (FIG. 17). This is repeated at each level

(Fig. 18), and in this way the total number of axial bundles diminishes distally in proportion to the number of branches. There is some slight tendency to restore the number by occasional splitting of vertical bundles but this process is too infrequent to effect the distal diminution. It should be noted that elsewhere in the axis of *Rhapis* splitting of vertical bundles is equally rare and insignificant except in the seedling (Tomlinson & Zimmermann, 1966b).

DISCUSSION

The vascular contact between an inflorescence and its subtending leaf has not been described previously in palms. This is the shortest possible pathway for assimilates to move from leaf to inflorescence. Since it is such a remarkably direct physiological adaptation it may be of value to know if the arrangement described for *Rhapis* is typical of palms generally. Our study of vascular continuity has not been restricted to *Rhapis*. Two approaches to a comparative survey have been made. The simplest is to examine single transverse sections of a wide variety of palms and look for the characteristic well-developed "halo" of satellite bundles aggregated around the larger leaf traces. This arrangement is common and evidently a uniform property of many palms. For example, inflorescence traces are recognizable in some of von Mohl's illustrations such is their accuracy and clarity. These observations suggest a vascular supply to the inflorescence derived, at least in part, from the leaf trace system as in *Rhapis*. It must be remembered, however, that many palms undergo a long period of vegetative growth without producing any kind of lateral branch. Sections taken from the lower part of a palm stem commonly show no satellites, although they may be evident in the upper part of the same stem. Thus the change from vegetative to reproductive phase of growth in the axis (Tomlinson, 1964) may be reflected anatomically. This in turn means that satellite bundles in a palm stem may not be revealed by examining one level.

The only certain method of demonstrating that a palm has the *Rhapis*-type of inflorescence supply is to follow the distribution of vascular bundles in three dimensions. Analysis of a number of palms (*Chamaedorea*, *Chamaerops*, *Phoenix*, and *Ptychosperma*) shows essentially the same inflorescence trace system as in *Rhapis* but with important quantitative differences. In *Chamaedorea* for example, the "satellite" bundles diverge from the leaf trace very much lower than in *Rhapis* and also before, rather than after, the vertical bundle. This suggests differences in inflorescence supply which may be taxonomically significant. However, such considerations must await a detailed survey which, in view of the labor involved, will be a lengthy undertaking. Our experience does suggest, on the other hand, that other types of inflorescence supply may exist. In *Washingtonia*, for example, despite a thorough analysis of many single sections from different levels, we have seen no satellites associated with leaf traces.

The practical value of an accurate knowledge of connections between inflorescence and foliage leaf can be readily grasped. Our observations

TABLE I. **Dimensions of representative male and female inflorescences in Rhapis excelsa**

Bract	MALE				FEMALE			
	Length of bract (mm.)	Length of internode below (mm.)	No. ax_2† corresponding branch (ax_1)	Total no. ax_3 on all ax_2	Length of bract (mm.)	Length of internode below (mm.)	No. ax_2 on corresponding branch (ax_1)	Total no. ax_3 on all ax_2
Prophyll (1)	120	16	. .	. .	108	20	. .	. .
2	115	61	19	6	118	55	10	2
3	95	48	16	5	80	80	10	1
								↑
4	78	48	14	1	75	68	6	simple
5	50*	47	6	simple	40*	62	2	(rachillae)
6	< 2	32	↑	(rachillae)	5	33	↑	↓
7	< 2	0			3	4	simple	
8	< 2	9			4	13	(rachillae)	
9	< 2	7	simple		< 2	7		
10	< 2	9	(rachillae)		< 2	7	↓	
11	< 2	7			ends in			
12	< 2	4			rachilla			
13	< 2	5						
14	< 2	5	↓					
	ends in							
	rachilla							

† ax_1 = axis of first-order branch; ax_2 = axis of second-order branch; ax_3 = axis of third-order branch.
* Bracts marked with an asterisk are lowest which do not encircle the axis completely.

suggest that an inflorescence may be approached directly through its subtending leaf. It might under these circumstances be possible to influence the development of an inflorescence at an early stage. Leaf and associated inflorescence do not mature at the same rate. The apex of the subtending leaf is exposed many plastochrones before the inflorescence itself. In the Date palm, for example, the youngest leaf which is exposed may subtend an inflorescence bud only 5 to 7 millimeters in length, but which will not expand for a further 22 plastochrones (Hilgeman, 1954).

Of particular interest to the morphologist is the contrast between the method of vascular attachment of inflorescence to main axis on the one hand, compared with attachment of lateral to main inflorescence axis, on the other (cf. upper and lower diagrams of FIG. 13). Morphologically the two are equivalent but developmentally they are dissimilar. We cannot comment on this difference until the development of root and vegetative branch insertion has been analyzed. For the moment, it is interesting to speculate that the reapportionment of vascular bundles between parent and branch axis in the inflorescence may well account for the apparent dichotomy of the vegetative axis in a number of other palms, long familiar in *Hyphaene* (Schoute, 1909) and more recently demonstrated in other palms (e.g. Tomlinson & Moore, 1966). Satisfactory answers to such speculative questions depend on a thorough understanding of developmental processes in palms.

SUMMARY

In *Rhapis* there is a direct vascular link between the inflorescence and the leaf which subtends it. Inflorescence traces are mostly attached to dorsal traces which supply the subtending leaf. Some inflorescence traces are attached to peripheral vertical bundles of the main axis. Branching within the inflorescence is racemose throughout but with marked adnation between branch and parent axis. Distal bracts are reduced to minute scales. Inflorescence anatomy is essentially like that of the main vegetative axis. The cortical system is quite well developed, especially in distal regions where bracts largely make vascular contact with the cortex only. Bract traces are otherwise derived from the axial system in the same manner as traces to rhizome scales. At each branch of the inflorescence part of the vascular system of the parent axis passes directly into the branch without reference to the corresponding bract. Different kinds of vascular supply to morphologically equivalent organs indicates different methods of development. Distal reduction in the size of bract and branch is paralleled by a corresponding reduction in vascular supply.

ACKNOWLEDGMENTS

We are indebted to Miss Priscilla Fawcett, Botanical Illustrator at Fairchild Garden for FIGURES 1–12, and to Miss Lesley Jackson for the preparation of the serial sections on which this study is based. Mrs. B. M. McCurda's clerical assistance is much appreciated.

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ANATOMY OF THE PALM RHAPIS EXCELSA, VI. ROOT AND BRANCH INSERTION

P. B. Tomlinson [1] and M. H. Zimmermann

In palms, as in all woody monocotyledons without secondary vascular tissues, there are limitations to the method by which a lateral organ can be attached to the parent axis so as to make an effective vascular union. Schoute has discussed this problem at a morphological level in a series of papers on branching in Pandanaceae, Palmae, and woody Liliiflorae (e.g. Schoute, 1903; 1918; see also Tomlinson, 1964). Anatomical details, however, still remain undescribed. In the preceding paper in this series (Tomlinson & Zimmermann, 1968) two distinctive methods of branch-axis union were described in relation to inflorescence. On the one hand, the inflorescence axis is basally supplied from the main axis by numerous bundles which diverge from dorsal leaf traces, together with bundles which are attached directly to peripheral vertical bundles. On the other hand, branching within the inflorescence itself involves a simple redistribution of existing vascular bundles between parent axis and branch. It is obvious that although these two types of branch are morphologically equivalent, they must develop differently. However, we have not yet investigated inflorescence development. To complete the study of vascular continuity the present article describes the anatomy of root and branch insertion.

Although these constructional aspects of palms are of fundamental physiological significance, previous investigation has been limited. Von Mohl (1824) and Karsten (1847) made some general observations without describing anatomical details. Mangin (1882) in a notable paper, described various methods of attachment of roots to parent axis in monocotyledons, including a number of palms. Drabble (1904) dealt specifically with the same problem in palms in his lengthy survey of the general anatomy of palm roots. Our own observations on *Rhapis* have confirmed the findings of these earlier botanists.

METHODS

Attachment of root and vegetative branch has been revealed to a large extent incidentally during analyses of rhizome and seedling axis. Methods of serial analysis using microcinematography have been described fully in several previous articles (Zimmermann & Tomlinson, 1965; 1966; 1967b). In addition, continuous series of sections through root insertions

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[1] Research by P. B. Tomlinson on the anatomy of palms is supported by National Science Foundation Grant GB-5762-X.

(in both longitudinal and transverse planes) and the insertion of a branch at the base of an erect shoot were specially cut and analyzed by the same methods. Photographs which form FIGS. 1–9 were made from these additional series of sections.

MORPHOLOGY

The distribution of adventitious roots and lateral vegetative branches on seedlings, rhizomes, and at the base of the aërial stem has been described and illustrated in the second and third articles of this series (Tomlinson & Zimmermann, 1966a, b). Briefly, roots are abundant and closely crowded on the seedling axis, widely and irregularly spaced on the rhizome and again numerous at the base of erect shoots; vegetative branches develop either from buds in the axils of transitional leaves on the juvenile axis or at the base of erect shoots. Buds may grow out (usually in order of their age) into rhizomes but many are strongly inhibited, persisting as reduced structures within the protective, somewhat woody prophyll. The subsequent account refers largely to the attachment of roots on rhizomes and of branches to the base of erect shoots. Their attachment to seedlings is briefly commented upon (cf. also Tomlinson & Zimmermann, 1966b).

ROOT ATTACHMENT

Roots originate endogenously, rupturing the surface of the stem and modifying its peripheral tissues (FIG. 2). There is a discontinuity between surface tissues of root and stem. The epidermis and wide sclerotic layers of the outer cortex of the root penetrate deeply into (more strictly, differentiate first within) the stem cortex. Cortex of root and stem, however, are continuous. The root endodermis ends blindly in the outer cortex of the stem. Root development also locally stimulates expansion and some division of ground parenchyma cells in the outer part of the central cylinder in such a way that peripheral vascular bundles bulge outwards (FIG. 2).

In a transverse section of the root, close to its insertion (FIG. 1), a peripheral system made up of the normal polyarch xylem and phloem strands can be distinguished from an irregular series of medullary strands which include metaxylem only. These two systems are attached somewhat differently and may be described separately. It must be emphasized initially that *no root traces end blindly.*

Peripheral system. Peripheral xylem and phloem strands of the root may become attached independently of each other. More commonly the two tissues form discrete vascular strands (root traces) uniformly sheathed by short, thin-walled fibers with a common attachment to one stem bundle (FIGS. 3 & 4). However, root traces commonly divide into two strands, each with its own xylem and phloem. The vascular strands of this peripheral root trace complex fan out tangentially and make contact with peripheral bundles of the stem. For a vigorous root this tangential spread

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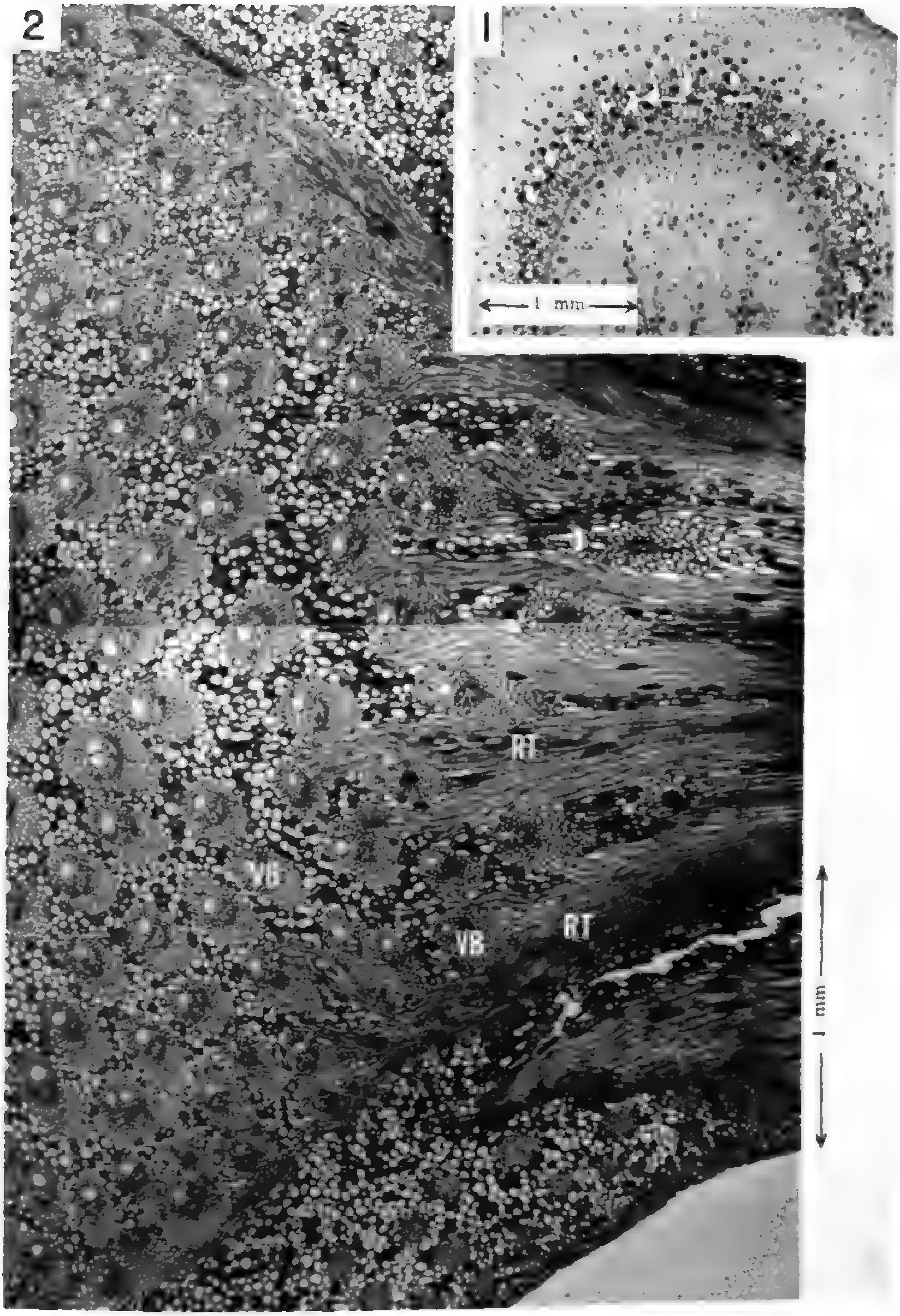


FIGS. 1 and 2. Root insertion in *Rhapis excelsa*. FIG. 1. Transverse section of root close to its insertion. FIG. 2. Transverse section of rhizome, including root insertion, in approximate median longitudinal section. RT — root trace; VB — vertical bundle of rhizome.

may be up to one-half the total circumference of the central cylinder (FIG. 2). Close to the root insertion some of the root traces (or branches of root traces) penetrate shortly into the central cylinder to make their attachment. Otherwise traces run in the boundary between cortex and central cylinder. They have been recognized as frequent "girdling traces" in the rhizome (Tomlinson & Zimmermann, 1966a, p. 255), remote from the root attachment.

Medullary system. Each strand consists of a single wide metaxylem vessel surrounded by a fibrous sheath. The strands penetrate directly into the central cylinder of the rhizome and are attached to peripheral vertical bundles (FIGS. 2; 5 & 6).

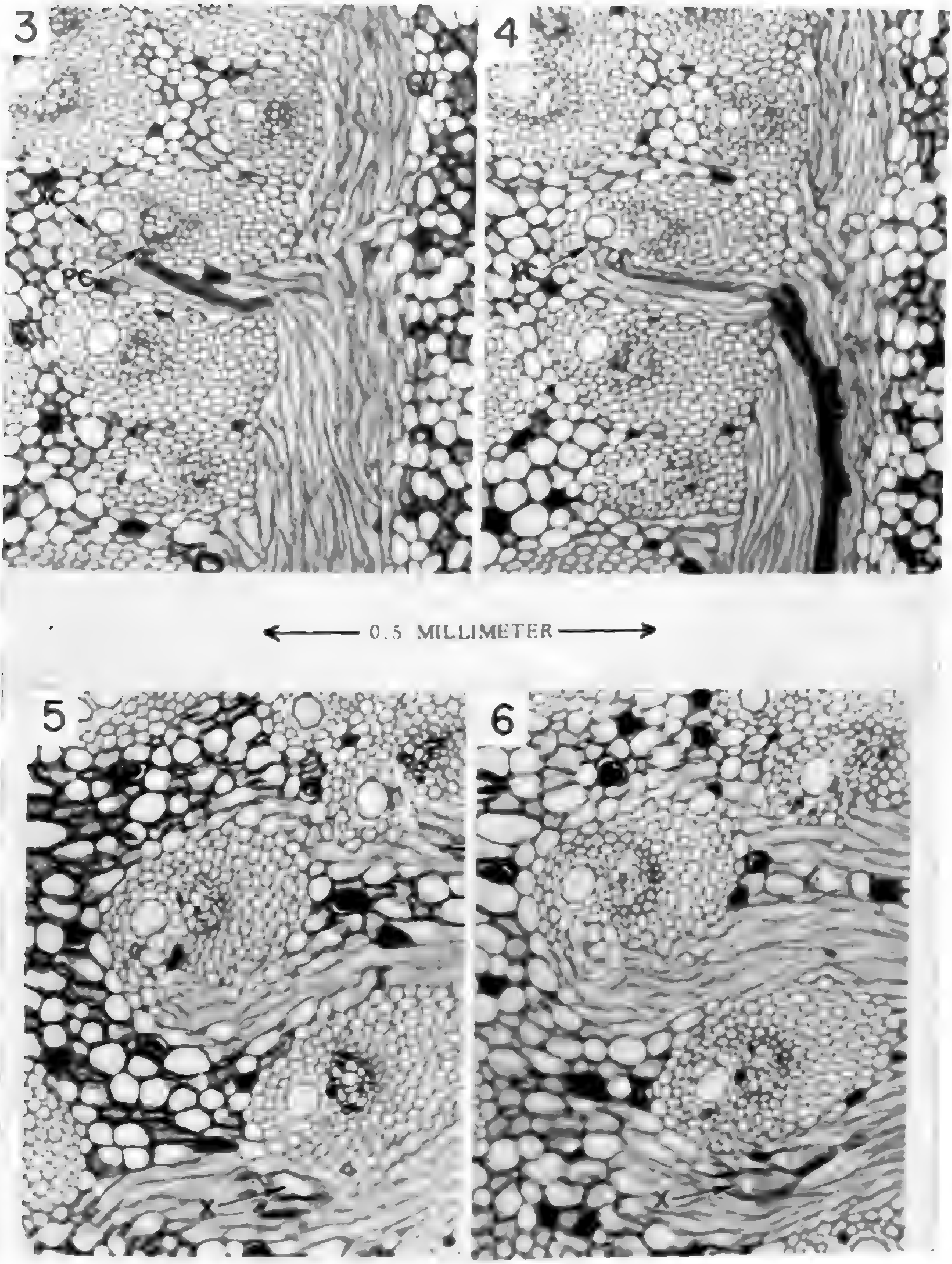
Vascular connection. It is not usually possible to see direct continuity between xylem of root trace and stem bundle in a single section, but only in a continuous series of thin sections. The xylem vessel of the root trace breaks up into an aggregate of narrower elements which run parallel to the stem bundle (FIGS. 3 & 5). The distal elements of this cluster are applied to the metaxylem vessel of the stem bundle. This terminal cluster of root trace elements frequently spreads, often nearly 180 degrees, around the circumference of the stem vessel, so making a very wide contact. The metaxylem of the stem bundle is not usually itself modified. This contrasts with vessel-to-vessel contact in the leaf-trace system of the stem, e.g. between bridges and vertical bundles, where bridge attachment induces a characteristic break-up of the metaxylem into several narrow elements. This is the probable result of a difference in the relative time of differentiation of vessels in the two contrasted types of contact.

Phloem to phloem contact in the peripheral system is usually more direct and can often be seen in a single section (e.g. FIG. 3).

In the attachment of a mature root, traces are uniformly and fully differentiated throughout their length. Many roots, however, abort or are suppressed. Traces from these root buds connect with the vascular system of the stem. These traces are fully differentiated proximally (at their attachment to the stem) but remain in a procambial state distally (at their attachment to the undeveloped root).

The deep penetration of traces was described by Mangin (1882) as a characteristic feature of root attachment in Palmae and Pandanaceae. Drabble (1904) confirmed these observations on the palms and noted that in many species with larger roots separate strands or aggregates of separate strands may persist into the root well beyond its insertion (see also Tomlinson, 1961, pp. 49–50). In *Rhapis* the deep penetration of central root traces is particularly noticeable in the seedling. Here they contribute extensively to the anastomosing bridge system which characterizes this part of the stem (Tomlinson & Zimmermann, 1966b). Undoubtedly, this deep penetration is the result of early root development.

We have not traced the course of the medullary xylem bundles into the root in *Rhapis* but the observations of Drabble (1904) suggest that these may unite with the peripheral metaxylem strands of the polyarch stele.



FIGS. 3–6. Details of root insertion in rhizome of *Rhapis excelsa*; attachment of root traces to rhizome bundles. FIG. 3. Attachment of peripheral root trace to peripheral rhizome bundle. Phloem continuous. FIG. 4. Same bundle at a level 40μ higher, xylem continuous with metaxylem of stem bundle via irregular cluster of tracheal elements. FIG. 5. Attachment of central root trace to rhizome bundle. Cluster of tracheal elements continuous with metaxylem vessel of rhizome bundle. FIG. 6. Same bundle seen 60μ below FIG. 5. Cluster of tracheal elements here free of vessel in rhizome bundle but continuous into root trace. The root trace in the lower half of both figures shows part of a vessel. PC — phloem continuity; XC — xylem continuity; X — xylem.

However, medullary vessels remain as a feature of the distal parts of *Rhapis* roots (Tomlinson, 1961).

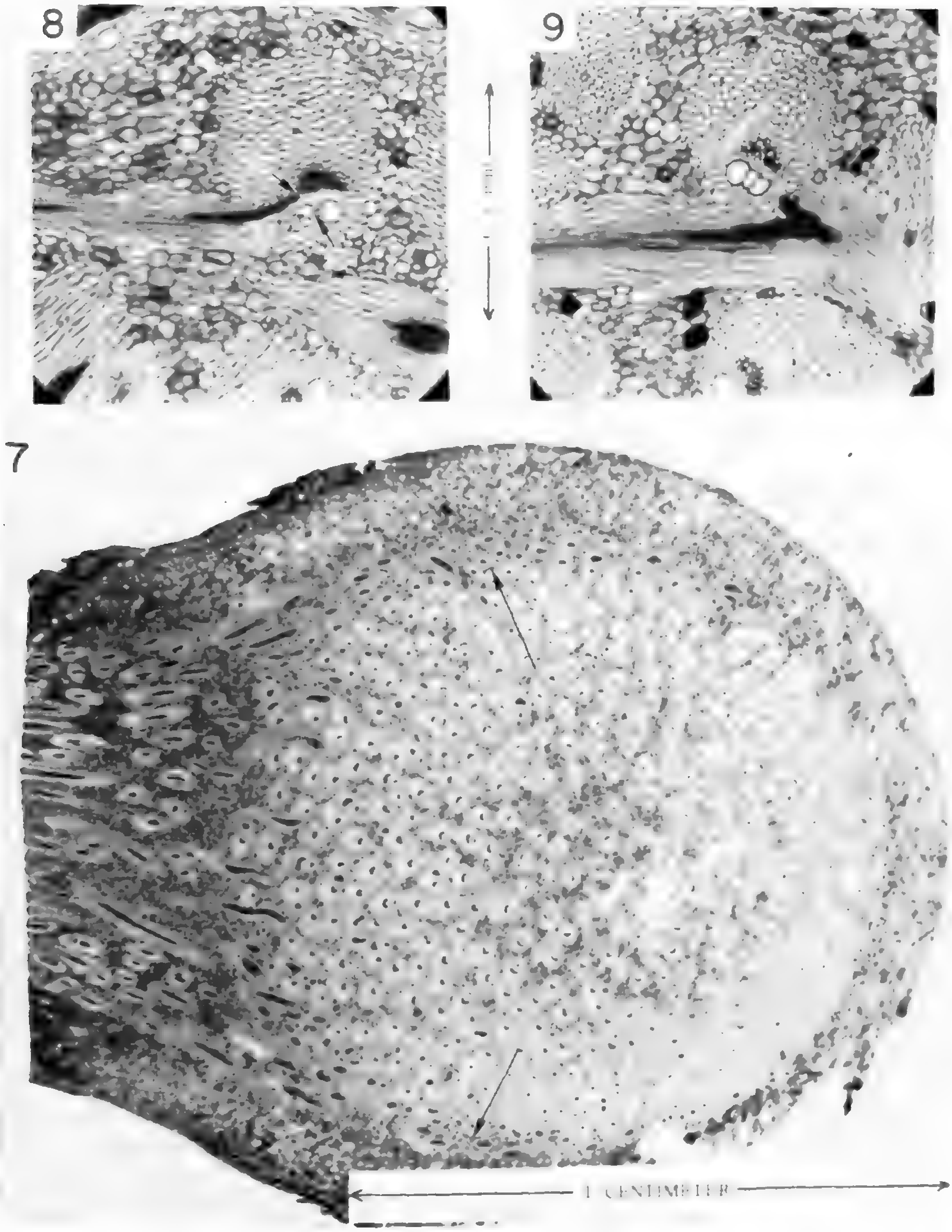
BRANCH ATTACHMENT

Vegetative axillary buds which produce branch rhizomes differ from roots in having an exogenous origin. The rhizome itself has a vascular system of discrete strands which are inserted into the parent axis very much like root traces (FIG. 7). Individual branch traces are all alike, each with both xylem and phloem; there are no traces with xylem only, as in the root. The strands run from the branch and anastomose irregularly and at random with the bundles of the parent stem (FIG. 8), often forking distally (FIG. 9). *None of them end blindly.* Central branch traces penetrate deeply into the stem to make their attachment; peripheral bundles spread markedly around the circumference of the stem forming a distinct layer of vascular bundles between the cortex and the central cylinder (FIG. 7). Vessel to vessel attachment between branch trace and stem bundle is often much more direct than that between root trace and stem bundle. This indicates approximately simultaneous development of vessels in the two strands. However, the contact between branch trace and stem bundle sometimes involves an intermediate plexus of terminal elements as in the root, indicating later development of the branch trace (e.g. FIG. 8).

Many vegetative buds are inhibited but the suppressed primordia still make extensive vascular contacts with the parent stem via branch traces which remain at a procambial stage of development in the bud itself, although the same traces in the axis are fully differentiated.

DISCUSSION

Physiological significance of vascular continuity. It is obvious that the discrete vascular bundles represent the pathway for translocation of water and nutrients throughout the palm. The present article completes a description of the continuous vascular system in *Rhapis*. The channels for long distance conduction throughout the palm are now quite evident. Water from the roots passes into the stem via the numerous linkages at the root insertion. A continuous channel along the rhizome and up the aërial stem is afforded by the axial bundle system which links directly with each leaf via leaf traces. Cross-linkage is effected by the frequent bridge bundles associated with outgoing leaf traces. In the aërial stem the helical path of the central bundles further promotes lateral and more uniform distribution of water. Vascular continuity into the inflorescence is provided by inflorescence traces which diverge either directly from the peripheral vertical bundles or as "satellites" from the major leaf traces. In this way the inflorescence links with both peripheral and central bundles. New vegetative branches are also connected directly to the axial system



FIGS. 7–9. Branch insertion in *Rhapis excelsa*. FIG. 7. Transverse section of base of erect stem with branch (rhizome) attachment to left. The layer of branch traces between cortex and central cylinder of the parent axis is conspicuous (arrows). FIGS. 8 and 9. Details of attachment of branch traces to bundles of erect stem. FIG. 8. Showing direct continuity of phloem, and xylem continuity via an intermediate cluster of elements. FIG. 9. A forked branch trace. PC — phloem continuity; XC — xylem continuity.

of the parent stem through which they must derive their water supply until such time as they produce an independent root system.

The pathway from foliage leaves for products of photosynthesis is equally continuous. At the node the downward-descending nutrients may be redistributed in three possible ways. First, they may pass from the leaf trace to the vertical bundle, or via bridges to other vertical bundles and thence upwards to the shoot apex. This pathway is clearly demonstrated in our illustration of the developing vascular system in the crown (*Fig. 2*, Zimmermann & Tomlinson, 1967a). Second, assimilates may move directly to an axillary inflorescence via satellites. This pathway is very significant and is discussed in further detail below. Third, assimilates may move downwards into the stem. Much of this material is stored as starch in ground parenchyma, particularly in the rhizome, but some must be available for developing roots and additional rhizomes.

Vascular continuity in developmental terms. An important aspect of the analysis of the insertion of lateral organs carried out in this article and the previous one in the *Rhapis* series (Tomlinson & Zimmermann, 1968) is the demonstration of dissimilar kinds of vascular union in the attachment of morphologically equivalent kinds of branch attachment and similar kinds of union in the attachment of dissimilar organs. Any idea that morphologically equivalent parts must necessarily have a similar vascular supply must be abandoned. Roots and vegetative branches are attached in essentially the same way. The attachment of vegetative branch, inflorescence axis, and inflorescence branch are all dissimilar although in morphological terms these organs are all equivalent. An explanation for these apparent discrepancies must be sought in developmental terms.

We have suggested in a paper in this series in which development of the axial system was described (Zimmermann & Tomlinson, 1967a), that the distribution of procambial strands in the developing crown can best be understood in terms of competing centers of growth, in which the shoot apex proper, leaf primordia, and inflorescence primordia each represent a growth center. The time of appearance of one growth center in relation to another is of major significance. Centers all receive a vascular supply by which they are fed. Those that appear early receive a procambial supply which is continuous with centers of supply of assimilates. These may be termed "supply" bundles. Centers which appear relatively late may initially lack continuity with existing bundles. This is established by bundles originating in the belated growth center and making a late contact with relatively mature bundles. These may be termed "demand" bundles. It is probably more useful in a physiological sense to speak of developing vascular traces in terms of "supply" and "demand" rather than of traces which grow "towards" or "away from" a growth center (or upwards, or downwards) since this implies a direction of differentiation which may not exist.

Differing types of organ are supplied by one or other of these types of bundle, sometimes by both in combination. Growth centers may, therefore, be categorized developmentally according to their type of vascular attachment to the parent axis. Root primordia and branch primordia arise late in relation to the maturation of the axis. They are clearly connected to the main axis by "demand" bundles which seemingly grow towards existing vascular strands. The vascular tissue of these existing strands is at a relatively late stage of maturation and is little influenced by the late attachment of a trace. We have shown how vessel-to-vessel contact from root trace to stem bundle involves a plexus of narrow elements around the vessel of the bundle which otherwise remains little altered. This reflects a late attachment of the trace.

Root and branch primordia on seedlings develop earlier than their counterparts on mature axes. This is indicated by the deeper penetration of root and branch traces into the seedling axis.

Branch and root primordia whose development is inhibited complete a vascular union with stem bundles in such a way that the fully differentiated attached end of each trace is immature distally. It is important to realize that this sequence of maturation is by no means an indication of a "direction" of differentiation.

The shoot apex proper and primordia of branches on the inflorescence axis may serve as examples of growth centers wholly vasculated by "supply" bundles. The latter example is particularly instructive (see *Fig. 13*, Tomlinson & Zimmermann, 1968), part of the axial system of "supply" bundles of the inflorescence is simply channeled towards the new growth center represented by the branch primordium.

The insertion of inflorescence on the main axis serves as an example of a union which involves both kinds of vascular attachment. The inflorescence primordium is initiated early. Contact with the developing stem system is established via "supply" bundles in the form of "satellites" which diverge from major leaf traces towards the growth center represented by the inflorescence primordium. Commonly at this stage the inflorescence aborts and remains as a vestigial axillary structure a few millimeters long. The satellite bundles, however, persist as a vascular system out of all proportion to the organ they supply. However, should normal development of the inflorescence continue, the vascular system is necessary and moreover is supplemented by an additional series of "demand" bundles visible as the inflorescence traces directly attached to peripheral stem bundles. These must appear late in inflorescence development *because no evidence of them is found in aborted inflorescences.*

SUMMARY

Vascular connection between either a root or a rhizomatous branch, on the one hand, and the main axis, on the other, is effected in essentially the same way. Root or branch traces are attached directly to axial vascular bundles, often penetrating deeply into the stem. An extensive peripheral attachment via girdling traces is also present. No bundles end blindly. The relative times of maturation of main and lateral organ determine the extent and type of connection. This is in turn reflected in the way in which vessel-to-vessel continuity is established, either directly or via an intermediate plexus of tracheal elements. Comparison with types of branching in the inflorescence suggests that the vascular union between main axis and lateral organ must all be understood in developmental

terms. For this reason morphologically equivalent organs may have different attachments if they develop differently and dissimilar organs may have similar attachments if their development is the same.

ACKNOWLEDGMENTS

The assistance of Miss Lesley Jackson who prepared all the series of sections on which this study is based is gratefully acknowledged.

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COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENIACEAE, III. THE CARPELS *

William C. Dickison

Information regarding floral morphology and anatomy of the Dilleniaceae is surprisingly scarce. Floral studies on *Dillenia*, *Hibbertia*, and *Doliocarpus* by Wilson (1937), Ozenda (1949), and Sastri (1958) provide only incomplete data. Recently, Professor C. L. Wilson has undertaken an extensive investigation of the floral anatomy of the entire family. The first contribution toward this goal (Wilson, 1965) deals with the genus *Hibbertia*.

In the present study, no attempt was made to delve into the area of floral anatomy. Instead, concentration was focused on a comparative morphological survey of the dilleniaceous carpel.

As a result of intensive morphological studies on the woody ranalian families, the nature of the primitive carpel and its initial trends of specialization have been suggested by Bailey and Nast (1943); Bailey and Swamy (1951); Swamy and Periasamy (1964). The verification and development of these trends, however, will be obtained only by extensive comprehensive investigations of all orders and families of angiosperms (Bailey & Swamy, loc. cit.).

Since the combination of characters encountered in the Dilleniaceae has suggested a position among other presumed primitive taxa (see Dickison, 1967a), the family is thought to occupy a key position in angiosperm phylogeny. With this in mind, the present investigation was carried out with a twofold objective: (1) to attempt to uncover relationships and trends of specialization within the family, and (2) to provide additional evidence to help clarify the phylogenetic affinities of this assemblage.

MATERIALS AND METHODS

Carpels of representatives of all ten genera presently considered to compose the Dilleniaceae were examined. Material was obtained largely from the author's personal collection of preserved and dried specimens. This was augmented only when necessary by flowers derived from herbarium sheets.

The most convenient method of studying carpel vascularization was through the use of cleared specimens. Successful clearing was accomplished with 5 to 8 per cent hot NaOH (Bailey & Nast, 1943) for a period ranging from twelve hours to five days. Sclerified hairs on the

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* I wish to thank Dr. James E. Canright for reading the manuscript.

highly pubescent carpels of *Schumacheria* and *Curatella* had to be meticulously removed prior to clearing, before details of vascularization could be observed. When phlobaphene pigments obscured the vascular traces, it was often necessary to use an overnight treatment of Stockwell's bleach (Johansen, 1940). After clearing, the carpels were washed and stained with saturated aqueous basic fuchsin.

Serial sections of floral buds were obtained by the standard paraffin methods. Dried specimens were first re-expanded in 2.5 per cent hot NaOH, after which they were washed, fixed in FAA, and treated as preserved material. Staining was accomplished with safranin or a safranin-fast green combination.

OBSERVATIONS

Dillenia. The gynoecium of *Dillenia* consists of from four to twenty carpels arranged in a whorl around a conical receptacle. The carpels are sessile, cylindrically ovate in shape and have elongate, free, characteristically abaxially recurved styles. The gynoecium is glabrous or occasionally sparsely covered with unicellular unbranched trichomes. Calcium oxalate crystals in the form of raphides or crystal sand, and enlarged secretory cells are common in the wall tissue of some species.

The stigmatic region in those species investigated was indistinct and restricted to the terminal portion of the style. Hoogland (1952) reports, however, that two species (*Dillenia serrata* and *D. celebica*) have distinct, knob-like stigmas. The ovular number varies from four to about 80. The ovules are bitegmic, anatropous or apotropous and generally borne in single or double submarginal rows (FIG. 12). In *D. parviflora* it was observed that the micropylar openings in the two integuments do not always correspond. This interesting feature was first brought to my attention by Dr. G. L. Stebbins (personal communication), although it has been reported and illustrated in *Acrotrema* (Swamy & Periasamy, 1955) and *Hibbertia* (Sastri, 1958), and has now also been observed in *Davilla* and *Curatella*.

The conduplicate carpels exhibit various syncarpous tendencies. Young carpels have their ventral margins closely appressed but retain a distinct ventral suture. At maturity, the ventral suture opens but the carpel remains closed by the adnation of the free ventral margins to the conical receptacle (FIG. 12). Carpellary fusion between the ventral margin and the torus in the lower three-fourths to one-half of the gynoecium results in a solid core of tissue and isolated locules of individual carpels. There may also occur, simultaneously, varying degrees of lateral concrescence between carpels. The extent and type of syncarpy changes with carpel age and level of examination in the gynoecium. A small ventral notch is all that is evident of conduplicate folding in the stylar region of the mature carpel.

The carpels of all seven species of *Dillenia* examined were uniformly vascularized by three bundles which depart from a eustele in the receptacle

(FIG. 1). The dorsal trace extends through the style and terminates in the stigmatic region, whereas both ventrals end within the top of the ovary. Each ovule is supplied by a vein originating from the corresponding ventral trace. When there are double submarginal rows (as in *D. indica*), the original trace bifurcates to supply both ovules. In some species (e.g., *D. suffruticosa*), the ovular trace may become considerably branched within the ovule. Lateral veins depart at regular intervals from the dorsal bundle to vascularize the ovary wall.

Acrotrema. From approximately ten known species of this rare, semiherbaceous genus, only flowers of a collection by Thwaites (US *1576875*) were available for examination. The gynoecium is composed of three rather small (ca. 3 mm. in length) glabrous carpels. Basally, the open conduplicate carpels are laterally concrescent along their inner surfaces, resulting in a single internal cavity. At the level of ovular insertion, the gynoecium becomes completely apocarpous with the suture of each individual carpel closed. A slender, adaxially recurved style is terminated by an indistinct stigmatic surface.

The number of ovules in the genus ranges from two to six to ten to twenty (Hoogland, 1951). Swamy and Periasamy (1955) report that the ovules of *Acrotrema arnottianum* are typically anatropous, but following fertilization become completely amphitropous. A comparable situation occurs in *Hibbertia* (Sastri, 1958).

The vascular pattern in the single species investigated (FIGS. 2, 13) is similar to that described for *Dillenia*, with the exceptions that in *Acrotrema* the ventral bundles approximate the dorsal in length, and there is a noticeable absence of lateral carpellary wall veins.

Hibbertia. The bisexual flowers of the largest dilleniaceous genus have one, two, three, five or rarely (in *H. crenata*), ten carpels (Wilson, 1965). This genus has often attracted attention because it is thought to contain members with the least specialized floral structure in the family. In some species the gynoecium is entirely apocarpous but frequently it displays varying degrees of basal syncarpy. The carpels are differentiated into a swollen ovary which is projected distally into a narrow, elongated, often abaxially orientated style; at the tip of the style is an indistinct, or slightly enlarged, stigmatic surface. The carpels vary from glabrous to densely pubescent and may contain numerous raphides crystals (e.g., H. *exutiacies*). In addition, the presence of a single druse crystal in the ovules of certain species (e.g., *H. tetrandra* and *H. cuneiformis*) is very striking. One to 25 bitegmic, anatropous, submarginal ovules are present in each ovary. As has been noted previously, the micropylar openings in the two integuments do not always correspond.

Wilson (loc. cit.) has described two distinct types of gynoecia within the bicarpellate species. He arbitrarily designates these as "opposite" and "oblique" forms. In an "opposite" gynoecium, the carpels normally have their dorsal bundles lying directly opposite each other and the ventral sutures remain centrally located throughout the length of the carpel. In "oblique" carpels, however, the dorsal bundles depart at an angle, with a subsequent displacement of the ventral traces and sutures to one side of the carpel. The occurrence of these two morphologically dissimilar gynoecial types is clearly observable. Wilson considers the oblique condition to be specialized and suggests it may have arisen more than once within the genus.

All specimens studied were vascularized by three traces: a dorsal and two ventrals. In material of such species as *Hibbertia scandens* (FIG. 3), the dorsal bundle supplies numerous lateral veins to the ovary wall before ending at the style apex. The vascular supply to the ovules is derived from the ventral bundles.

A well documented trend of reduction in carpellary vascularization is present within the genus. For example, in *H. tetrandra* (FIG. 4) only two lateral wall veins originate from the dorsal, and the ventral bundles are much reduced. The culmination of this specialization can be found in the greatly reduced carpel of the genus *Pachynema* (see FIG. 5).

Pachynema. Two species of this Australian genus were available for investigation. The bisexual flowers contain two glabrous carpels with only slight basal fusion. Each carpel is differentiated into an enlarged ovary and a narrow, slightly reflexed, vascularized style. A very localized, apical stigmatic surface is quite indistinct. Secretory cells are very common in the ovary wall.

Reduction in the sterile ventral borders results in the conduplicate nature of these carpels becoming obscured. The bicarpellate gynoecium is best described as opposite, although this appears to be a rather unstable character with tendencies toward obliqueness being observed. The ventral sutures are typically open at the level of ovular placentation, but closed below and above this location. Variations in the degree of closure reflect differences in carpel maturity.

The reduced nature of the gynoecium in this genus is very pronounced in the pattern of carpel vascularization (FIG. 5). One dorsal and two ventral bundles enter the base of the carpel. Four major lateral veins are derived from the dorsal bundle and supply the ovary wall. The status of the ventral traces is considerably reduced with each one serving as the vascular supply to one of the two basal ovules.

Didesmandra. The gynoecium of the single species, *Didesmandra aspera*, is bicarpellate with only slight basal connation present. The carpels are very characteristically differentiated into a large, swollen, glabrous ovary and an elongate (15–20 mm.), filiform style. A stigmatic region is restricted to the style apex. Numerous enlarged secretory cells are scattered throughout the ovary wall.

The two conduplicate carpels are oblique in their orientation (FIG. 14). Even though the oblique condition is clear, it is not as pronounced as in some hibbertias. The conduplicate nature of the carpels is somewhat obscured by the reduction and fusion of the ventral margins rendering the gynoecium permanently closed along its entire length.

The vascular system (FIG. 7) at the base of each carpel is eustelic. A dorsal bundle departs initially from the stele, closely followed by a pair of ventral traces. Following the departure of the dorsal and ventral carpel bundles, the stele contracts to a pithless condition and continues distally to vascularize the single, comparatively large, basal ovule. The ovular trace terminates in a series of short branches. The ovary wall is supplied by lateral veins from both dorsal and ventral bundles.

Schumacheria. All observations on this endemic Ceylonese genus were made from *S. castaneifolia.* Although the flowers are often described as possessing three carpels, bicarpellate flowers are quite common. In either case, the gynoecium is densely covered with sclerified hairs. The presence of calcium oxalate crystals in the form of either raphides or crystal sand, in addition to large secretory cells, is also characteristic for this species. The ovary, containing a single basal ovule (FIG. 16), projects distally into an elongate, abaxially recurved style which narrows at its tip to form a terminal stigma.

In bicarpellate gynoecia, the carpels are distinctly oblique in orientation. In such cases, syncarpy occurs between carpels throughout the length of the ovary by fusion of only one of their ventral borders. Also, one carpel of the gynoecium may open at maturity while the other remains closed.

In tricarpellate flowers, one carpel was found to develop at a higher level than the other two which are initially somewhat oblique. As the third carpel develops, the "obliqueness" evident basally is lost. This observation suggests that in *Schumacheria* the third carpel is in the process of being lost and the oblique condition is a result of this process. A developmental study of the flower of *Schumacheria* would perhaps aid in clarifying the origins of the oblique gynoecium.

The vascularization of *Schumacheria* carpels is quite complex but resembles *Didesmandra* in that following the departure of the dorsal and ventral carpel traces, the stele becomes pithless and forms a thick, stout ovular trace which "fans out" in the ovule into numerous small veinlets (FIG. 6). Three traces leave the stele at approximately the same level. These bundles branch and bifurcate almost immediately, however, so the carpel, for all practical purposes, is vascularized by more than three major traces. The two ventral traces do not contribute to the vascularization of the ovule. The ventrals extend to the summit of the style with the dorsal trace. Numerous lateral veins anastomose throughout the ovary wall.

The suggested close relationship of *Schumacheria* and *Didesmandra* (Hoogland, 1951) is supported by carpel morphology, pollen morphology, and wood anatomy.

Tetracera. This genus is particularly noteworthy in possessing both unisexual and bisexual flowers in an otherwise entirely bisexual family. It is interesting in this regard that Hoogland (1953) refers to the flowers of the Indo-Malayan tetraceras as bisexual, whereas Hunter (1966) calls the flowers of the Panamanian forms unisexual. The small number of African specimens I examined possessed bisexual flowers; thus, unisexuality appears to be confined to the New World. However, additional collections will have to be studied to support such a basic distinction.

The apocarpous gynoecium is composed of one to five pyriform carpels. The carpels vary from glabrous to densely pubescent, and possess from one to twenty anatropous, bitegmented ovules arranged in two to six submarginal rows. An erect, occasionally abaxially directed, style is terminated with an undifferentiated or slightly peltate stigmatic surface. Calcium oxalate crystals in the form of raphides or crystal sand and large secretory cells are quite common in the wall tissue of some species (e.g., *Tetracera indica*).

The conduplicate nature of the carpels is apparent in both the ovary and the solid style where a persistent ventral fold remains. Characteristically, the carpels are completely closed and fused basally. Progressing distally, the ventral suture becomes histologically more pronounced with the ventral region becoming open in some species.

Carpel vascularization is as follows (FIG. 8): following the departure of sepal, petal, and stamen traces, the vascular system in the torus forms large, isolated bundles corresponding in number to the carpels. Thus, each carpel is supplied by a single, large toral trace. Upon entering the carpel base, the dorsal bundle departs first, closely followed just below the initiation of the locule by the bifurcation of the remaining toral trace into two ventral bundles. Many carpels observed had accessory carpel bundles originating from the toral bundle. These accessory veins are usually quite reduced and either end blindly or connect with other lateral wall veins. The occurrence of numerous, highly anastomosing, lateral wall veinlets between the ventral and dorsal bundles is well developed in the genus. The ovules are supplied by veins branching from the ventral traces.

Curatella. The flowers of the monotypic *Curatella americana* are normally bicarpellate, although Hunter (1966) reports that the number of carpels may rarely be one to five. The gynoecium is very densely pubescent. Syncarpy occurs between carpels by complete fusion of the adaxial ovary surfaces. The erect styles are typically free and terminated by a peltate stigmatic surface. Raphides crystals and large secretory cells are present throughout the gynoecium.

In addition to fusion between carpels, the ventral sutures of both carpels are also closed basally (FIG. 15). The ventral suture becomes more distinct at the level of placentation and may even become completely open. In the solid style a notch remains in the ventral region. The orientation of the bicarpellate gynoecium is strictly opposite.

As seen in FIG. 10, the carpel of *Curatella* is vascularized by five major bundles: a dorsal, two ventrals, and two large accessory traces. Occasionally, additional smaller supernumerary traces are distinguishable so that seven carpel traces are present. Each carpel trace arises independently in the toral stele; however, in some gynoecia the ventrals were observed to diverge from a common sympodium. At the base of the carpel, complex anastomosing and branching occurs in the stelar system before the major carpel traces emerge. A similar situation has been reported in the Winteraceae (Nast, 1944; Tucker & Gifford, 1964). The dorsal bundle, which bifurcates at the base of the style, and the two ventrals terminate just below the stigma. The accessory bundles usually connect with other lateral wall traces departing from the dorsal. Each ventral trace supplies the vascularization to one of the two, bitegmented, basal ovules. The micropylar openings in the two integuments do not always correspond.

Davilla. This genus is uniformly characterized by monocarpellate flowers. The glabrous gynoecium is distinguished by a slightly clavate style and a flattened, peltate, stigmatic surface. Two basal, bitegmic ovules are present in each carpel, along with the rather frequent occurrence of raphides crystals. The micropylar openings in the two integuments do not always coincide.

In the Dilleniaceae, *Davilla* appears to be unique in that the ventral carpel margins are involute and not conduplicately folded. At the carpel base, the ventral region begins to open along the outer ventral surface in what would be considered a conduplicate manner. Slightly higher, however, the ventral margins become distinctly involute (Fig. 11 b), with the outer carpel surfaces being brought inside. At this level the carpel may either be closed or open. Above the point of placentation the involuted margin begins to fuse internally and eventually all evidences of the ventral suture and folding are lost (Fig. 11 c).

The vascularization of *Davilla aspera* is rather simple (Fig. 11 a) when compared to other New World genera. Three carpel traces are present at the base of the locule. The dorsal bundle extends unbranched along the length of the style, except for the departure of two lateral wall veins. Both ventrals are reduced but give rise to the vascular supply to the ovules.

Doliocarpus. With the exception of the bicarpellate *D. coriaceus*, this genus is also unicarpellate (Hunter, 1966, reports the Panamanian species may rarely possess two carpels). All species have carpels with well-differentiated ovaries and extended styles terminated by peltate stigmatic surfaces of varying size. The gynoecium is either glabrous or densely pubescent (e.g., *D. major*). Similar to many other Dilleniaceae, the carpel wall frequently contains large secretory cells. *Doliocarpus dentatus* (Fig. 9) is readily distinguished from other species by the presence of raphides crystals, which were often so numerous they obscured details of vascularization in cleared carpels.

The carpels of *Doliocarpus* are conduplicate although the ventral borders may be considerably reduced. Slight variations were observed in the degree of carpel closure. The ventral margins of *D. dentatus* and *D. guianensis* are closed basally, but at the level of locule formation begin to open internally until they become completely distinct at the level of ovular insertion. Above the level of placentation, the carpel begins to close centripetally. *Doliocarpus major*, by contrast, remains open along the entire ovary length.

Doliocarpus coriaceus shows complete adnation between the two opposite carpels. At the level of ovular placentation, the ventral suture of each carpel opens, creating a continuous internal cavity within the gynoecium. Immediately above this point, the ventral region fuses solidly leaving no evidence of sutural structure. Separation of the style is initiated by an internal cleft which proceeds outward.

Each carpel of *Doliocarpus coriaceus* is supplied by three major bundles, a dorsal and two ventrals. The dorsal trace is well pronounced and vascularizes the style. The weaker ventrals terminate within the ovary after initiating traces to the two basal ovules. Small lateral wall veins occasionally originate from and anastomose between the ventral and dorsal bundles, as well as from the toral region.

All the monocarpellate species examined were vascularized by more than three major traces departing from the stele. Generally a distinct dorsal bundle is recognizable, which, upon entering the style, undergoes a series of bifurcations resulting in a rich vascularization of the style. Although ventral traces can often be discerned, they are not at all pronounced or distinguished from the other four to six accessory bundles. The pair of ovules is supplied by veins originating directly from the receptacle. Numerous lateral wall veins are present throughout the ovary. The complex basal branching and anastomosing observed in *Curatella* is also present in *Doliocarpus*.

DISCUSSION

Among the various species of Dilleniaceae examined, the following primitive gynoecial features were observed: (1) complete or nearly complete apocarpy; (2) visible conduplicate folding; (3) open ventral sutures; and (4) large numbers of ovules. It is clear, nevertheless, that no extant dilleniaceous carpel is closely comparable to the primitive ranalian megasporophyll.

On the other hand, the Dilleniaceae are more readily characterized by a larger number of moderately to highly advanced phylogenetic specializations which parallel those that occur in angiosperms as a whole: (1) reduction in number of carpels to one; (2) differentiation and elongation of a narrow, vascularized style; (3) formation of a restricted, terminal, often peltate stigmatic surface; (4) reduction in number of ovules to two or one; (5) varying degrees of basal adnation and/or lateral concrescence; (6) complete fusion of the ventral suture; (7) reduction or amplification of the basic three-veined carpel vascularization; and (8) tendency toward involute closure. The occurrence of the oblique gynoecium in many bicarpellate Old World species is an intriguing feature of possible phylogenetic significance.

The least specialized carpels in the family are found among the apocarpous species of *Hibbertia.* When considered *as a whole,* the subfamily Dillenioideae is less specialized in carpel morphology than the Tetraceroideae. This information may be correlated with that obtained from other lines of evidence, e.g., wood anatomy. The fact that direct correlations do not always hold true can be demonstrated in *Didesmandra* and *Schumacheria,* which have very primitive wood but rather specialized gynoecia, and *Tetracera,* with more advanced wood but comparatively primitive carpels. Most frequently, dilleniaceous species have various combinations of advanced and primitive characters present simultaneously. For this reason, no one subfamily or genus retains exclusively primitive or advanced features. The opinion of Hoogland (1951) that the gynoecium of *Dillenia* is the most advanced in the family is not substantiated.

According to the classical concept, the primitive carpel is a three-trace organ (Eames, 1931). The primitive nature of the three-trace condition was generally accepted in light of studies on the woody Ranales (e.g., Bailey & Swamy, 1951). From the three-trace condition, a multitrace carpel would be derived by amplification, whereas a two-trace organ would result from loss of one of the ventrals.

With the discovery of multitrace carpels in some otherwise primitive families — Degeneriaceae, Lauraceae, Winteraceae, Myristicaceae, and Annonaceae among others, the primitive nature of the three-trace carpel was questioned. Some authors, e.g., Swamy (1949), suggested that the presence of additional bundles in the monocarpellate gynoecia of *Degeneria* was indicative of a multicarpellate ancestry with the extra bundles being considered remnants of missing carpels. In reviewing the vascularization in ranalian carpels, Sastri (1959) has specifically warned against the assumption that the three-trace carpel is primitive for all angiosperms. Tucker and Gifford (1966b) are of the opinion that the three-trace concept is not essential to an understanding of carpel vascularization, and point to Sterling's (1953) conclusion that the basic pattern in the Rosaceae is five-trace.

When the vascular pattern in the Dilleniaceae is correlated with other indices of advancement such as closure, ovule number, degree of syncarpy, etc., there is little question that the three-trace condition is primitive. Specializations in vascularization have subsequently occurred toward reduction (particularly in the ventral bundles) and amplification. It appears, accordingly, that there exists a fundamental distinction in carpel vascularization between the Dilleniaceae and the Rosaceae, a family often derived through, or allied to, the dillenias.

In many species of Dilleniaceae with reduced carpel numbers, weak supernumerary traces occur which could be interpreted as remnants of a multicarpellate ancestry. However, I believe the well developed accessory bundles in the monocarpellate species of *Doliocarpus* and the bicarpellate *Curatella* are the result of phylogenetic amplification. It is entirely possible that both processes have occurred simultaneously. It should be emphasized in this connection that not all solitary dilleniaceous carpels are multitrace, a tendency noted by Tucker and Gifford (1966a). In contrast, the unicarpellate hibbertias have three prominent traces (Wilson, 1965), whereas the New World genus *Davilla* retains the three-trace condition in a considerably reduced form.

My conclusions (Dickison, 1967a & b), based on wood anatomy and pollen morphology, that previous magnoliaceous ranalian affinities ascribed to the Dilleniaceae are not well founded also gain support from the vascular anatomy of the carpels. In some Magnoliaceae and Annonaceae, the ovules are vascularized by traces from the dorsal bundle (Canright, 1960; Periasamy & Swamy, 1956). Although there is no uniform method of ovular vascularization in the Dilleniaceae, ovular traces never originate from the dorsal bundles. The cortical system characteristic of many Ranales is also lacking in the dillenias. Likewise, the compound gynoecia and axile placentation of the Theaceae show little similarity to the Dilleniaceae.

A more comparable situation is found in *Paeonia*. The gynoecium of *Paeonia* is apocarpous with each carpel vascularized by three principal bundles, a dorsal and two ventrals, accompanied by a variable number of smaller secondary veins. Each of the two ventral traces bifurcates at the base of the style resulting in a richly supplied stigma. It is particularly noteworthy that Brouland (1935) diagrammed a bicarpellate gynoecium of *P. delavayi* as being oblique. Since this species is more commonly tricarpellate, it again indicates that the oblique condition probably results from reduction within the gynoecium. Also, the occurrence of the oblique gynoecium in *Paeonia* suggests that this character might have phylogenetic significance in the Dilleniaceae and allies.

Unfortunately, the scanty, or nonexistent information on the floral morphology and anatomy of many families putatively related to the Dilleniaceae prevents a critical comparison.

MATERIAL EXAMINED[1]

Acrotrema sp. CEYLON: *Thwaites* CP *3899* (US *1576875*).
Curatella americana L. BRAZIL: *Irwin 5470* (NY).
Davilla aspera (Aubl.) Benoist. BRAZIL: *N. T. Silva 16.*
Davilla sp. BRAZIL: *Irwin 5570* (NY).
Didesmandra aspera Stapf. SARAWAK: *Burtt & Woods B.2540* (E); SAR *18297.*
Doliocarpus coriaceus (Mart. & Zucc.) Gilg. COLOMBIA: *Haught 1655* (US).
Doliocarpus dentatus (Aubl.) Standl. BRIT. HONDURAS: *Gentle 1418* (MO); BOLIVIA: *Krukoff 10407*(UC).
Doliocarpus guianensis (Aubl.) Gilg. COSTA RICA: *Skutch 3980* (US).

[1] Material studied was obtained from the State Herbarium of South Australia, Adelaide (AD); The Forest Herbarium, Bangkok (BFK); Botanic Museum and Herbarium, Brisbane (BRI); Commonwealth Scientific and Industrial Organization, Canberra (CANB); Royal Botanic Garden, Edinburgh (E); Royal Botanic Gardens, Kew (K); Missouri Botanical Garden, St. Louis (MO); Animal Industry Branch, Northern Territory Administration, Alice Springs (NT); New York Botanical Garden (NY); Sarawak Museum, Kuching (SAR); Botanic Gardens, Singapore (SING); University of California, Berkeley (UC); and the United States National Herbarium, Washington (US).

Doliocarpus major Gmel. PANAMA: *Stern et al. 223* (US).
Dillenia aurea Sm. THAILAND: BKF *s.n.*
Dillenia indica L. AUSTRALIA: Cult. BRI *s.n.*
Dillenia ovata Wall. ex Hook. f. & Thoms. SINGAPORE: Cult. SING *s.n.*
Dillenia papuana Martelli. NEW GUINEA: *Darbyshire & Hoogland 8039* (CANB).
Dillenia parviflora Griff. THAILAND: BKF *s.n.*
Dillenia philippinensis Rolfe. PHILIPPINES: *J. V. Pancho s.n.*
Dillenia suffruticosa (Griff.) Martelli. SINGAPORE: Cult. SING *s.n.*
Hibbertia cuneiformis (Labill.) Gilg. Cult. K *s.n.*
Hibbertia dentata R.Br. Cult. K *s.n.*
Hibbertia exutiacies Wakefield. AUSTRALIA: *Eichler 17965* (AD).
Hibbertia scandens (Willd.) Dryand. Cult. K *s.n.*
Hibbertia tetrandra (Lindl.) Gilg. Cult. E *C3544.*
Pachynema dilatatum Benth. AUSTRALIA. Northern Territory: NT *6129.*
Pachynema junceum Benth. AUSTRALIA. Northern Territory: NT *6750.*
Schumacheria castaneifolia Vahl. CEYLON: *Abeywickrama s.n.*
Tetracera akara (Burm. f.) Merr. BORNEO: UC *290527.*
Tetracera indica (Houtt. ex Christm. & Panz.) Merr. SINGAPORE: *Keng s.n.*
Tetracera podotricha Gilg. ANGOLA: *Gossweiler 9135* (US).
Tetracera scandens (L.) Merr. MALAYA: *s.n.*
Tetracera volubilis L. PANAMA: *Allen 2039* (MO).

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EXPLANATION OF PLATES

PLATE I

Explanation of symbols: c., druse crystal; d.b., dorsal bundle; e.p., stigmatic surface; l.b., lateral bundle; ov.b., ovular bundle; ov.t., ovular trace; t., trichome; v.b., ventral bundle.

FIGS. 1–6. Vascularization of dilleniaceous carpels; only one of the ventral bundles and half the lateral veins are shown. 1, *Dillenia parviflora* (BKF *s.n.*), from Thailand. 2, *Acrotrema* sp. (US *1576875*). 3, *Hibbertia scandens* (Cult. K *s.n.*). 4, *Hibbertia tetrandra* (Cult. E *C3544*). 5, *Pachynema dilatatum* (NT *6129*). 6, *Schumacheria castaneifolia* (*Abeywickrama s.n.*), from Waga, Ceylon.

PLATE II

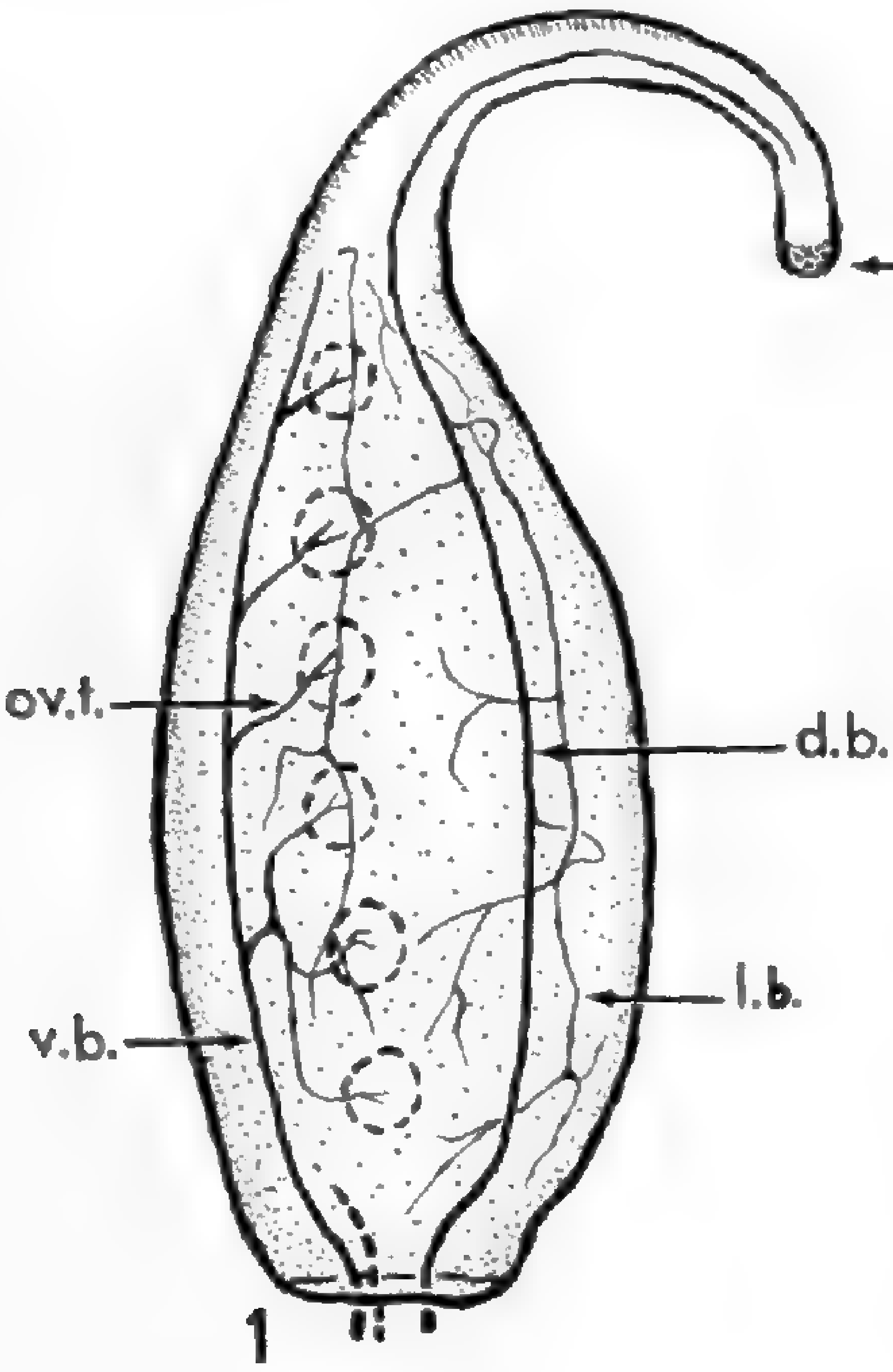
Explanation of symbols: a.b., accessory bundle; d.b., dorsal bundle; e.p., stigmatic surface; l.b., lateral bundle; ov., ovule; ov.b., ovular bundle; r., raphides; t., trichome; v.b., ventral bundle.

FIGS. 7–11. Vascularization of dilleniaceous carpels, continued: only one each of the ventral bundles and accessory bundles, and half the lateral veins are shown. 7, *Didesmandra aspera* (SAR *18297*). 8, *Tetracera akara* (UC *290527*). 9, *Doliocarpus dentatus* (*Krukoff 10407*), only the major lateral wall veins are illustrated. 10, *Curatella americana* (*Irwin 5470*). 11 a, b, c, *Davilla aspera* (*N. T. Silva 16*), from Belém, Brazil.

PLATE III

Explanation of symbols: d.b., dorsal bundle; ov., ovule; ov.t., ovular trace; s.t., stamen trace; v.b., ventral bundle; v.s., ventral suture.

FIGS. 12–16. Dilleniaceous carpel morphology. 12, *Dillenia philippinensis* (*J. V. Pancho s.n.*, from Makiling, Philippines), transverse section of carpel, × 27. 13, *Acrotrema* sp. (US *1576875*), cleared and stained flower showing details of vascularization; one carpel has been removed, × 30. 14, *Didesmandra aspera* (SAR *18297*), transverse section of gynoecium showing large, solitary ovule, enlarged secretory cells, and oblique orientation, × 25. 15, *Curatella americana* (*Irwin 5470*), transverse section of gynoecium in region of ventral sutures, showing complete fusion of the two opposite carpels, × 30. 16, *Schumacheria castaneifolia* (*Abeywickrama s.n.*, from Waga, Ceylon), longitudinal section of carpel showing solitary, basal ovule, × 27.



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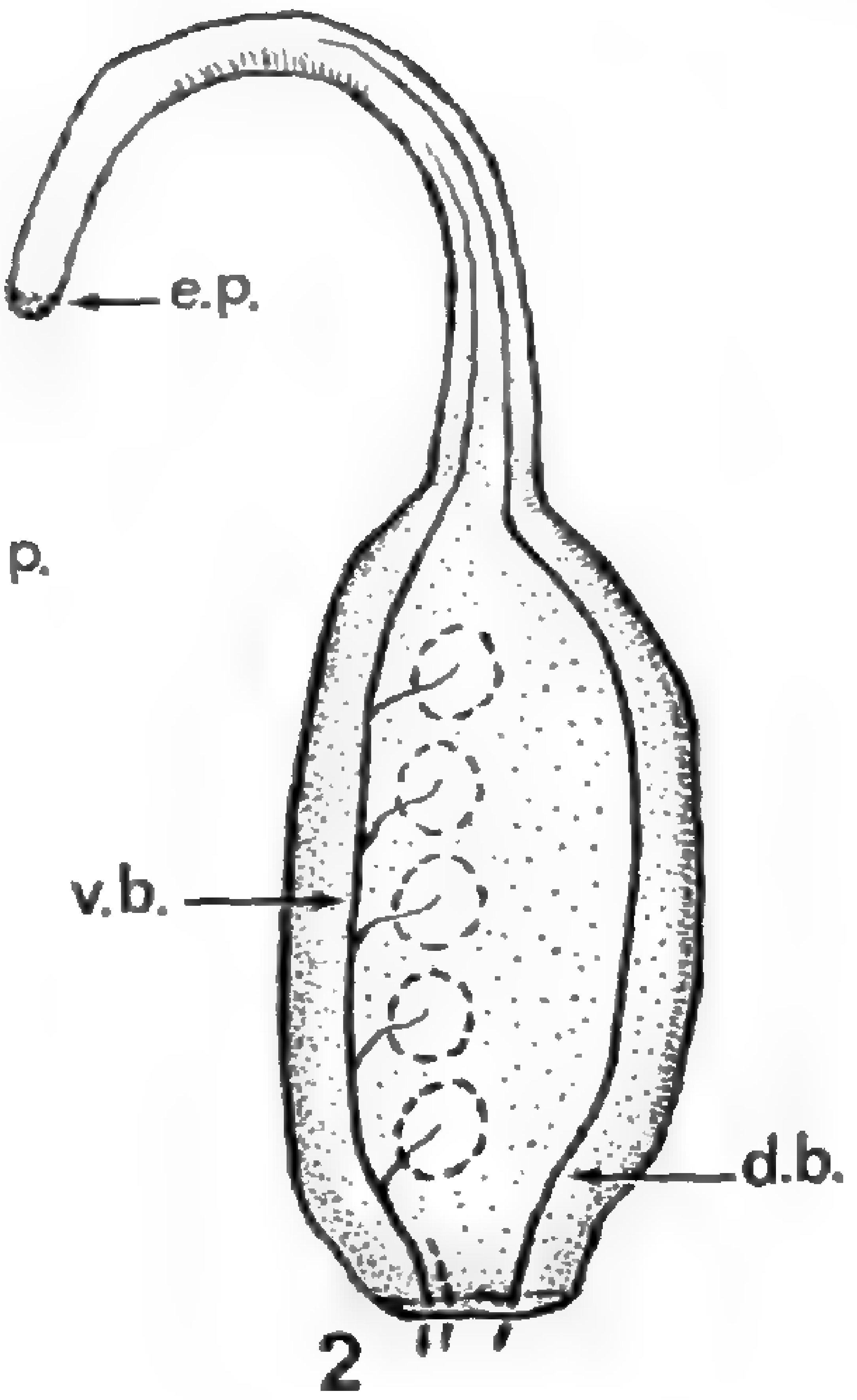

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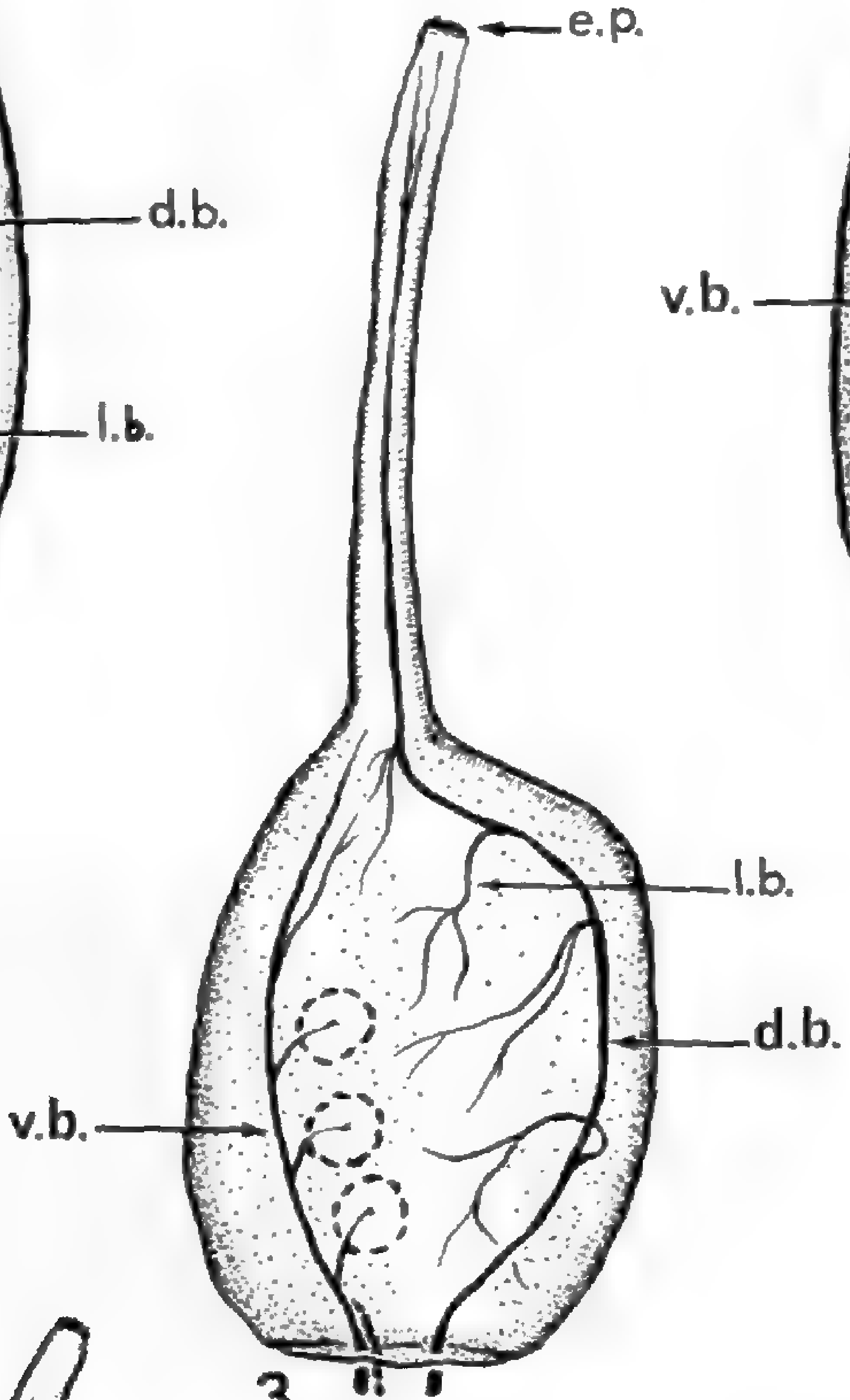

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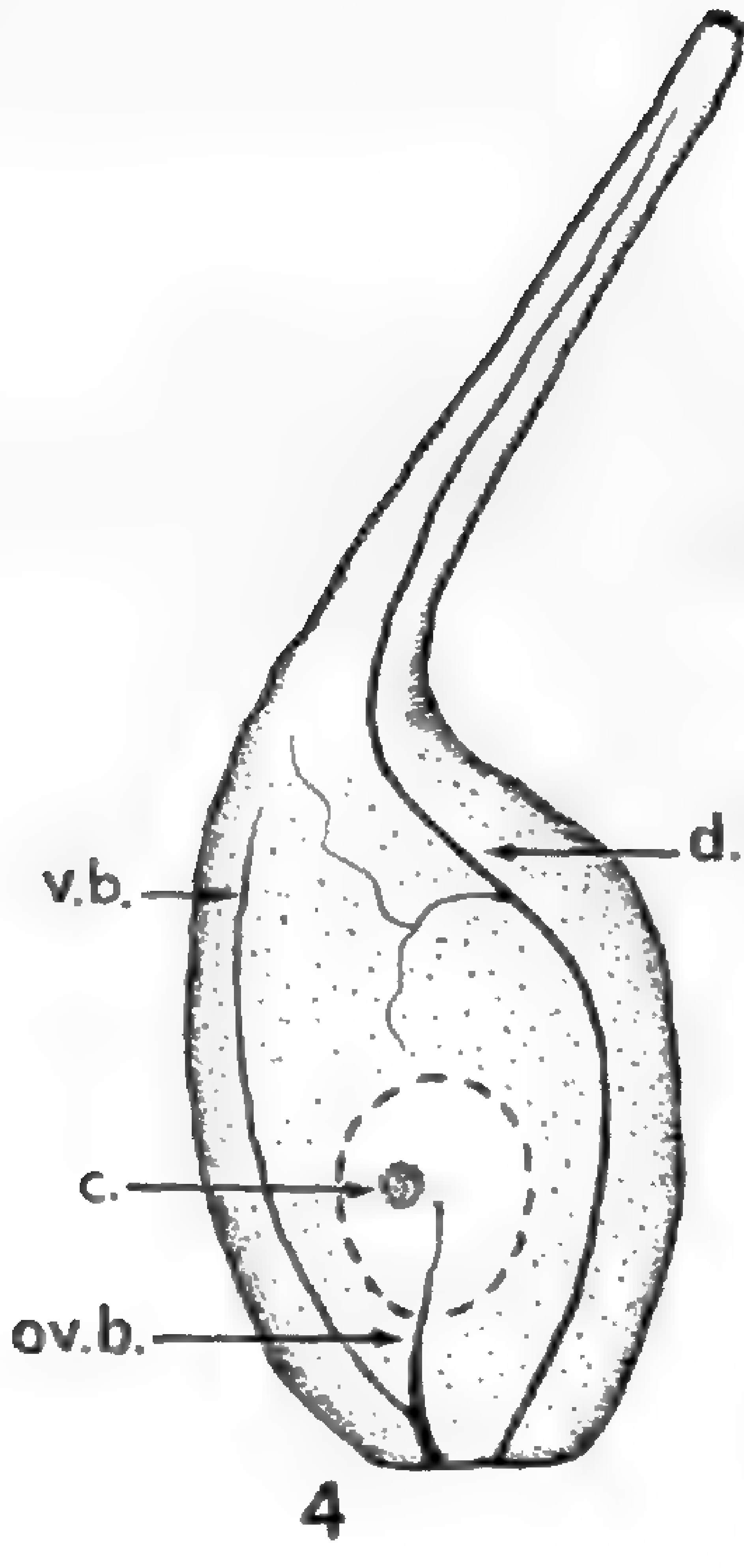

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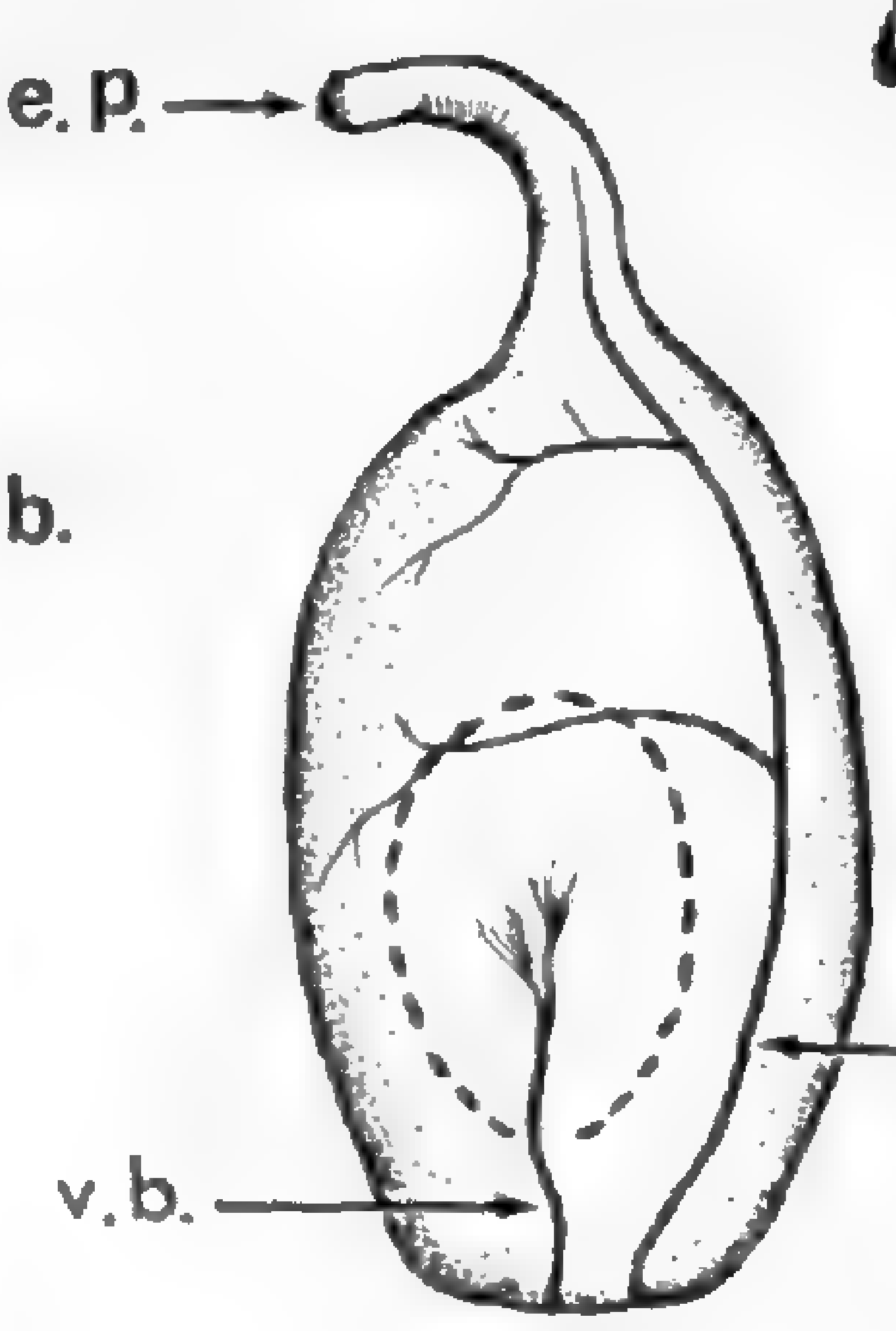

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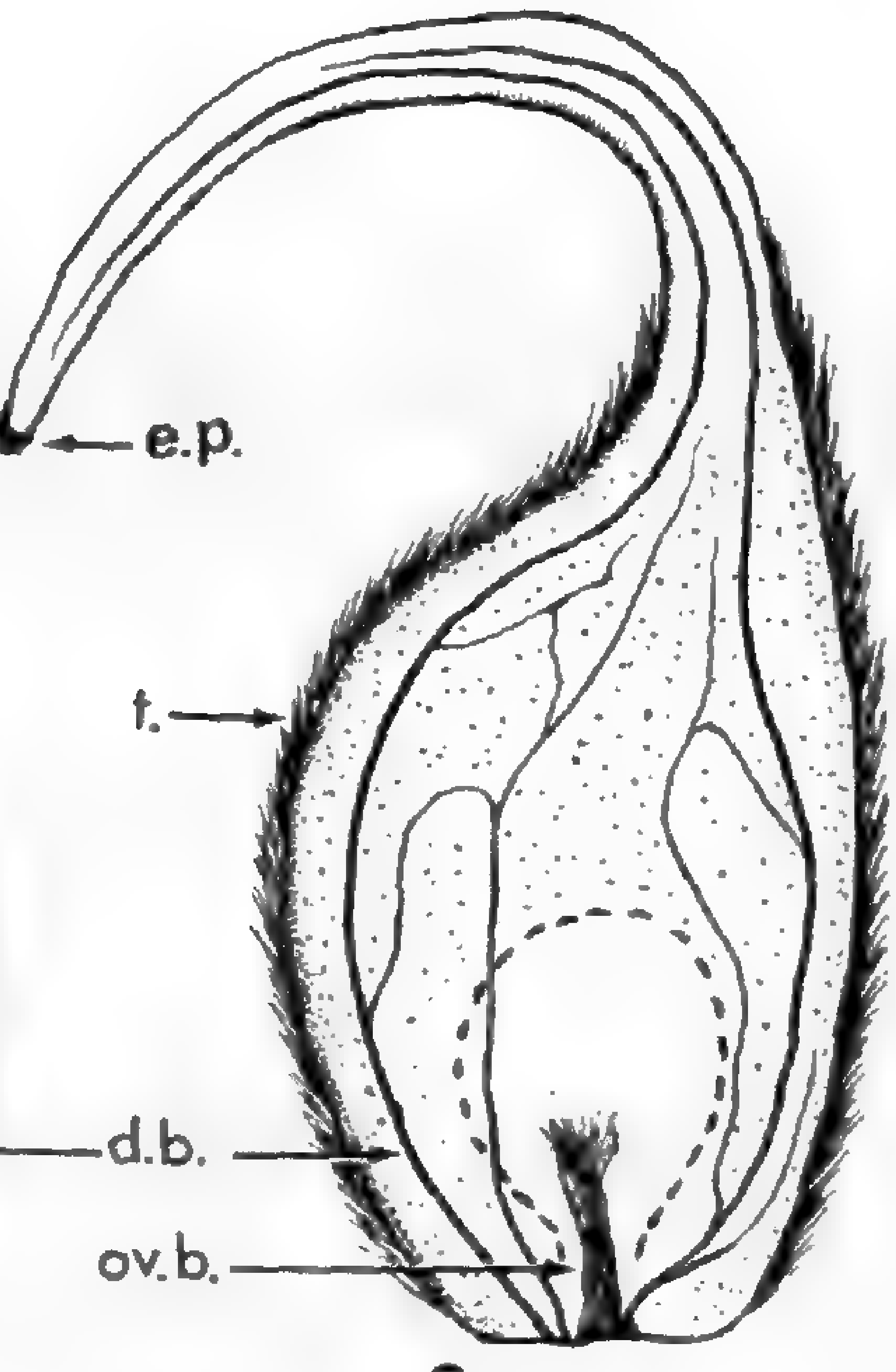
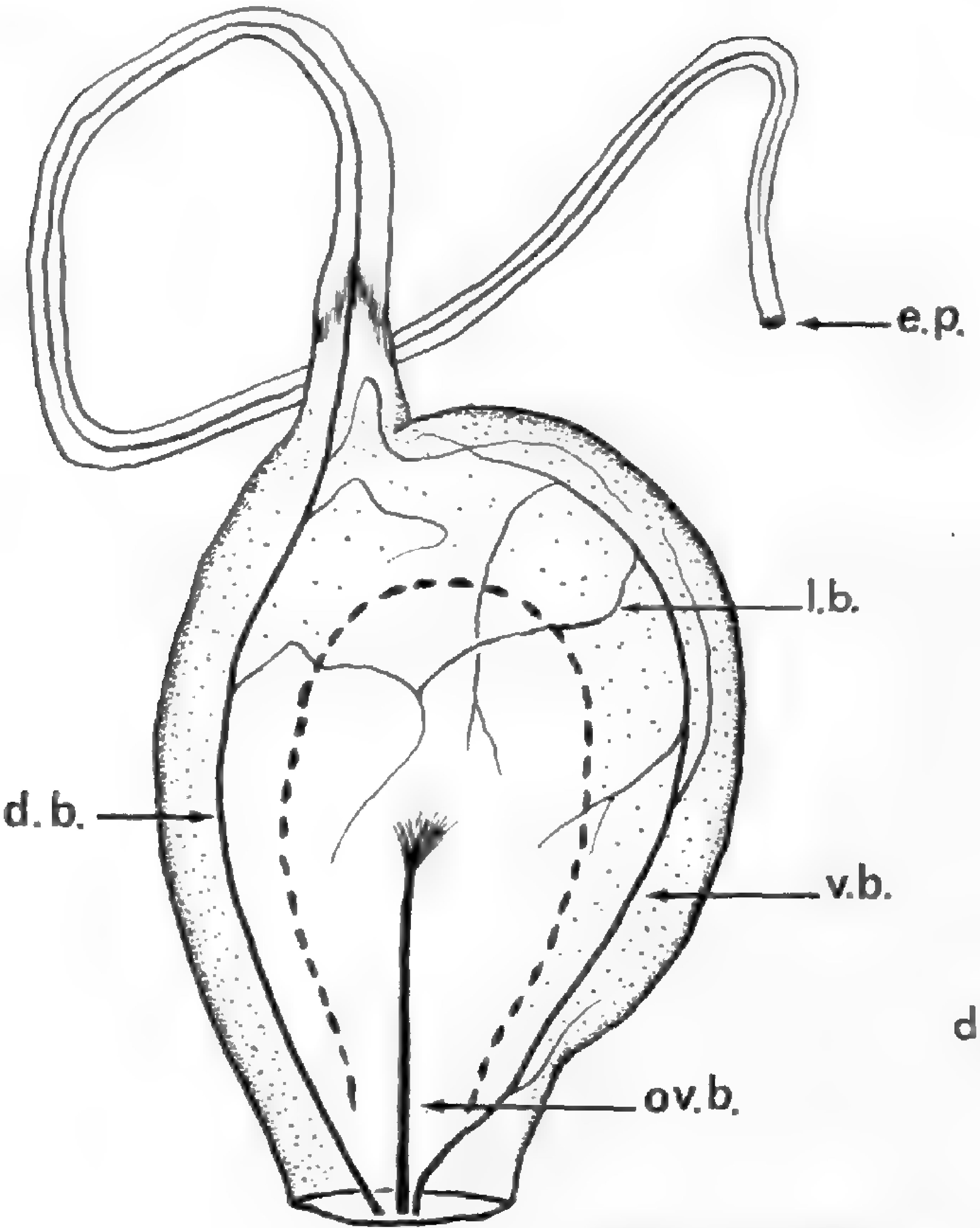


6

DICKISON, DILLENIACEAE, III



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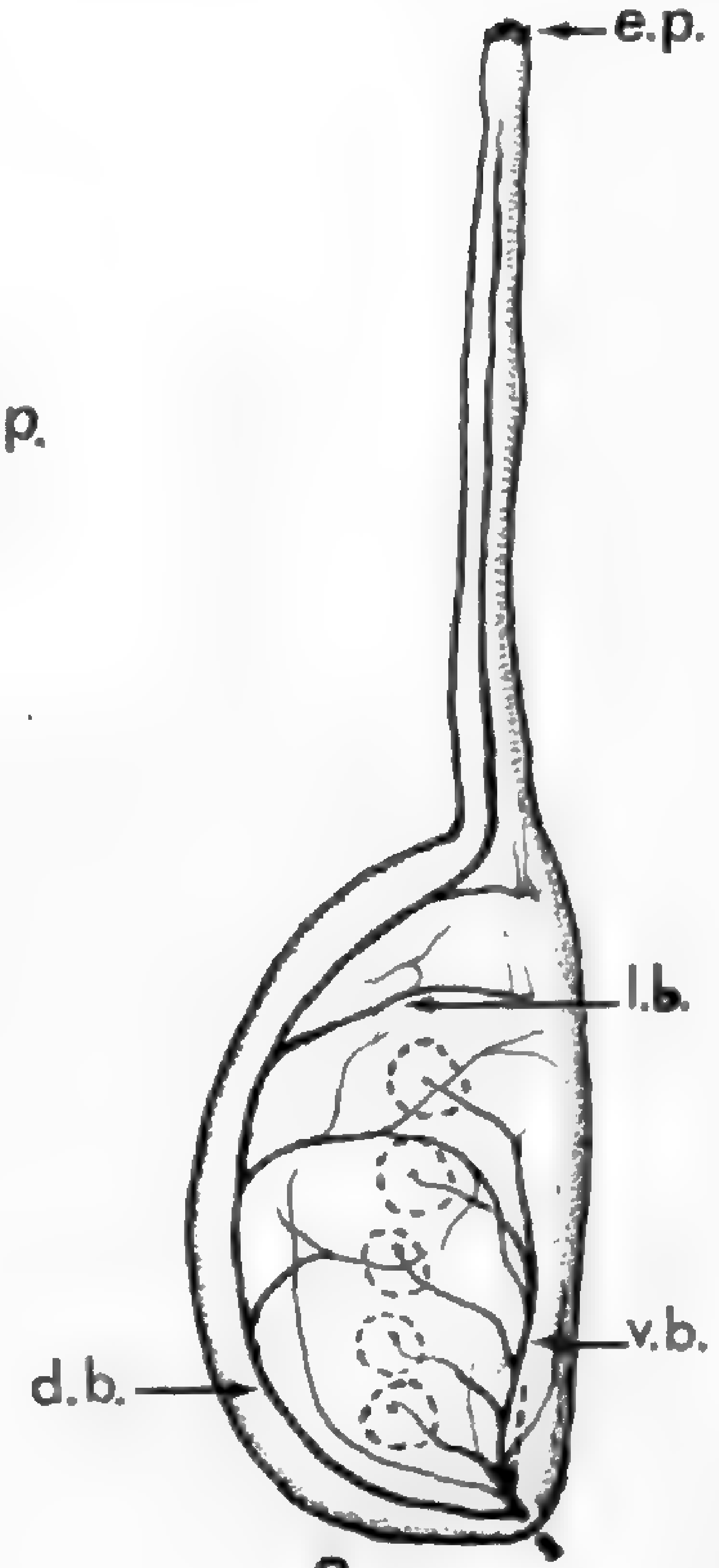

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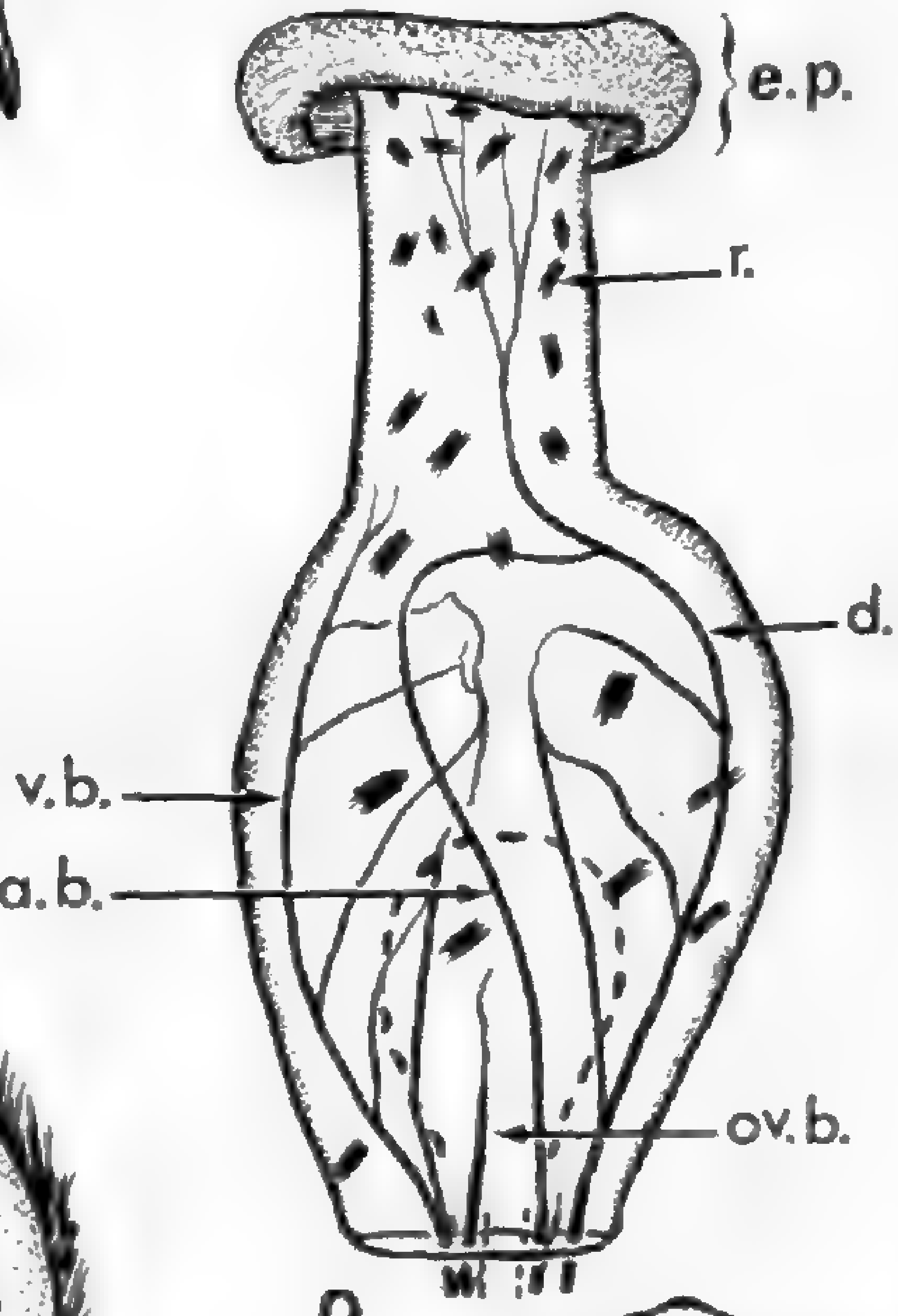

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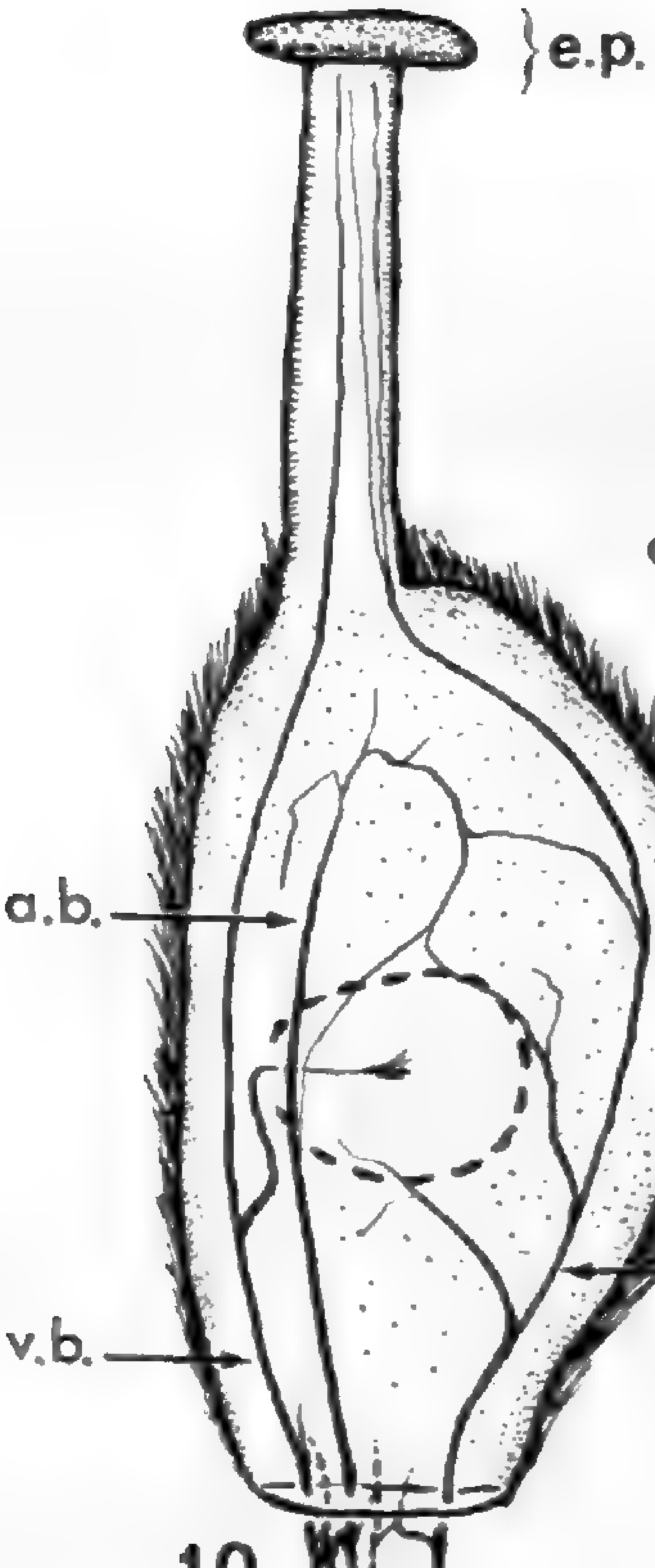

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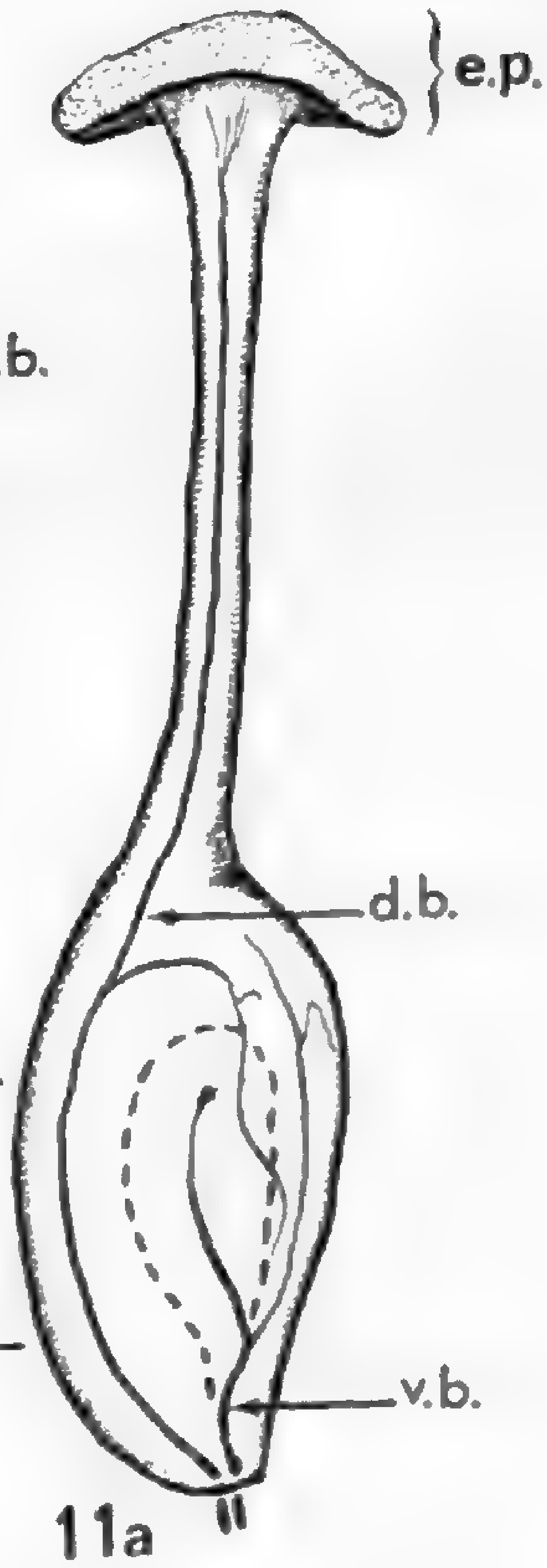

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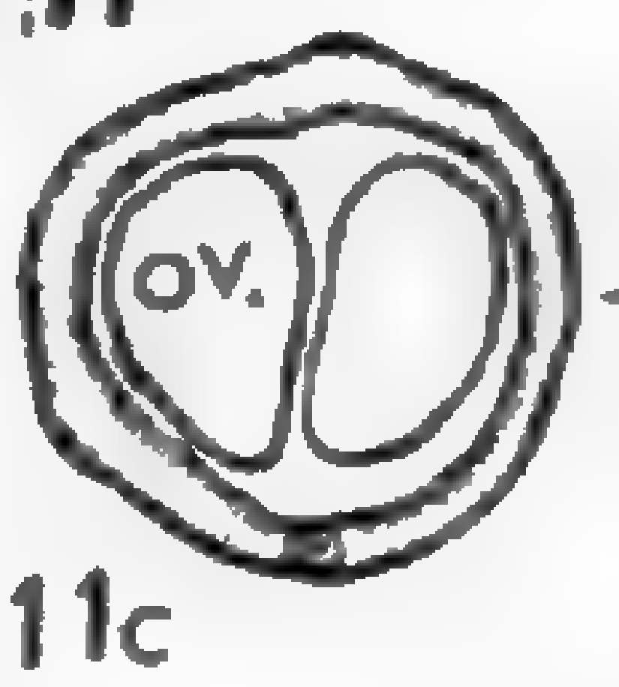
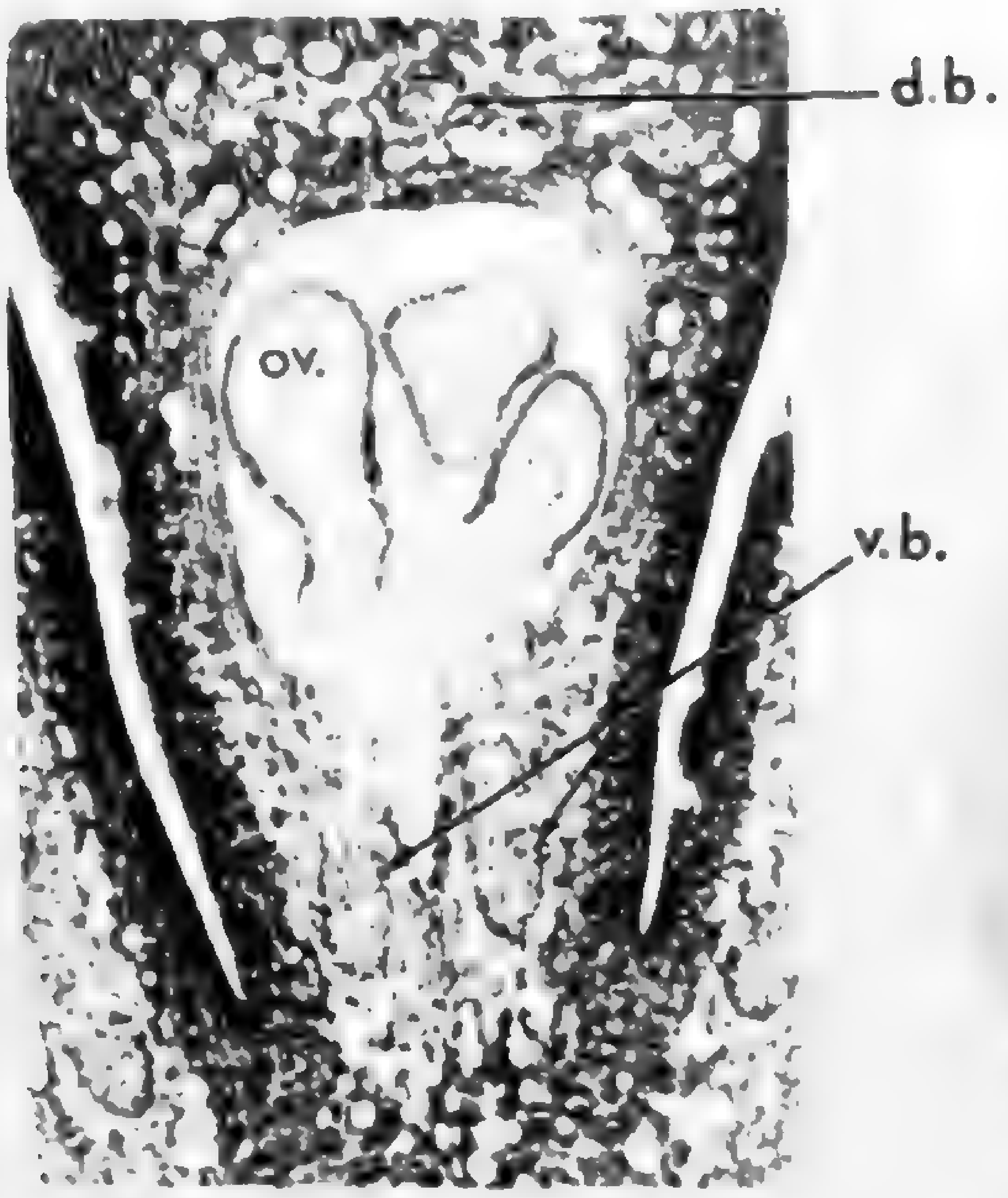


11c

11b

Dickison, Dilleniaceae, III



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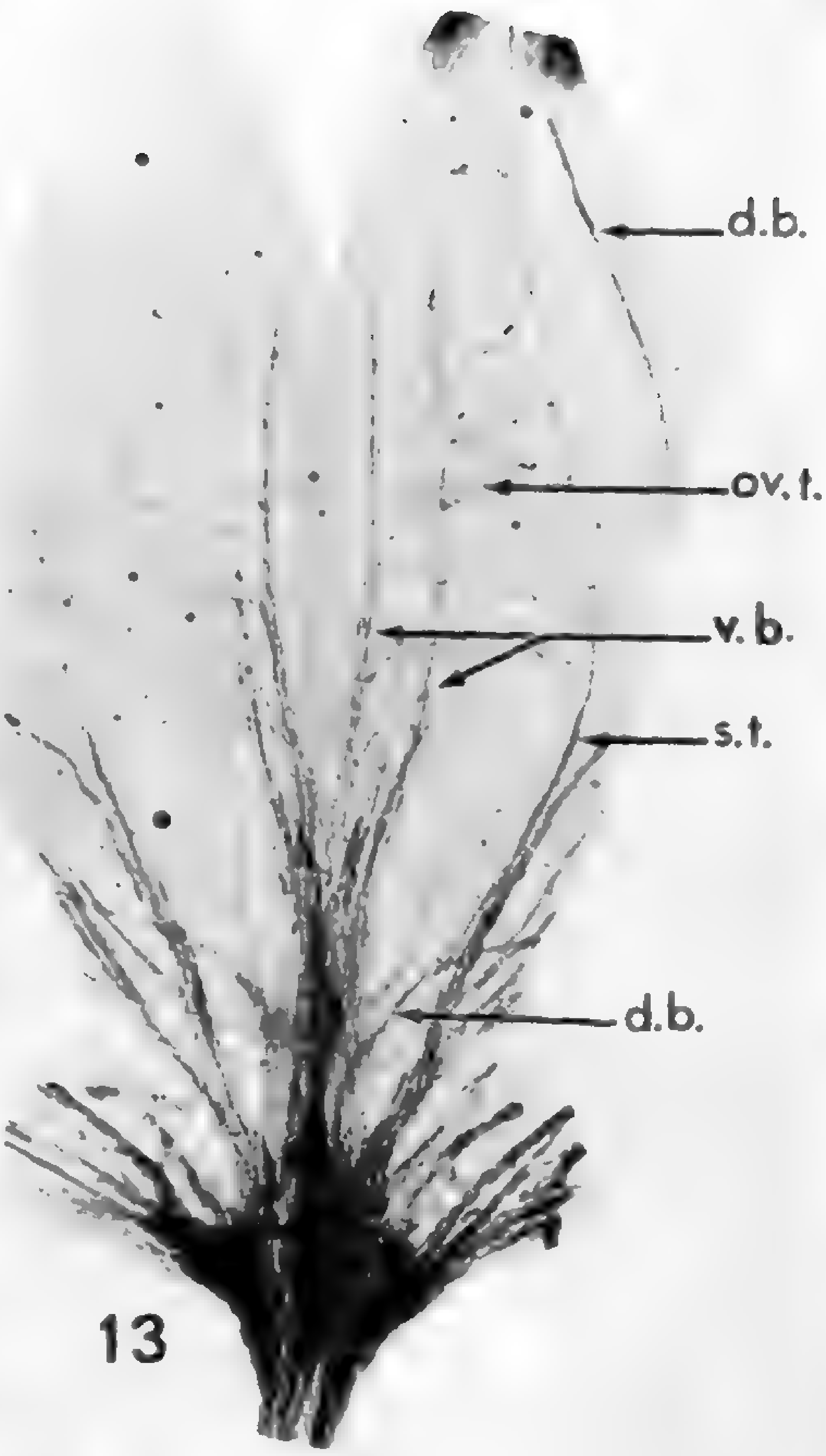

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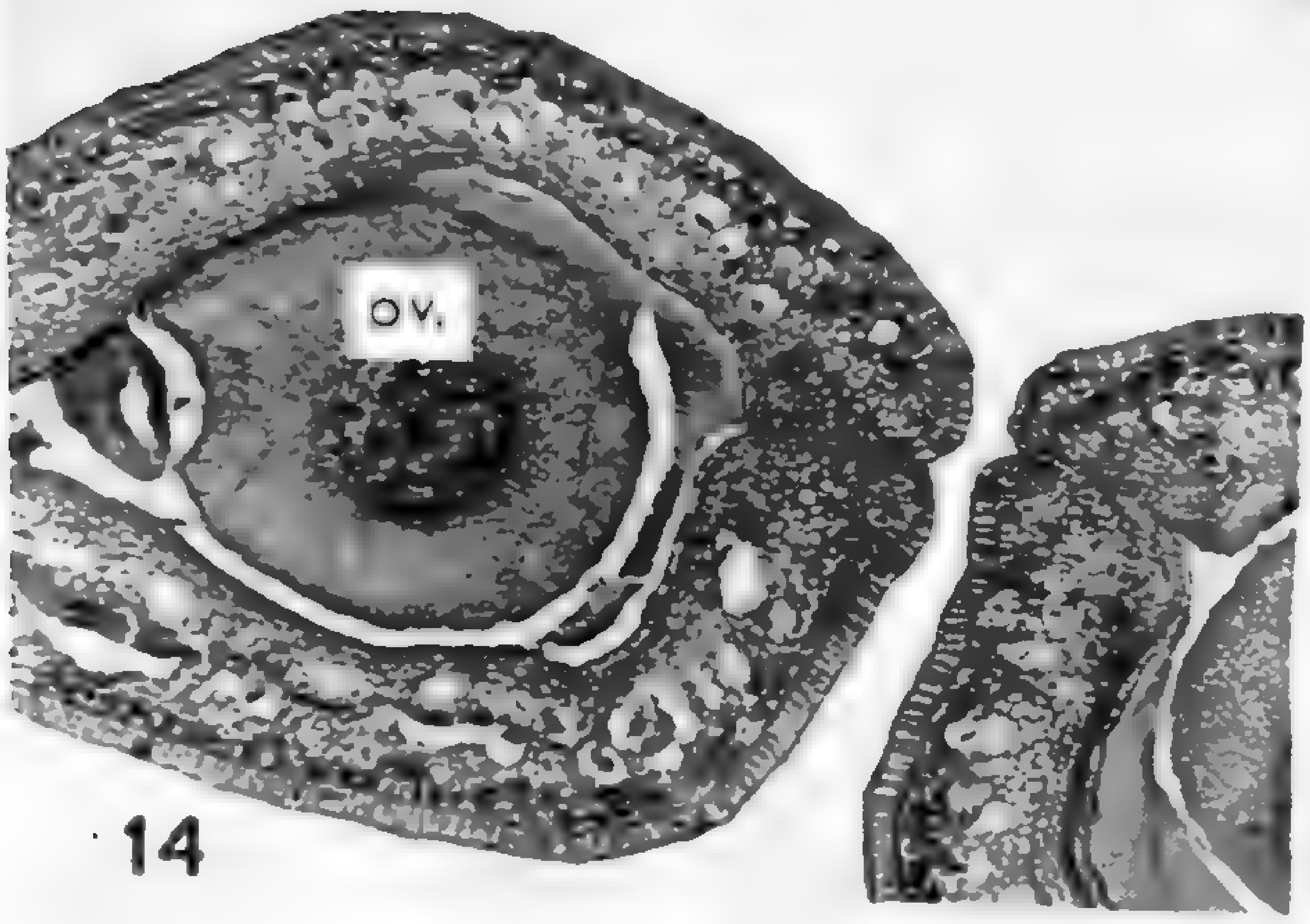

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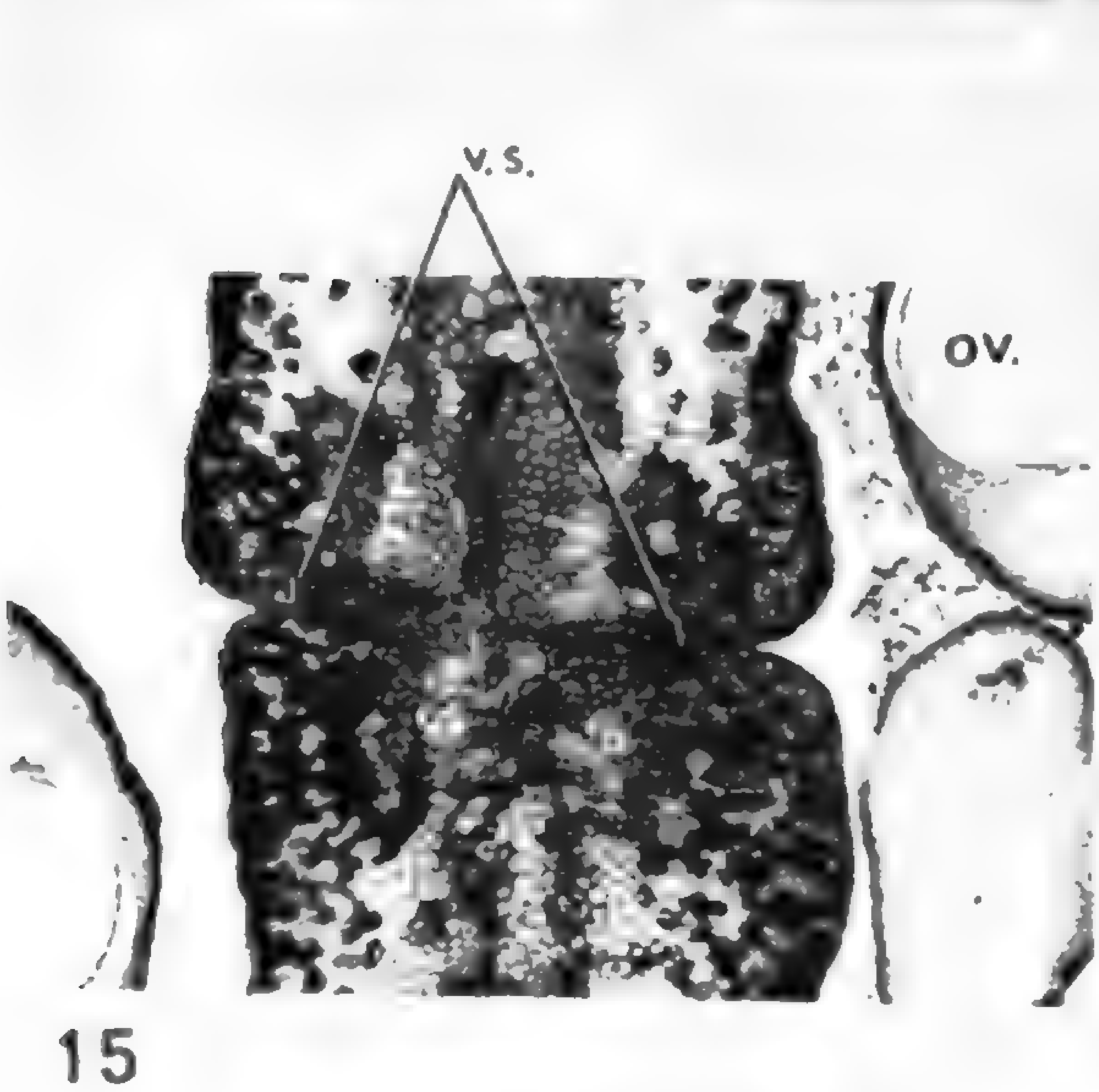

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16

REVISION OF THE GENUS NOTELAEA (OLEACEAE)

P. S. Green

The genus *Notelaea* is endemic to eastern Australia and Tasmania, although it was first described from a plant under cultivation in France, introduced from what is known today as New South Wales. As treated here the genus contains nine species only; those described from outside Australia being excluded and disposed of in other genera.

Seven species are very closely related and much confusion has existed in their recognition and differentiation. A critical redetermination of many misnamed specimens has helped to clarify the species' limits and the examination of a large range of herbarium material, together with a very limited, but invaluable, experience of some of the plants in the field, has led me to believe that the recognition of these seven taxa is justified at the rank of species. However, experimental and field studies, if and when they are carried out, may modify the rank at which the taxa are finally classified. The other two species, although related, are sufficiently distinct to warrant the establishment of two new sections for their accommodation; their differences from the seven species mentioned seem insufficient to justify generic separation.

Hybridization between closely related species has not been proved experimentally but the combination of characters exhibited by a very few specimens can only be explained on the assumption that this has occurred. Under *Notelaea microcarpa* mention is made of a putative hybrid with *N. ovata*, and *N. microcarpa* is thought to have introgressed with *N. longifolia* on occasion, as shown, for example, by the variation in a relict population near Dorrigo, New South Wales (represented by the range of specimens in *Green 1519 a–l*) cited below under *N. longifolia* f. *intermedia*.

Field experience of two or three species was made possible for me by funds from the Arnold Arboretum (where I had the honor of being a staff member at the time) together with National Science Foundation Grant No. GB1545, and most grateful acknowledgment is made for this generous support. I should also like to express my sincere thanks to Mr. L. A. S. Johnson of the Royal Botanic Gardens, Sydney, for much information gleaned from his knowledge of the species in the field and especially for the many valuable annotations he attached to the herbarium material when it was sent on loan from Sydney; to Messrs. A. G. Floyd and H. C. Hayes of the Forestry Commission of New South Wales, Coff's Harbour, for their generous help with time, transport, and local knowledge of the species in northern New South Wales; and to Miss Mary Grierson and Miss Judy Appenzeller for the maps and figures. Finally, I should like to record my grateful appreciation to the directors and curators of the cited herbaria for the loan of material or facilities for study. All the material

cited has been examined, and the respective herbaria are indicated by the abbreviations published in the *Index Herbariorum*, Ed. 5, 1964.

Notelaea Ventenat, Choix de Plantes 25. *t.25* 1804; R. Brown, Prodr. 523. 1810; Endlicher, Gen. Pl. 572. 1838; A. DC. in DC. Prodr. **8**: 290. 1844; Bentham, Fl. Austral. **4**: 298. 1868 & in Bentham & Hooker f. Gen. Pl. **2**: 678. 1876; C. Moore, Handb. Fl. New S. Wales 320. 1893; Knoblauch in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 10. 1892; F. M. Bailey, Queensl. Fl. **3**: 972. 1900; Johnson, Contr. New S. Wales Natl. Herb. **2**: 411. 1957.

Rhysospermum Gaertner f. Fruct. **3**: 232. *t.224. fig. 2.* 1807.
Postuera Rafinesque, Sylv. Tellur. 10. 1838.

Evergreen shrubs or small trees. *Leaves* opposite, simple, glabrous to velutinous, lamina thickish or coriaceous, entire or crenulate, venation obscure or clearly reticulate. *Inflorescence* axillary, decussate with terminal flower, from 1–3 superposed buds, bracts broadly ovate to narrowly lanceolate, early deciduous. *Flowers* hermaphrodite. *Calyx* 0.3–1.2 mm. long with 4 more or less triangular lobes 0.1–1 mm. long. *Corolla* of 4 petals joined in two pairs at the base of the stamens, the pairs free, or only just joined at the base (in *N. ligustrina*), lobes 1.2–2.5 mm. long, broadly ovate, rounded or more or less acute (in *N. ligustrina*), induplicate-valvate or slightly imbricate in the bud (in *N. ligustrina*), concave and enclosing the stamens, closely so and raised on a common "stalk" at maturity in *N. johnsonii*. *Stamens* 2, anthers 0.8–1.5 mm. long (0.3 mm. in *N. johnsonii* and closely invested by the corolla), filaments short 0.1–0.5 mm. long. *Ovary* triangular flask-shaped, 0.8–2 mm. long without well differentiated style, terminal stigma more or less bilobed 0.1–0.5 mm. long. *Drupe* ellipsoid to more or less globose, 5–20 mm. long by 4–16 mm. broad; mesocarp soft when ripe and purplish-black, but white, pink or red in some species; endocarp hard, 0.1–0.6 mm. thick.

TYPE SPECIES: *Notelaea longifolia* Vent.

KEY TO SECTIONS

1. Corolla lobes induplicate-valvate in the bud (FIG. 1, A & B).
    2. Paired corolla lobes and stamens sessile at maturity, the bases of adjacent pairs touching or almost touching, and surrounding the ovary; anther lobes about the same size as the connective (FIG. 2, B & C); flowers yellow, cream or white. .... NOTELAEA.
    2. Paired corolla lobes and stamens stalked at maturity, the bases of adjacent pairs separate and not surrounding the ovary, even in bud; anther lobes small in proportion to the connective (FIG. 4, D & E); flowers purplish-pink. .... MISCHOPETALA.
1. Corolla lobes imbricate in the bud (FIG. 3, B). .... LIGUSTRINA.

KEY TO THE SPECIES OF NOTELAEA

1. Venation of leaf clear and more or less reticulate above.

2. Leaf venation below raised and clear, at least as prominent or almost as prominent as that above, unless masked by a velutinous indumentum.
   3. Veins, after the primary ones, showing progressive diminution in size, coarsely reticulate, secondary veins merging with the approximately equal-sized marginal thickening to the lamina, ripe fruit broadly ovoid to subglobular, only a little longer than broad.
      4. Lamina narrowly ovate to narrowly lanceolate, (3.5–)6–10(–16) cm. long, margin usually entire, except for juvenile or sucker growth, base acute or obtuse and long acuminate into the decurrent base, reticulation below usually at least a little less prominent than that above, with primary veins usually curving forward slightly towards the leaf apex before dividing, even in the broadest leaves; inflorescence usually borne in the axil of the subtending leaf, the lowest pedicels arising in the lower half of the inflorescence, often near the base; shrub or small tree to 7 m. high. .... 1. *N. longifolia.*
      4. Lamina broadly ovate or ovate to, occasionally, narrowly ovate (rarely lanceolate or elliptic), (2.5–)3–9(–14) cm. long, margin more or less crenulate, base rounded, although some of the largest and narrowest leaves with acute leaf bases, but even then with distinct if sometimes shallow and irregular crenulations, reticulation below usually as prominent as that above with primary veins more or less straight until they divide, not curving forward towards the leaf apex; inflorescence usually a little above the axil of the subtending leaf, pedicels often arising only in the upper half of the inflorescence; low shrub to 1 m. high. .... 2. *N. ovata.*
   3. Veins, after the primary ones, all more or less evenly, finely, and prominently reticulate, secondary ones not clearly merging with the marginal thickening to the lamina; ripe fruit ellipsoid-ovoid, clearly longer than broad. .... 3. *N. venosa.*
2. Leaf venation below usually more obscure than above, unless masked by a velutinous indumentum.
   5. Outline of leaves lanceolate or elliptic, (1–)1.5–5 cm. broad.
      6. Reticulation of veins raised and more or less prominent above, the surface minutely but prominently punctate below; inflorescence 1–3 cm. long; paired corolla lobes, with stamens, sessile at maturity; fruit 7–9 mm. long; central and northern east Queensland. .... 4. *N. punctata.*
      6. Reticulation of veins not raised above, often obscure, the surface below not prominently punctate; inflorescence 4–8 cm. long; paired corolla lobes, with stamens, stalked at maturity (FIG. 4, D & E); fruit 18–20 mm. long; limited area of northeasternmost New South Wales and southeasternmost Queensland. .... 9. *N. johnsonii.*
   5. Outline of leaves narrowly or very narrowly lanceolate to linear, (0.2–)0.3–1.5(–3) cm. broad.
      7. Venation of upper leaf surface more or less clear and raised, the primary veins making an angle of 15°–30° with the midrib; lamina (3–)5–15(–30) mm. broad; Queensland and the central and northern western-slope country of New South Wales. .... 5. *N. microcarpa.*
      7. Venation of upper leaf surface more or less obscure, except for

slightly raised primary veins which make an angle of about 40° with the midrib; lamina (2–)3–8(–14) mm. broad; central tablelands country of New South Wales. .... 7. *N. neglecta.*

1. Venation of leaf obscure above.
  8. Leaves linear to narrowly lanceolate, more than 7, usually at least 10 times as long as broad; ripe fruit 5–7 mm. long.
    9. Breadth of leaf (1.5–)2–5(–7) mm., venation totally obscure; inflorescence 4–10 mm. long; southern Queensland and northern tablelands country of New South Wales. .... 6. *N. linearis.*
    9. Breadth of leaf (2–)3–8(–14) mm., venation obscurely visible; inflorescence 10–20 mm. long; central tablelands of New South Wales. .... 7. *N. neglecta.*
  8. Leaves broadly to narrowly lanceolate, up to 7 times as long as broad; ripe fruit 8–20 mm. long.
    10. Primary and other veins obscure above and below, leaves (2–)3–6(–8.5) cm. long; inflorescence 1.5–3.5 cm. long; petals more or less acute (FIG. 3, A); fruit 8–12 mm. long, varicolored; Tasmania, Victoria, and southeasternmost New South Wales. .... 8. *N. ligustrina.*
    10. Primary veins just visible below, leaves (4–)7–10(–12) cm. long; inflorescence 4–8 cm. long; petals rounded, enveloping the stamens (FIG. 4, D & E); fruit 18–20 mm. long, bluish-black; northeasternmost New South Wales and southeasternmost Queensland. .... 9. *N. johnsonii.*

Notelaea sect. Notelaea

Sect. *Eunotelaea* Knoblauch in Engler & Prantl, Nat. Pflanzenfam. **4**(2): 10. 1892.

The largest and most widespread section, characterized by the induplicate-valvate aestivation of the corolla. It is closely related to sect. LIGUSTRINA which, however, exhibits imbrication of the corolla in the bud. In most species the ripe fruit is invariably purplish-black in color but in *Notelaea punctata* it has been recorded as "varicolored," in *N. linearis* as "white and translucent" or "rich blue" and in *N. punctata* as white and red, as well as dark purple to blackish.

1. **Notelaea longifolia** Ventenat, Choix de Pl. 25. *t.25.* 1804; Desfontaines, Hist. Arbr. **1**: 120. 1809; R. Brown, Prodr. 523. 1810; Sprengel, Syst. Veg. **1**: 35. 1824; A. DC. in DC. Prodr. **8**: 291. 1844; Ettingshausen, Blatt-Skel. Dikot. 69. *t.26, fig. 9.* 1861; Reichenbach f. Neuholl. Pfl. Amelia Dietrich 9. 1866; Bentham, Fl. Austral. **4**: 229. 1868; F. Mueller, Fragm. Phytogr. Austral. **8**: 43. 1873, & Syst. Census Austral. Pl. 92. 1882; F. M. Bailey, Synop. Queensl. Fl. 303. 1883; F. Mueller, Key Syst. Vict. Pl. **2**: 39. 1885, & **1**: 357. 1887–8; F. M. Bailey, Queensl. Woods, 85. 1888 & 97. 1889; F. Mueller, Second Syst. Census Austral. Pl. 156. 1889; Maiden, Useful Native Pl. Austral. 579. 1889; F. M. Bailey, Cat. Pl. Queensl. 29. 1890; C. Moore, Handb. Fl. New S. Wales 320. 1893; F. M. Bailey, Queensl. Fl. **3**: 973. 1900;

Dixon, Pl. New S. Wales 214. 1906; Guilfoyle, Austral. Pl. 40 [1911]; F. M. Bailey, Comprehensive Cat. Queensl. Pl. *311, 319. fig. 292.* [1913]; Maiden & Betche, Census New S. Wales Pl. 172. 1916; Ewart, Handb. Forest Trees Vict. Foresters 407. 1925; Francis, Austral. Rain-Forest Trees 327. 1929; Domin, Bibliot. Bot. 22(89) (Beitr. Fl. Pflanzengeogr. Austral. 1(3): 512): 1066. 1929; Ewart, Fl. Vict. 941. 1930; Audas, Native Trees Austral. 242 [1935]; Anderson, Trees of New S. Wales, ed. 2. 132, 271, 338. 1947; Bean in Chittenden, Dict. Gard. 3: 1379. 1951; Beadle, Evans & Carolin, Handb. Vasc. Pl. Sydney Distr. & Blue Mts. 348. 1963.

Evergreen shrub or small tree up to 7 m. tall (sometimes to 14 m. *fide* Anderson, *loc. cit.*), bark finely fissured, finely pustular to fairly smooth, mid to dark gray-brown, blaze granular; young stems densely puberulent or velutinous to glabrous. *Leaves* glabrous, glabrate, puberulous or velutinous above or below; petioles glabrous to velutinous, (2–)5–15(–25) mm. long; lamina lanceolate, narrowly ovate or elliptic, occasionally narrowly lanceolate or ovate, (3.5–)6–10(–16) cm. long by (1–)2–3.5(–5.5) cm. broad; margin somewhat thickened, entire or obscurely and somewhat irregularly crenulate; apex acute or long acute, finely pointed if undamaged; base acute to obtuse, long acuminate into the petiole; venation reticulate and raised above and below, except when obscured if densely velutinous, veins below usually a little less prominent than those above, (5–)6–8(–10) primary veins per side arising at an angle of 40°–70° with the midrib, usually curving forwards slightly towards the apex before branching, even on the broadest leaves, basal pair of primary veins usually arising at an acute angle in the decurrent base of the lamina. *Inflorescence* axillary, 1(–2) per axil, decussate, lowest pedicels usually in the lower half, often near the base, glabrous or puberulous, often minutely so and scattered, 1–2.5 cm. long, lengthening after anthesis, (5–)7–11(–13)-flowered; upper bracts 1–2 mm. long, thin, ovate to lanceolate, puberulous or glabrous and minutely ciliolate, early deciduous; basal pair thick, pubescent to glabrous (in northeastern plants), 1–3 mm. long, acute-acuminate, deciduous except for the persistent fused basal portion. *Flowers* hermaphrodite, yellow or pale yellow; pedicels 1–4 mm. long, accrescent in fruit. *Calyx* glabrous, 0.5–1 mm. long with 4 more or less triangular lobes, often acutely pointed, 0.5–0.8 mm. long. *Corolla* induplicate-valvate, lobes 4, 1.5–2.5 mm. long, in pairs joined in the lower half with the filament, concave. *Stamens* 2, 1–2 mm. long, more or less enclosed within the concave petals; anthers 1–1.5 mm. long with a distinct terminal appendage 0.2–0.3 mm. long; filaments short, 0.5 mm. long. *Ovary* flask-shaped, 1.2–1.5 mm. long, tapering into a style about 0.5 mm. long with 2 short stigmatic lobes 0.2 mm. long. *Drupe* ovoid, dark purple or bluish black, 1–1.6 cm. long by 0.8–1.2 cm. broad; endocarp hard, pointed ovoid, 8–12 mm. long by 5–8 mm. broad, 0.3–0.5 mm. thick.

Notelaea longifolia is the best known and most widespread species of the genus, with a distribution stretching from the area of Bateman's Bay in southern New South Wales to the southern part of the Wide Bay district of Queensland. A number of formal taxonomic varieties have been described but the most striking, var. *velutina*, is here transferred to *N. microcarpa* (see below under that species). When this is done, and a large number of specimens are critically redetermined, especially after the careful delimitation of *N. ovata, N. venosa, N. punctata* and *N. microcarpa,* one is left with a far more homogeneous species in which the only obvious variation is that in degree of pubescence. When the localities for the specimens are plotted on a map, together with a symbol to indicate their hairiness in three simple categories of pubescent, glabrate or glabrous, it is found that *N. longifolia* occupies a coastal strip and exhibits a cline in the degree of pubescence, with velutinous or pubescent plants in the south and glabrous plants in the north (MAP 1). The southernmost specimens are most densely hairy, often velutinous, while around Sydney the amount of pubescence varies greatly; often densely velutinous and only slightly velvety specimens being found in the same area (e.g. *Johnson & Constable* NSW 52347 & 52348 from Little Forest, 7 miles WNW. of Milton, 10 Sept. 1960). In northernmost New South Wales and in Queensland, *N. longifolia* is quite glabrous, and in the intervening area the leaves of the specimens examined are all glabrate with a fine puberulence on the young stems and bud scales only. Considerable thought has been given to the question of whether this cline should be divided taxonomically; clearly any division will be artificial, but it is believed that names would be useful, for frequently it may be convenient to refer to a plant exhibiting one of the extremes of pubescence. This then raises the question of the taxonomic rank to be employed. None of the formal infraspecific ranks are particularly suitable yet the appropriate biosystematic term of clinodeme expressly excludes a nomenclatural connotation. Diagnosis, in this case, is dependent on variation in one character only, that of degree of pubescence, so although a distinct distributional pattern in this character exists, the ranks of subspecies and variety seem of too great a consequence so the conventional rank of form is chosen and appropriate names are published below. (Incidentally, the use of variety would compel the employment of Domin's highly inappropriate epithet of *decomposita* for the glabrous plant from the northern end of the range — see below.)

In annotations on the Sydney herbarium covers L. A. S. Johnson has summarized the habitat occupied by *Notelaea longifolia*: "Sometimes found within rainforest and often on rainforest margins but also commonly in eucalypt forest, though not on the poorest siliceous soils. In the poor Hawkesbury sandstone country it is found chiefly in the gullies or near salt-water estuaries (often on rocky slopes here) where there is some enrichment of the soil nutrients." Also, "in gullies in wet sclerophyll forest — sometimes in patches of rainforest."

In addition to being the most widespread species, *Notelaea longifolia* also appears to be central in its relationship to the others. Perhaps it represents the descendants of the basic stock from which the other species

MAP 1. Distribution of *Notelaea longifolia* and forms.

have evolved, for each of the other species of sect. NOTELAEA appears very closely related. Where they meet, hybridization seems to take place occasionally with *N. microcarpa*, a species characteristic of the western-slope country. The distribution of those specimens of possible hybrid origin examined in this revision is indicated on MAP 1.

Forma **longifolia**

"*Olea apetala*" Andrews, Bot. Rep. **5:** *t.316.* 1803, *non* Vahl (1794).
Rhysospermum nervosum Gaertner f. Fruct. **3:** 232. 1807.
R. ellipticum Gaertner f. *loc. cit. t.224, fig. 2.* 1807.
Notelaea rigida Desfontaines, Hist. Arbr. **1:** 120. 1809.
Postuera longifolia (Vent.) Rafinesque, Sylv. Tellur. 10. 1838.
Notelaea "ovata" Endlicher, Icon. Gen. Pl. xi. *t.55.* 1838, *non* R.Br. (1810); Lindley, Veg. Kingdom 616. *fig.* 1846.
N. nervosa (Gaertner f.) Steudel, Nomencl. ed. 2. **2:** 198. 1841; A. DC. in DC. Prodr. **8:** 291. 1844.
? *N. laurifolia* Kunth, Index Sem. Hort. Berol. 12. 1846, & in Walpers, Repert. Bot. Syst. **6:** 742. 1847.
N. longifolia Vent. var. *candolleana* Domin, Bibliot. Bot. **22**(89) (Beitr. Fl. Pflanzengeogr. Austral. **1**(3): 514): 1068. 1929.
N. longifolia Vent. var. *rigida* (Desf.) Domin, *loc. cit.* 1066. 1929.
N. longifolia Vent. var. *typica* Domin, *loc. cit.* 1929.

Young stems, petioles, leaves (especially below) and inflorescence rachides more or less densely pubescent to velutinous. The pubescence of the leaf sometimes short and inconspicuous but more or less persistent, at least below.

SELECTED EXSICCATAE. **New South Wales.** Bateman's Bay, June 1906, *Boorman* (NSW 33491); Boyne State Forest, NE. of Nelligen approx. 180 m. alt., 22 Nov. 1966, *Pullen 4203* (CANB 161997–9); Currawon State Forest, near Bateman's Bay, June 1959, *L.J.W. & J.G.T. 3663* (BRI 35461); Lake Burrill, S. of Milton, 12 Jan. 1937, *Hadley 2404* (*Rodway 6239*) (K, NSW 33416); near Canjola, South Coast, 6 Dec. 1937, *Hadley 2620* (*Rodway 6236*) (K, NSW 33412); Comerong Is., Shoalhaven R., 18 Sept. 1932, *Rodway 880* (*6231*) (K, NSW 33408); Cabbage-tree Creek, against the road between Nowra & Currarong, 22 May 1964, *Willis* (MEL 19628); gully near Barber's Creek (Tallong), *Forsyth & Hamilton* (NSW 33483); Illawara ("Sydney woods"), *Macarthur 174* (K, syntype of var. *candolleana*; BM, isosyntype); Cronulla, Oct. 1919, *Cheel* (NSW 33528); Sydney, *Clowes* (K, syntype of var. *candolleana*); Port Jackson, 1803, *R. Brown* ("*2849*") (BM, K); Manley Beach, Nov. 1863, *Wilhelmi* (LE, P); The Spit, Middle Harbour, Sydney, 14 Nov. 1949, *Constable* (K, NSW 11316); Hornsby, May 1917, *Blakely* (A, BRI 7934, C, NSW 33453); near Harry's R., central Cox's R., S. of Blue Mts., 23 Dec. 1951, *Whaite 1096* (K, NSW 22139); Little Wheeny Creek to Kurrajong Heights, about 350 m. alt., 10 Aug. 1953, *Johnson* (K, NSW 24963); Pulbah Island, Lake Macquarie, 27 Oct. 1941, *Messmer, Bryce & Rupp* (NSW 33447); 6 miles N. by W. of Raymond Terrace, 1 May 1960, *Story 7275* (CANB 80051); Flyer's Creek, near Buladelah, Apr. 1924, *Rupp 21* (NSW 33555); Crawford R., near Buladelah, Oct. 1902, *Cheel* (NSW 33442); Wallamba State Forest, near Nabiac, 12 Aug. 1955, *McDonald* (NSW 33516); Waukivory Creek, Gloucester, Sept. 1897, *Maiden* (NSW 33500); 16 miles W.

of Dungog, 5 May 1960, *Story 7346* (CANB 80364); 10 miles NNE. of Ravensworth, 23 March 1960, *Story 7145* (CANB 80379). Without locality: 1770, *Banks & Solander* (BM, E, ? isotypes of *Rhisospermum nervosum*); Hb. Hornemann, ded. Desfontaines (C, ? isotype of *N. rigida*); *Caley* (BM, G).

Cultivated. AUSTRALIA: Botanic Gardens, Sydney, Feb. 1917, *Blakely* (NSW 33549); Botanic Gardens, Adelaide, 20 Dec. 1930, *J. F. Bailey* (K); Botanic Garden, Hobart, 31 Jan. 1932, *White 8246* (A, BRI 7944); Botanic Gardens, Melbourne, *F. Mueller* (BM, MEL 19623). FRANCE: ex hort. Cels, *ex herb. Ventenat* (G, lectotype) & *ex herb. Desfontaines* (FI, ? isolectotype); Hort. Paris, Orangerie, 23 Oct. 1819, *ex herb. J. Gay* (K, topotype of and labelled as *N. rigida* Desf. Arb.); Jardin des Plantes de Paris, 1818, *Perrottet* (G). GERMANY: Hort. Berlin, without collector (C). GREAT BRITAIN: Hort. Kew, 1794, without collector (BM); Isles of Scilly, Tresco Abbey, 18 Sept. 1953, *Dorrien-Smith* (K).

This form is distinguished from the others by the more or less densely pubescent or even velutinous indumentum on the young stems, leaves, and inflorescence rachides. The type, a cultivated specimen, is distinctly hairy (although less pubescent than much of the wild material) and, at the turn of the 18th century, was almost certainly introduced from the Port Jackson area, from which most of the early introductions of Australian plants were made.

Typification has not been straightforward. In all probability *Notelaea longifolia* was originally described by Ventenat from a living plant grown in the garden of M. Cels and it is possible that no type specimens, as we know them today, were prepared. However, there is no doubt about the identity of the species for the protologue was beautifully illustrated and, thanks to the help of M. Gilbert Bocquet of Geneva, to whom I express my thanks, I learned that a specimen from M. Cels' garden, which had been in the Ventenat herbarium, is today in the Geneva herbarium. This I have examined on loan and designated as lectotype.

Notelaea rigida was similarly described from a cultivated plant, this time from the Orangery in the Jardin des Plantes in Paris and a specimen, although collected some nine years later, has been seen in the Kew Herbarium with this origin and this name attached. The genus *Rhisospermum*, described by C. F. Gaertner, was based on fruit from the collection of Sir Joseph Banks, who accompanied Capt. Cook on the first of his famous voyages; no authentic type has been seen but there is a Banks & Solander collection at the British Museum (Natural History), with a duplicate in Edinburgh, unfortunately without fruit in both cases.

Notelaea laurifolia, described by Kunth in 1846 from a plant cultivated in the Berlin Botanic Garden, was attributed to New Zealand, but, as far as is known, none of the related New Zealand plants had been introduced at that time and the admittedly somewhat inadequate description fits *N. longifolia*. The type in the Berlin Herbarium was presumably destroyed during the war, so that the exact identity of Kunth's plant must remain uncertain until a duplicate or other authentic specimen is perhaps found elsewhere. For the present the best disposition of the name seems to be under *N. longifolia*.

The typification of the varieties described as new by Domin was more difficult at first sight but, on learning that the specimens upon which he had based his new taxa, other than those which were in his own collection, are often at Kew, and usually without annotation, the types were easily located by comparison of the labels with his protologues. *N. longifolia* var. *decomposita* is dealt with under f. *glabra* below. Var. *candolleana* is a hairy form with narrowish leaves. The reference to "Sydney woods" on the label of the Macarthur syntype seems to have been taken by Domin as a locality whereas the reference is to a timber or wood specimen, No. 174, sent from Sydney to the Paris Exhibition of 1854. Finally, var. *pedicellaris* was found to belong to *N. venosa*, under which species it is now included.

A specimen, *Cambage 2702*, collected on 15 May 1911, between Baerami and Dunman in the region of the Upper Hunter in New South Wales (NSW 33540) appears of hybrid origin with *N. microcarpa*. The leaf shape is like that of *N. microcarpa* but the fruit, which is immature, is too large for this species and looks as though it would have developed to the size normal for *N. longifolia*.

The extent to which the foliage of juvenile, sucker or other strongly growing shoots differs from that of adult plants cannot be settled with certainty from herbarium collections, unless these are specially made, but in *Notelaea longifolia* they appear to be larger and broader than usual, more markedly reticulate and with the margin crenulate. *Pullen 4203* from Boyne State Forest, New South Wales, is represented in the Canberra Herbarium by three sheets, two of which show normal adult foliage, one with fruit, while the third (CANB 161998) has large broadly ovate-lanceolate leaves, 10–13 cm. long by 4.5–5.5 cm. broad with rounded base and short petioles 2–3 mm. long. The field notes say "leaves of sterile branch larger than those of adult branches." Specimens in the Sydney Herbarium annotated as juvenile consist of unattached leaves 18–25 cm. long by 8.5–9.2 cm. broad with petioles 10–15 mm. long which, although not particularly rounded at the base, are strongly reticulate and more crenulate than usual. These specimens are: Patonga, N. bank of Hawkesbury R. near the mouth, N.S.W., Sept. 1936, *Blakely* (NSW 33449) and Bulbararing Lake, near Kincumber, N.S.W., 17 June 1905, *Maiden* (NSW 33448).

Forma **intermedia** P. S. Green, f. nov.

Caulibus junioribus et bracteis externis gemmarum minute puberulis; inflorescentiarum rachidibus minute et dissite puberulis; foliis junioribus et petiolis glabratis dinoscenda.

SELECTED EXSICCATAE: **New South Wales.** Wattagan State Forest, W. of Dora Creek, 15 Sept. 1954, *Constable* (K, NSW 30732); Port Stephens, Aug. 1911, *Boorman* (NSW 33445); Dungog to Clarencetown, 29 May 1934, *Fraser* (NSW 33443); Clarencetown, 7 Nov. 1936, *Fraser & Vickery* (NSW 33444); 16 miles ENE. of Singleton, 26 March 1960, *Story 7195* (CANB 78754, K); Port Macquarie, Oct. 1892, *Maiden* (A); Ellenborough to Long Flat, 19 Oct. 1953, *Johnson* (K, NSW 26257); Ralf's Riverlet, Nov. 1897, *Maiden* (NSW 33441); Carrai Carrai State Forest, 30 miles approx. W. of Kempsey, 11 June 1958, *Constable*

(K, holotype; BM, NSW 46234, isotypes); Nambucca Heads, June 1910, *Boorman* (NSW 33440); Bellingen, Dec. 1938, *Hewitt* (NSW 33437); Dorrigo State Forest, about 750 m. alt., 4 Oct. 1930, *White 7513* (BRI 7937); Coff's Creek, Coff's Harbour, 4 Nov. 1963, *Hayes* in *Green 1515* (A, K); Glenugie Peak, 6 Nov. 1963, *Green 1525* (A); Brickmaker's Creek, 4 miles SE. of Ramornie Crossing, July 1922, *Blakely & Shiress* (NSW 33476); Smith's Creek, 7 miles NE. of Ramornie Crossing, July 1922, *Blakely & Shiress* (NSW 33473); Coal Ridge, 10 miles N. of Ramornie Crossing, July 1922, *Blakely & Shiress* (NSW 33472); Harwood Is., Clarence R., 10 Feb. 1922, *Helms 458* (A, C); Ballina, Sept. 1892, *Bäuerlen 853* (A, NSW 33464, Z); Dunoon Road, 7 Nov. 1963, *Hayes & Floyd 1* (A); Casino, Dec. 1916, McAuliff (NSW 33468–33470); Koyogle, Dec. 1917, *McLean* (G, NSW 33467); Drake, Oct. 1901, *Boorman* (NSW 44087); Acacia Creek, via Killarney, May 1905, *Dunn 112* (NSW 44088).

Cultivated. AUSTRALIA: Garden Palace Grounds, Sydney, Apr. 1898, *Camfield* (NSW 44057); Botanic Gardens, Melbourne, *F. Mueller* (MEL 19624).

Introgression between *Notelaea longifolia* f. *intermedia* and *N. microcarpa* var. *velutina* appears evident from the small population of *Notelaea* I examined on 5 Nov. 1963 adjacent to the Nymboida River near Dorrigo, New South Wales. Specimens were collected from each of the small trees seen, *Green 1519 a–l* (A), which exhibit a considerable degree of intermediate variation in leaf shape, veining, and pubescence. It is suggested that in the not too distant past, with the felling of the forest and establishment of agriculture, there has been considerable ecological upheaval in this area and that *N. longifolia* and *N. microcarpa*, which were formerly separated, came into contact. Hybridization between f. *intermedia* and *N. microcarpa* seems likely for a few other intermediate collections from New South Wales which are cited here.

Paddy's Land State Forest, about 900 m. alt., 12 Apr. 1955, *Turner 39* (NSW 33535); Unumgar State Forest, 13 March 1963, *Jones 2370* (CANB 136002); & near Mt. Lindsay, Dec. 1943, *Jones* (BRI 7924); and from the Moreton District of Queensland: the Ranch, foot of Wilson's Peak, 17 Jan. 1933, *Michael 1983* (BRI 7920, NSW 33532).

Forma **glabra** P. S. Green, f. nov.

Caulibus junioribus, foliis, bracteis externis gemmarum et inflorescentiarum rachidibus manifeste glabris.

Notelaea reticulata A. DC. in DC. Prodr. **8**: *291*. 1844; Ettingshausen, Blatt-Skel. Dikot, 69. *t.22*, *fig*. 5. 1861.

N. longifolia Vent. var. *decomposita* Domin, Repert. Sp. Nov. **12**: 96. 1913 & Bibliot. Bot. **22**(89) (Beitr. Fl. Pflanzengeogr. Austral. **1**(3): 514): 1068. 1929.

SELECTED EXSICCATAE: **Queensland.** MORETON DISTRICT: Mouth of Currumbin Creek, 7 Nov. 1929, *White 6509* (BRI 7931, holotype; A, isotype); Tamborine, 21 Feb. 1963, *W. T. Jones 2346* (CANB 136129); Stacks Creek, Logan R., 2 Dec. 1931, *Michael 1934* (BRI 7938); near Beenleigh, about 1 mile along Barr's Road, 4 Nov. 1964, *L. S. Smith 12238* (BRI 64517–9, K) & *12239* (BRI 64522–3); Goodna (Woogaroo Creek), Dec. 1916, *White* (BRI 9701, NSW 33462); Taylor Range, 15 July 1943, *Clemens 42465* (A); Brisbane River, *F. Mueller* and *Hill & F. Mueller* (K, syntypes of var. *decomposita*) & Apr. 1876, *Bailey* (BRI 7935, K); Ithaca Creek, Brisbane, 30 Oct. 1949, *White 13149* (BRI 42314); between Brisbane and Redcliffe, bank of South Pine R., 16 Dec. 1930, *Hubbard 5499* (BRI 7922; K); Moreton Bay, Sept. 1829, *A. Cunningham* (G, type of *N. reticulata*; K, isotype) & islands, Moreton Bay, Sept. 1829, *A. Cunningham 8* (A, BM, K, ? isotypes of *N. reticulata*); at the creek of Mr. Archer's Station (E. of Kilcoy), 15 Sept. 1843, *Leichardt* (NSW 33459); Eumundi, Nov. 1892, *Simmonds* (A); Noosa Heads, 26 May 1951, *Johnson* (NSW 33460). WIDE BAY DISTRICT: Lake Cootharaba, *Keys* (BRI 7910 & 7930); Imbil, March 1918, *Weatherhead 393* (BRI 7933).

New South Wales. Dunoon, 7 Nov. 1963, *Green 1527* (A, K); mouth of Brunswick R. by Pacific Highway, Brunswick Heads, 30 May 1964, *Schodde (& Hayes) 3549* (CANB 135634–5); Tweed Heads, Nov. 1903, *Maiden & Boorman* (NSW 33463).

Cultivated. AUSTRALIA: Botanic Gardens, Sydney, Dec. 1895 & Feb. 1898, *Camfield* (NSW 33557) & Dec. 1925, *Blakely & Anderson* (NSW 33558).

At the northern end of its range *Notelaea longifolia* f. *glabra* is not always easy to distinguish from *N. punctata*. The distributions of the two overlap slightly, as represented, for example, by the collections of *Keys* from Lake Cootharaba (BRI 7910 & 7930), *Francis* from Cootharaba (BRI 7932) and *Weatherhead* from Imbil (BRI 7933 & 9697), all in the Wide Bay District of Queensland. Where there is fruit there is little difficulty in identification: BRI 7932 & 9697 have small fruits characteristic of *N. punctata*, whereas BRI 7933 has the larger ones typical of *N. longifolia*. Vegetatively the prominence of the secondary veins below appears to be the best character for distinguishing most material, at least in the dried condition, for in both species the leaves are punctate. Habit appears significant and herbarium studies alone are inadequate to settle satisfactorily the problem of specific differentiation in this instance. Careful field observations, coupled, perhaps, with biosystematic studies, are called for.

Examination of the type of *Notelaea reticulata* DC. from Moreton Bay showed it to be the glabrous expression of the species, as might be expected from the locality from which it was collected. Similarly, the type of Domin's var. *decomposita*, from the Brisbane River, is the glabrous form and was found to be based in part on a very floriferous specimen (actually with the flowering stage just past) from the flowering shoots of which the leaves had just dropped, so that the inflorescences might, at first glance, be interpreted as compound.

2. **Notelaea ovata** R. Brown, Prodr. 524. 1810; Sprengel, Syst. Veg. **1**: 35. 1824; A. DC. in DC. Prodr. **8**: 291. 1844; Ettingshausen, Blatt-Skel. Dikot. 69. *t.26, figs. 7 & 8.* 1861; Bentham, Fl. Austral. **4**: 299. 1868; F. Mueller, Fragm. Phytogr. Austral. **8**: 43. 1873, & Syst. Census Austral. Pl. 92. 1882; F. M. Bailey, Synop. Queensl. Fl. 303. 1883; F. Mueller, Second Syst. Census Austral. Pl. 156. 1889; Maiden, Useful Native Pl. Austral. 580. 1889; F. M. Bailey, Cat. Pl. Queensl. 29. 1890; C. Moore, Handb. Fl. New S. Wales, 320. 1893; F. M. Bailey, Queensl. Fl. **3**: 972. 1900; Dixon, Pl. New S. Wales, 214. 1906; F. M.

Bailey, Comprehensive Cat. Queensl. Pl. 311. 1913; Maiden & Betche, Census New S. Wales Pl. 172. 1916; Audas, Native Trees Austral. 242. [1935]; Bean in Chittenden, Dict. Gard. 3: 1379. 1951; Beadle, Evans & Carolin, Handb. Vasc. Pl. Sydney Distr. & Blue Mts. 348. 1963.

N. longifolia Ventenat var. *ovata* (R. Br.) Domin in Bibliot. Bot. 22(89) (Beitr. Fl. Pflanzengeogr. Austral. 1 (3): 513): 1067. 1929, quoad syn., excl. fig. et spec. cit.

Evergreen *shrub* 0.5–1 m. tall, usually with several stems from an old common stock; young stems densely puberulous, sometimes minutely so. *Leaves* glabrous or minutely puberulous above and below when young, especially on the midrib and veins, rarely subvelutinous; petioles puberulous, sometimes minutely so, 1–6(–10) mm. long; lamina thickish, more or less coriaceous, punctate, very broadly ovate to ovate to narrowly ovate, more rarely lanceolate or broadly elliptic to elliptic (or even narrowly elliptic), (2.5–)3–9(–14) cm. long by (1.2–)1.8–3(–6) cm. broad; margin crenulate, sometimes irregularly so, rarely almost entire, somewhat thickened; apex acute, sometimes obtuse, occasionally slightly acuminate, tip often minutely apiculate; base rounded (to rarely subcordate, or, on the narrowest leaves, more or less acute), attenuate into the petiole; venation reticulate and raised above and below, (5–)6–7(–11) primary veins per side. *Inflorescence* axillary, 1(–2) per axil, in the case of a single inflorescence up to 5 mm. above the axil with an unopened bud in between, decussate, lowest pedicels often in the upper half, puberulous or scattered and minutely puberulous, especially towards the base, (1–)1.5–3.5 cm. long, (3–)5–9(–11)-flowered; occasionally freakish, up to 6 cm. long with secondary branching and 15 or more flowers per inflorescence; upper bracts

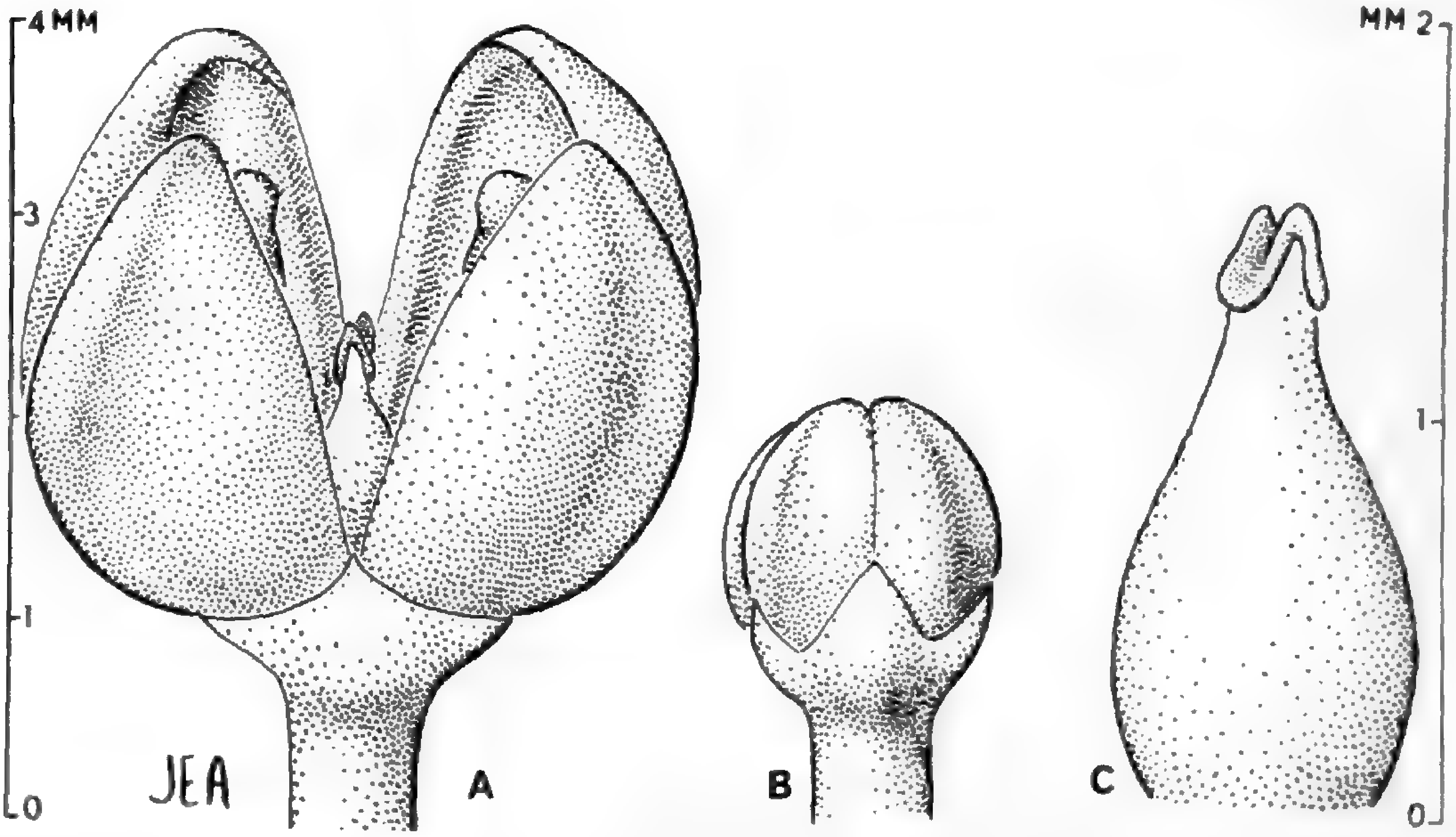


FIG. 1. *Notelaea ovata.* A, flower; B, young bud; C, ovary. (Drawn from *Green 1522a*).

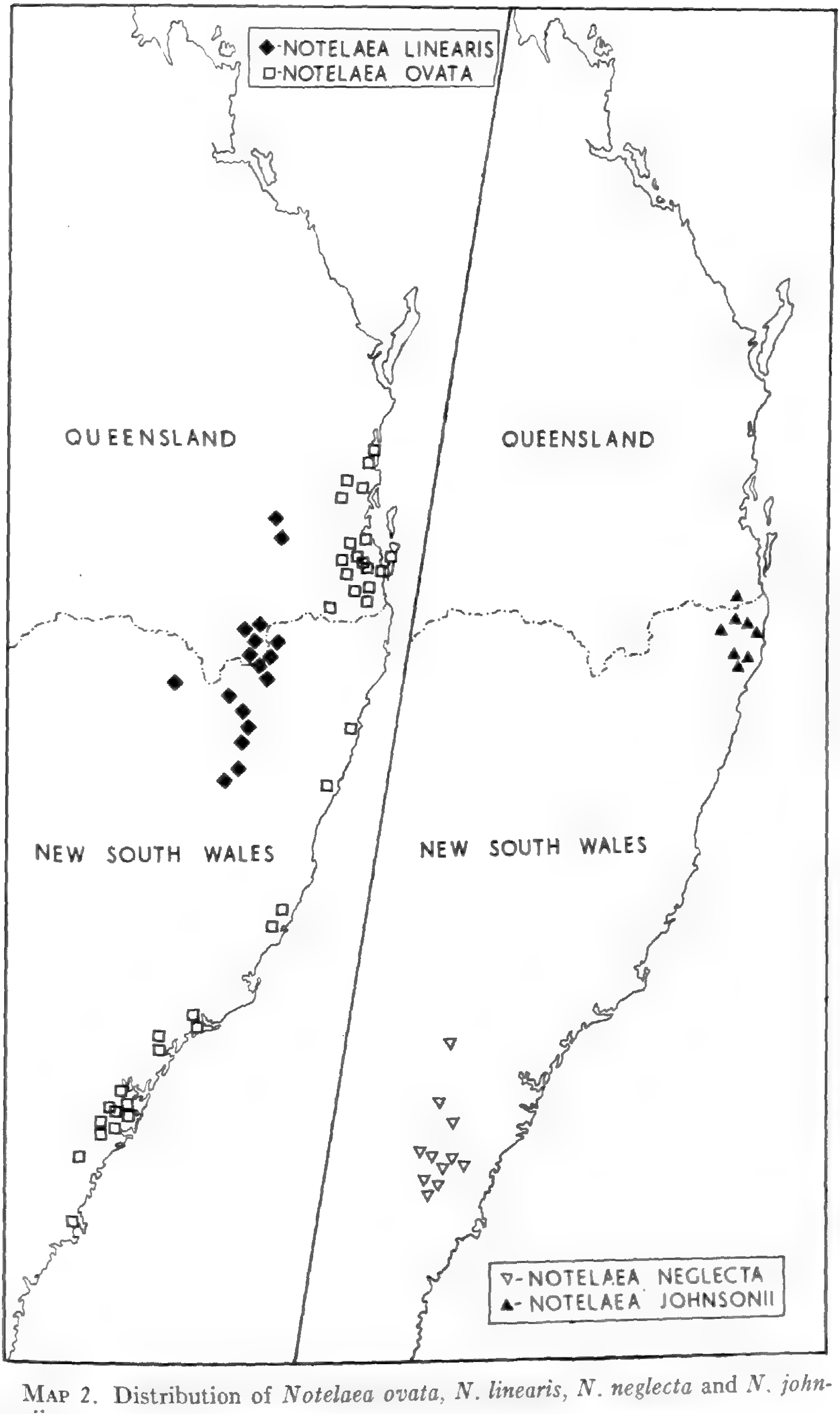
1–3 mm. long, lanceolate, sometimes almost subfoliaceous, minutely puberulous, early deciduous; basal bracts, thickish puberulous, but most often raised above the axil 3–10 mm. on the inflorescence axis. *Flowers* hermaphrodite (FIG. 1), pale yellow; pedicels 1.5–6 mm. long. *Calyx* glabrous 0.5–1 mm. long, with 4 more or less triangular lobes, slightly erose or sometimes minutely ciliolate, 0.5–0.7 mm. long. *Corolla* induplicate-valvate, lobes 4, 1.5–2.5 mm. long, in pairs joined in the lower half, concave. *Stamens* 2, 1–1.75 mm. long more or less enclosed within the concave petals, with a slight terminal appendage; filaments short 0.5 mm. long. *Ovary* flask-shaped, 1–1.5 mm. long tapering into a style 0.3–0.5 mm. long with 2 short stigmatic lobes 0.2 mm. long. *Drupe* ovoid with whitish semitransparent sarcocarp (*fide* B. S. Cole) 1–1.25 cm. long (?) by 0.8–1 cm. broad (?); endocarp hard, pointed ovoid, 7 mm. long by 5 mm. broad, 0.3 mm. thick.

SELECTED EXSICCATAE. **Queensland.** MORETON DISTRICT: Coolum, April 1945, *Clemens* (BRI 9704); Mt. Coolum, 24 March 1945, *Clemens* (K); Beerwah, Sept. 1919, *White* (BRI 9718); Elimbah, 4 Dec. 1961, *McKee 9731* (CANB 120610); top of Mt. Tunbubudla, Glass House Mountains, about 300 m. alt., 10 Aug. 1930, *Hubbard 3606* (A, K); Kedron, near Brisbane, *Shirley* (BRI 9720); Dinmore Pottery, 19 Oct. 1964, *L. S. Smith 12171* (BRI 64521, K); Taylor Range, near Brisbane, about 200 m. alt., 24 Aug. 1930, *Hubbard 3757* (A, K); Brisbane River, 1863–1865, *Dietrich* (BM); hills near Mt. Gravatt, near Brisbane, 11 July 1930, *Hubbard 3317* (A, BRI 9708, K); about 5 miles SE. of Ipswich, 16 June 1957, *Pedley* (K); Russell Island, Sept. 1913, *White* (BRI 9709, NSW 44035); Stradbrooke Island, *Scortechini & Bailey* (BRI 9710); Mount Maroon, NE. gorge, about 840 m. alt., 10 March 1962, *Everist 7111A* (BRI 38264); Coomera R., near Canungra, 9 Oct. 1949, *White 13124* (BRI 42315).

New South Wales. Trial Bay, Feb. 1882, *Betche* (NSW 33551); Barcoogere State Forest, about 6 miles N. of Corindi, 6 June 1957, *Johnson & Constable* (NSW 47501) & 6 Nov. 1963, *Green 1522 a–f* (A); Hastings River, *Beckler* (K); Kendall, Sept. 1932, *Bailey* (A, NSW 44036); Nelson's Bay, Port Stephens, 6 Feb. 1937, *Vickery* (LE, NSW 44037); Wallsend, Oct. 1899, *Boorman* (NSW 44039); Killara district, Oct. 1948, *Price* (NSW 44042); North Rocks, Sept. 1803, *Caley* (BM); Lindfield, 23 Oct. 1927, *White 5139* (BRI 9717, K); Port Jackson, *R. Brown* (BM, holotype; E, K, P, isotypes); Hurstville, April 1901, *Camfield* (NSW 44050); Bargo River, Dec. 1902, *Boorman* (A, NSW 44052); Huskisson, Jarvis Bay, Dec. 1925, *Rodway* (K).

Although the epithet borne by this species is very appropriate for most individuals and specimens, the leaves are fairly variable, both in size and in the proportions of length and breadth, so that on occasion the outline closely resembles that of *Notelaea longifolia*. However, the species may be separated by the more regular and prominent reticulation of the veins in *N. ovata* and the more definitely crenulate margin.

MAP 2 shows that *Notelaea ovata* is a coastal species, where it is found in Eucalypt forest on sandy soils or, in the Sydney district, according to L. A. S. Johnson, on soils derived from argillaceous shale, and in Queensland, to judge from the field notes with herbarium specimens, on sandstone hills and ridges. The tallest growth recorded on the labels of all the speci-



MAP 2. Distribution of *Notelaea ovata*, *N. linearis*, *N. neglecta* and *N. johnsonii.*

mens examined is 4 feet (1.2 m.) but whether the species ever attains higher growth than this is not recorded. There is no doubt, both from personal observation in the field and from the notes and comments on labels, that plants are often cut back by fire and then regenerate from a woody basal stock, often of considerable age. Plants flower when only a foot or so tall but, to judge from the specimens examined, rarely fruit. In fact the range in fruit size and color is somewhat uncertain. A specimen in the Sydney herbarium collected at Medowie by R. S. Cole (NSW 44038) has fruits in an envelope which appear as though they were fleshy when ripe; the mesocarp has shrivelled and it is difficult to be sure of the exact dimensions when they were fresh, so that the sizes given in the description above are only an estimate. The fruits on this specimen are said to have been whitish with a semitransparent sarcocarp, although purplish-black is the color one might expect from related species, and the field notes with a specimen collected by Pedley near Ipswich, Queensland (K) state that the fruits are purple. Unfortunately, there are no fruits still attached to the specimen of this collection at Kew, so that it is impossible to compare them with those of the Cole collection and impossible to be certain of the correctness of the statement in Bentham's *Flora Australiensis* (**4**: 299) that this species has the "fruit of *N. longifolia*." Just how variable the fruit color and size can be is not known but it is worth bearing in mind that the fruit of *N. ligustrina* may vary from purple through red and pink to white. Observations on fresh fruiting material are badly needed.

In Barcoongere State Forest, New South Wales, I collected shoots from six different plants in a population scattered over a small area in order to record the variation in leaf size (*Green 1522 a–f*). Lanceolate-elliptic leaves 11 cm. long by 3.5 cm. broad, broadly ovate leaves 6.5 by 5 cm., and diminutive but ovate leaves 3.5 by 2 cm. were all represented, each from a different individual. Bud material was also fixed for cytological examination and given to Dr. Barbara Briggs of Sydney. From this she obtained a chromosome count of n = ca. 23. I am most grateful to Dr. Briggs for permission to publish this count.

The species of sect. NOTELAEA are closely related but it is not known to what extent they are interfertile. Chromosome numbers, such as they are known, appear to be uniform, $2n = 46$, but only one collection has been seen which appears to be a hybrid of this species. This was collected by L. S. Smith (no. *12180 a*) at Dinmore Pottery, Moreton Bay District, Queensland, on 19 Oct. 1964 in *Eucalyptus fibrosa-E. maculata* forest on hillside (BRI 64516, K). This specimen has the leaf shape of a large-leaved *N. microcarpa* but the margin and venation is that of *N. ovata*. L. S. Smith collected undoubted *N. ovata* at the same locality on the same day (his no. *12171*) and to judge from the distribution of *N. microcarpa* this species is to be expected in this area as well. The hybrid specimen bears a few very immature fruits and it is quite possible that the two species are interfertile.

3. **Notelaea venosa** F. Mueller in Trans. Vict. Inst. **1854–55**: 131

("Definitions of Rare or Hitherto Undescribed Australian Plants" 50). 1855, & in Hooker's Jour. Bot. & Kew Gard. Misc. **8**: 163. 1856; Anderson, Trees New S. Wales, ed. 2. 132. 1947; Beadle, Evans & Carolin, Handb. Vasc. Pl. Sydney Distr. & Blue Mts. 349. 1963.

N. longifolia Vent. var. *pedicellaris* Domin, Repert. Sp. Nov. **12**: 96. 1913 & Bibliot. Bot. **22**(89) (Beitr. Fl. Pflanzengeogr. Austral. **1** (3): 514): 1068. 1929.

Evergreen bushy *shrub* or *small tree,* 1.5–6(–9) m. tall; bark grayish, smooth or eventually rough, flaky gray-brown (fide *Schodde 3502*); stem glabrous or puberulous, especially when young, sometimes minutely so. *Leaves* glabrous or minutely puberulous at first above and below; petioles glabrous or minutely puberulous at first, 5–15(–20) mm. long (0.5–3(–8) mm. long in northern plants); lamina thickish, more or less coriaceous, obscurely punctate, lanceolate to occasionally narrowly ovate or elliptic, (4–)6.5–12.5(–17) cm. long by (1–)2–4(–6) cm. broad, in semi-juvenile shade leaves (NSW 44065 & MEL 19621) petiole 20–30 mm. long, lamina ovate, 15–21 cm. long by 7.5–9.5 cm. broad; margin slightly thickened, entire or very shallowly and finely crenulate, especially in the upper half, sometimes extremely shallowly so; apex acute, sometimes slightly acuminate; base acute, attenuate into the petiole, to obtuse (rounded or subcordate in northern plants); venation raised, finely and evenly reticulate, especially below, (6–)7–10(–11) primary veins per side. *Inflorescence* axillary, 1–2(–3) per axil with a bud or buds between it and the axil but usually not more than 1.5 mm. above the axil, decussate, 1–3(–7) cm. long, 7–11(–17)-flowered, often fairly dense and occasionally the terminal 5(–7) flowers subumbellate, glabrous; bracts 1.5–3 mm. long, broadly ovate, ciliolate, early deciduous, basal bracts 1–2.5 mm. long, blunt, glabrous, somewhat persistent or the fused bases persistent. *Flowers* hermaphrodite, yellow or greenish-white, pedicels glabrous, 2–5(–10) mm. long. *Calyx* 0.5 mm. long with 4 somewhat irregular, more or less triangular, lobes. *Corolla* induplicate-valvate, lobes 4, 1.5–2.5 mm. long, joined in pairs for about 0.5–1 mm., thickish, concave. *Stamens* 2, 1–1.75 mm. long with a broad filament 0.3 mm. long and a slight terminal appendage. *Ovary* broad flask shaped, 1–1.5 mm. long, tapering to an imperceptible style with bilobed stigma 0.2 mm. long. *Drupe* dark purple to blackish (-white and red, *fide* E. Gippsland 165–66, no collector, MEL 19626), slightly glaucous, ellipsoid-ovoid 1.5–2 cm. long by 1–1.4 cm. broad; endocarp ovoid, pointed 1.1–1.5 cm. long by 0.8–1 cm. broad, 0.4–0.6 mm. thick.

SELECTED EXSICCATAE. **New South Wales.** River Hastings, *Fraser* (K); Williams River, 7 Jan. 1934, *Fraser & Vickery* (NSW 44063); Mt. Scrumbo, 19 miles E. of Aberdeen, 11 Oct. 1960, *Story 7497* (CANB 85286, NSW 53859); Mt. Royal, 25 miles E. of Aberdeen, 25 Mar. 1960, *Story 7179* (CANB 80176, K, NSW 67494); ridge between Chichester R. and Kerripit R., NNW. of Dungog, 1 Apr. 1954, *McDonald* (NSW 43030); O'Sullivan's Gap, 10 miles N. of Bulahdelah, 30 Nov. 1946, *Gilbert* (NSW 6498); Mt. Warrowolong, Olney, 300 m. alt., 24 Aug. 1949, *Constable* (NSW 11517); Wandabyne, Nov. 1922, *Blakely &*

Shiress (NSW 44064); track between Victoria Falls Lookout and Falls, about 2 miles E. of Mt. Victoria, 6 May 1959, *Constable* (K, NSW 47326); Springwood, 5 Dec. 1953, *McKee 847* (K, NSW 26323); Cedar Creek, Central Kowmung R., 26 Mar. 1948, *Johnson 348/28* (NSW 5025); Blue Mountains, March 1910, *Domin 7757* (PR); near King's Fall, Oct. 1819, *A. Cunningham 94/1819* (K); Mt. Jellore, 16 Nov. 1912, *Cheel* (NSW 44071); Illawara, Oct. 1818, *A. Cunningham* (K), 1855 *Macarthur* (BM) & *Oldfield* (K); near Robertson, Nov. 1918, *Dunn 27* (NSW 44073); Jamberoo-Carrington Falls road, 22 Jan. 1955, *Constable* (BM, G, K, NSW 32245); Nowra-Kangaroo Valley, near top of pass on Nowra side, about 350 m. alt., 14 Jan. 1936, *Rodway 2113* (*6242*) (A, BRI 7929, K, NSW 33417); Milton, 8 Nov. 1914, *Cambage 4121* (NSW 44078); Sugar Loaf Mt., Monga, near Braidwood, Jan. 1915, *Boorman* (NSW 44079); Eurobodalla, 1 Jan. 1950, *Whaite 480* (NSW 44080); Ohlson's Creek, near Narooma, against the road to Tilba Tilba, 23 May 1964, *Willis* (K, MEL 19629); Quaama, Dec. 1915, *Dunn* (NSW 44082); near Tanja (Bega distr.), 1948, *Phillips* (NSW 44083); Eden to Pambula, Nov. 1901, *Maiden* (NSW 44085); Twofold Bay, Sept. 1860, *F. Mueller* (K, holotype of *N. longifolia* var. *pedicellaris*); Womboyn Lake, 135 m. alt., 12 Oct. 1954, *Constable* (A, K, NSW 36595).

Victoria. Genoa River, 1880, *Reader* (MEL 19607); Mallacoota, *Hart* (MEL 19609 & 19610); Mt. Drummer, 11 June 1959, *L. J. W. & J. G. T. 3619* (BRI 34850); sources of Delegate River, 1887, *Merrah* (MEL 19611); Broadribb River, Jan. 1855, *F. Mueller* (MEL 19620, holotype; K, MEL 19632, isotypes); Orbost, 20 Oct. 1903, *Grove* (G, K, LE); North Arm, Lakes Entrance, 17 Aug. 1944, *Willis* (MEL 19621)

This species is closely related to *Notelaea longifolia* and *N. ovata* and has often been misidentified as the former, although its main distribution is more southerly (MAP 3). However, it may readily be distinguished by the fine and even reticulation of the leaves, especially below. This species may also be recognized by the fruit which is relatively large and slightly longer in proportion to its width. When ripe the fruit is quite fleshy and bluish-black with a slight glaucous bloom, although the label with MEL 19626 from E. Gippsland says "white and red." According to annotations by L. A. S. Johnson it is characteristic of sandstone soils in or around rainforest, though often of the lower, poorer type, as in mountain gullies, etc., but sometimes in more open habitats or in patches of undergrowth of rainforest species in wet sclerophyllous forest.

Var. **A.**

Leaves subsessile or with very short petioles, 1.5–3 mm. long; leaf base subcordate or broadly rounded.

Queensland. MORETON DISTRICT: top of Mt. Mitchell, about 1050 m. alt., 19 July 1930, *White 6886* (BRI 9692); Wilson's Peak, *Peterson* (BRI 9706); top of Mt. Lindsay, about 1200 m. alt., 10 Aug. 1932, *Whitehouse* (BRI 9693).

New South Wales. Mount Mackenzie, Tenterfield, 4 Nov. 1963, *Goddard* (BRI 42938); near Hyland State Forest, 1375 m. alt., 5 Apr. 1955, *Turner* (NSW 44058); Orara West State Forest, E. Dorrigo, May 1946, *W. T. Jones 5* (BRI 42305–6); Bellangry State Forest, about 20 miles NW. of Wauchope, 2 Jan. 1957, *Cousins 180* (NSW 44059); Comboyne, Jan. 1934, *Chisholme* (NSW

MAP 3. Distribution of *Notelaea venosa*, *N. punctata* and *N. microcarpa*.

44060) & *Fraser* (NSW 44061); The Corker, Upper Williams River to Barrington Tops, 26 May 1934, *Fraser 19* (NSW 44062).

When studying the material of this species, certain specimens with subcordate leaf bases and very short petioles (1.5–3 mm. long) came to be put on one side as constituting a distinct entity. This seemed more probable when it was noted that one or two came from relatively high altitudes and that when their distribution was plotted on a map they were found only amongst the northernmost specimens (see MAP 3). However, with the limited material available there seem to be no other distinguishing characters and one of the southernmost specimens, *Miss L. Fraser* from Comboyne (NSW 44061), exhibits both types of leaf, in this case with the unusual short-stalked leaves together with inflorescences on the youngest shoots, and the typical leaves towards the base. Also, a specimen at Kew collected by Charles Fraser during the last century from about the same area, "native of the banks of the River Hastings," bears leaves somewhat intermediate in leaf base and petiole length (6–8 mm.). A comment, written upon another sheet, suggests that the unusual leaves are juvenile, but several of the specimens exhibiting them bear young fruit or the remains of flowers, while other undoubtedly juvenile collections bear leaves with typical bases and petioles, while a seedling collected on Mt. Drummer (BRI 34850), although with short petioles, has the typical acute leaf base. Further collections and field observations from the populations in northwest New South Wales and southernmost Queensland are desirable and may prove that they do merit nomenclatural differentiation after all.

4. **Notelaea punctata** R. Brown, Prodr. 524. 1810; Sprengel, Syst. Veg. 1: 35. 1824; A. DC. in DC. Prodr. **8**: 291. 1844; Reichenb. f. Neuholl. Pfl. Amelia Dietrich 9. 1866; Bentham, Fl. Austral. **4**: 300. 1868; F. Mueller, Syst. Census Austral. Pl. 92. 1882; F. M. Bailey, Synop. Queensl. Fl. 303. 1883; F. Mueller, Second Syst. Census Austral. Pl. 156. 1889; F. M. Bailey, Cat. Pl. Queensl. 29. 1890; C. Moore, Handb. Fl. New S. Wales, 320. 1893; F. M. Bailey, Queensl. Fl. **3**: 973. 1900; Dixon, Pl. New S. Wales 214. 1906; F. M. Bailey, Comprehensive Cat. Queensl. Pl. 311. 1913; Domin, Bibliot. Bot. **22**(89) (Beitr. Fl. Pflanzengeogr. Austral. 1(3): 514): 1068. 1929; Bean in Chittenden, Dict. Gard. **3**: 1379. 1951.

Bushy *shrub* to 1(–2) m. high (? more), branches glabrous or very minutely puberulous when young. *Leaves* glabrous; petiole 2–6(–10) mm. long, glabrous; lamina thickish, punctate above and below, especially below, narrowly ovate to lanceolate or elliptic to narrowly elliptic, (3.5–)5–9(–13) cm. long by (1–)1.5–3(–5) cm. broad; margin entire or occasionally slightly, very shallowly and irregularly crenulate, slightly thickened; apex acute or very slightly acuminate, tip acute; base acute or cuneate (rarely obtuse and rounded), attenuate or somewhat decurrent onto the petiole; venation raised and clearly reticulate above, usually less clearly so below, often obscure or visible as lighter lines or only slightly raised, 6–8(–10) primary veins per side. *Inflorescence* axillary, often up to 3 mm. above the axil with 1–2 dormant buds in between, 1(–2) per axil, decussate, (1–)1.5–3 cm. long, (7–)9–13-flowered, glabrous, except occasionally for a few minute scattered hairs towards the base; upper bracts 1–1.5 mm. long, thin, lanceolate to ovate, acute, early deciduous, ciliolate, basal pair thick, 1–2 mm. long, acute or acuminate, glabrous or with a few minute hairs towards the apex, persistent or at least the fused bases persistent. *Flowers* hermaphrodite, creamy white or pale yellow; pedicels 2–5(–8) mm. long. *Calyx* 0.5–1 mm. long, lobes 4, broadly and irregularly triangular, 0.3–0.6 mm. long, glabrous or ciliolate, sometimes subapiculate. *Corolla* induplicate-valvate, lobes 4, 2–3 mm. long, concave, joined in pairs above the base of the filaments for about 0.4 mm. *Stamens* 2, broadly ellipsoid, 1.5–2.5 mm. long, more or less enclosed within the concave petals, filaments 0.3–0.5 mm. long, with a terminal appendage about 0.1–0.3 mm. long, dehiscence lateral. *Ovary* 1–1.5 mm. long with 2 stigmatic lobes 0.2–0.3 mm. long on a short style about 0.2 mm. long. *Drupe* varicolored (fide *McLaughlin 22C*), pale (*fide* note with *Biddulph 63*), ovoid, 7–9 mm. long by 5–6 mm. broad; endocarp hard, 0.2 mm. thick.

Queensland. COOK DISTRICT: Middle Creek, about 6 miles SE. of Cairns, 30 Oct. 1949, *Flecker* in *N. Queensland Nat. Club 13331* (BRI 42304). NORTH KENNEDY DISTRICT: SE. slopes of Gt. Dividing Range, about 4 miles NNE. of Herberton, about 1060 m. alt., 7 Aug. 1948, *L. S. Smith 3729* (BRI 42313) & about 6 miles NNE. of Herberton, about 1100 m. alt., 26 Aug. 1954, *Smith 5301* (BRI 42302 & 42303); Herberton, 1918, *Michael 624* (BRI 7911); W. of Herberton, crest of Gt. Dividing Range, 1050 m. alt., 22 Aug. 1963, *Blake 22107* (BRI 42318); Rockingham Bay, *Dallachy* (BM, K, LE, NSW 44056). PORT CURTIS DISTRICT: Shoalwater Bay, 1802, *R. Brown "2846"* (BM, holotype; E, K, MEL 19631 isotypes). LEICHHARDT DISTRICT: Blackdown, about 12 miles SSE. of Bluff, Aug. 1961, *Gittins 389* (BRI 30808); Aug. 1964, *Gittins 887* (BRI 56856) & *887/2* (BRI 56855); Blackdown Tableland, south of Dingo, Sept. 1937, *Simmons* (BRI 7917); Rockland Spring, 30 miles ENE. of Springsure Township, 5 Sept. 1961, *Lazarides & Story* 121 (CANB 111988, K, NSW 67495); Expedition Range, Aug. 1960, *Gittins 360* (BRI 25421); Mt. Playfair, Springsure district, Sept. 1935, *McLaughlin 22c* (BRI 7914) & Nov. 1959, *Biddulph 63* (BRI 27107); 21 miles SE. of Bedourie, 14 Oct. 1963, *Speck 1858* (BRI 59772, CANB 137885, K); Isla Gorge between Theodore and Taroom, 1 Sept. 1963, *Hockings* (BRI 42317); 16 miles SSW. of Cracow Township, 10 July 1963, *Lazarides 6950* (BRI 51428–9, CANB 123629). BURNETT DISTRICT: Eidsvold, 1919, *Bancroft* (BRI 9700). WIDE BAY DISTRICT: Fraser Island, 6 Sept. 1916 & Dec. 1918, *Petrie 32* (BRI 9698 & 7927) & Oct. 1921, *White* (BRI 7936); Cootharaba, Dec. 1917, *Francis* (A, BRI 7932); Imbil, 27 March 1918, *Weatherhead* (BRI 9697, K).

Although in its typical state, with an obscure venation on the undersurface of the leaf and small fruits, *Notelaea punctata* is easily distinguished from typical *N. longifolia* (in which the leaves are clearly reticulate below with raised veins and the fruits are larger), the two species tend to merge where their areas of distribution meet (MAPS 1 & 3). The dotting of the leaf, so abundant and obvious on the type, and thus taken by Robert Brown as the basis for his specific epithet, is also found in *N. longifolia* (and other species) but usually much less obviously and abundantly so. Using leaf characters alone, it appears that there may be an area of transition, but too few specimens are in fruit and none from the intermediate areas. More collecting and further field observations are badly needed, especially in the Burnett and Wide Bay Districts of Queensland. This species is insufficiently well known and it may turn out that it would be better treated as a subspecies of *N. longifolia.*

C. Moore in his Handbook of the Flora of New South Wales of 1893 (p. 320), records *Notelaea punctata* from the northern coast district of New South Wales, but this is clearly an error and must have been based on a misidentification

In habit *Notelaea punctata* would seem, from the limited field notes available, to resemble *N. ovata,* usually growing as a low shrub, with many erect branches, from a rootstock which presumably survives bushfires. The only notes giving details of habitat indicate that *N. punctata* is found under *Eucalyptus* spp. on sandy soils on sandstone plateaux and ranges.

5. **Notelaea microcarpa** R. Brown, Prodr. 524. 1810; Sprengel, Syst. Veg. **1**: 35. 1824; A. DC. in DC. Prodr. **8**: 291. 1844; Bentham, Fl. Austral. **4**: 300. 1868; F. Mueller, Fragm. Phytogr. Austral. **8**: 43. 1873, & Syst. Census Austral. Pl. 92. 1882; Bailey, Synop. Queensl. Fl. 303. 1883, & Queensl. Woods 89. 1888 & 97. 1889; F. Mueller, Second Census Austral. Pl. 156. 1889; Maiden, Useful Native Pl. Austral. 580. 1889; C. Moore, Handb. Fl. New S. Wales 320. 1893; F. M. Bailey, Cat. Pl. Queensl. 29. 1890, & Queensl. Fl. **3**: 973. 1900; Dixon, Pl. New S. Wales 214. 1906; Guilfoyle, Austral. Pl. 100. [1911]; F. M. Bailey, Comprehensive Cat. Queensl. Pl. 311. 1913; Maiden & Betche, Census New S. Wales Pl. 172. 1916; Domin, Bibliot. Bot 22(89) (Beitr. Fl. Pflanzengeogr. Austral. 1(3): 514): 1068. 1929; Anderson, Trees New S. Wales, ed. 2. 69, 132, 338. 1947; M. Gray, Contr. New S. Wales Natl. Herb. **3**: 59. 1961.

Evergreen shrub or small tree to 10 m., usually round headed; bark gray, tessellated; branches puberulous when young, sometimes only minutely so. Leaves glabrous or scattered puberulous above and below, becoming glabrous, except occasionally near the midrib, or densely velutinous, especially below; petiole (1–)2–5(–10) mm. long, glabrous or puberulous, becoming glabrous; lamina thickish, scattered punctate, (lanceolate–) narrowly or very narrowly lanceolate (–linear), (2–)3–8(–15) cm. long by (0.3)0.5–1.5(–3) cm. broad; margin entire, scarcely thickened or occasionally somewhat thickened, usually flat; apex acute or obtuse-apiculate; base very narrowly cuneate, decurrent onto the petiole; venation usually raised and reticulate, especially above, less so, and sometimes almost obscure, below, 5–7 primary veins per side making an angle of about 15°–30° with the midrib and eventually running almost parallel to the margin.

Inflorescence axillary, 1–2 per axil, decussate (rarely and freakishly, terminal and then perhaps thyrsoid), 0.5–2 cm. long, (7–)9–13(–15)-flowered or rarely (more or less freakishly?) paniculate and many flowered (NSW *33512* & *33606*), puberulous, especially towards the base, to remotely scattered puberulous, rarely almost glabrous with a few hairs towards the base; upper bracts 1.5–2 mm. long, thin, more or less ovate or lanceolate, early deciduous, ciliolate, basal pair thick, their joined bases persistent, puberulous, rarely glabrous (in northernmost specimens), 1–1.5 mm. long, acute. *Flowers* hermaphrodite, greenish-yellow, yellow or cream; pedicels 0.5–4(–6) mm. long. *Calyx* 0.3–0.6 mm. long, lobes 4, usually with 2 long and 2 short (the longer at the base of the corolla pair), irregularly triangular, 0.1–0.5 mm. long, glabrous or margin bearing a few hairs. *Corolla* induplicate-valvate, lobes 4, 1.4–2 mm. long, concave, joined in pairs above base of filament for about 0.7–0.8 mm. Stamens 2, ellipsoid, (0.8–) 1–1.5 mm. long, more or less enclosed within the concave petals, subsessile or on filaments 0.1–0.2 mm. long, with blunt terminal appendage about 0.1–0.2 mm. long, lateral dehiscence. *Ovary* 1–1.5 mm. long, with 2 stigmatic lobes 0.2–0.3 mm. long on short style about 0.2 mm. long. *Drupe* dark blue or blackish (becoming soft and purple when ripe, *fide* Johnson), ovoid, (5–)7–10 mm. long by (4–)5–8 mm. broad (smallest dimensions immature?); endocarp hard, 0.2–0.4 mm. thick.

Var. **microcarpa**

Leaves glabrous or with only scattered pubescence above and below.

Selected Exsiccatae: **Queensland.** Cook District: Stannery Hills, Apr. 1909, *Bancroft* (BRI 8272, K) & Dec. 1908, *Bancroft 259* (BRI 8250, K); Lynd Scrub, approx. 40 miles SW. to SSW. of Mt. Garnet, 24 Aug. 1949, *L. S. Smith 3859* & *3869* (BRI 42307–8). North Kennedy District: St. Roman's Station, Mt. Garnet, 29 Apr. 1960, *Myers* (BRI 28627); Dickson Hill, Mt. Fox, 27 Sept. 1949, *Clemens* (K); Dalrymple Road, 12 miles N. of Charters Towers, *Flecker* (*Rodway 7933*) (NSW 33422). South Kennedy District: 3 miles W. of "Collin Downs" Station, 11 Aug. 1964, *Adams 1261* (CANB 143194, K). Port Curtis District: Sarina (Lotus Creek), 29 Sept. 1962, *Jones 2245* (CANB 136113); Broad Sound, 1803, *R. Brown* (BM, holotype; E, K, LE, NSW 33569, P, isotypes); Many Peaks, Shoalwater Bay, July 1919, *McEniery* (BRI 9695); Rockhampton, *Bailey 68* (BRI 8271, K), *Dallachy* (BM) & *ex F. Mueller* (GH, LE); Scubby Creek, near Rockhampton, July 1937, *Simmons* (A, BRI 8269 & 8270, K); Biloela, about 175 m. alt., 25 Oct. 1947, *L. S. Smith 3552* (BRI 42310–1). Leichhardt District: Croyden Station, 2 Nov. 1962, *Jones 2319* (CANB 136039); Gindie, Aug. 1916, *White* (BRI 8262, K, NSW 33571); Dawson, *Bancroft 56* (BRI 8275). Mitchell District: Enniskillen, 14 Nov. 1943, *White 12371* (A, BRI 8281); Victoria River, 17 Sept. 1846, *Mitchell 310* (BM). Warrego District: Warrego, *Bailey 55* (BRI 8253); Morven, 17 Apr. 1961, *Jones 1928* (CANB 107495). Maranoa District: 17 miles E. of Morven, 9 June 1937, *Everist 1525* (BRI 8283); 20 miles W. of Mitchell, 500 m. alt., 31 March 1936, *Blake 10935* (BRI 8257 & 8261, CANB 38903, K); Orallo, Oct. 1920, *Dunlop* (BRI 8274, K, NSW 33572); Roma, July 1915, *Bick* (BRI 8267, K, NSW 33574) & 25 Oct. 1933, *White 9510* (A, BRI 8255); Honeymah, about 40 miles SE. of Bollon, 16

July 1948, *Everist 3478* (BRI 8273, CANB 25566, K). BURNETT DISTRICT: Eidsvold, *Bancroft* (BRI 8278, K); Mt. Perry, *Keys 269* (BRI 9696); Dallarnil, 28 Dec. 1939, *L. S. Smith 665* (A, BRI 9699); Haley Creek Road, 21 Oct. 1947, *Mitchell 3050* (BRI 7915). WIDE BAY DISTRICT: Theebine, Nov. 1921, *White* (A, BRI 8265, K); Wide Bay, 1854, *Moore* (K). MORETON DISTRICT: Forestry Reservation, Yarraman, approx. 400 m. alt., Aug. 1944, *Clemens* (A, BRI 42312); Laidly Hills, 25 Jan. 1944, *Clemens 43476a* (A); Pine Mountain, N. of Ipswich, Oct. 1946, *Everist* (BRI 9575, K); 1 mile N. of Boonah, on Kalbar Road, 24 Nov. 1946, *Everist & Webb 1415* (BRI 9715, CANB 16733, K); mouth of Coomera R., 21 Jan. 1927, *White 3381* (A, BRI 7912, K). DARLING DOWNS DISTRICT: Glenmorgan, 19 July 1949, *Gordon 63* (BRI 42316); 2 miles W. of Condamine, 24 Aug. 1956, *Everist 5795* (BRI, CANB 100241, K); N. of Miles, 14 Aug. 1951, *Webb 1500* (CANB 30648); Chinchilla, 8 July 1912, *Bensley 1* (BRI 8258, K); Warwick, Aug. 1913, *Shirley* (BRI 8254, K, NSW 33575); Silverwood, Sept. 1922, *White 1763* (A, BRI 18276, K, NSW 33576).

New South Wales. 20 miles N. of Torrington, 12 Dec. 1951, *Jessup & Gray 23* (CANB 126269, NSW 42868); Mt. Mitchell, near Warialda, 28 July 1922, *de Beuzeville 12* (NSW 33580); Wallangra, Sept. 1929, *Rodway 6225* (K, NSW 33421); Moree, 29 Sept. 1912, *Brennan* (NSW 33582); Narrabri West, Aug. 1907, *Boorman* (GH, NSW 33590, Z); Warrumbungle Mountains, 640 m. alt., 26 May 1948, *Constable* (BM, K, NSW 6475); Little Sugar Loaf Mountain, near Gunnedah, 352 m. alt., 1 Nov. 1954, *Johnson & Constable* (K, NSW 32028); "Lowestoft," 27 miles S. of Tamworth, near highway, 684 m. alt., 18 Apr. 1956, *Constable 1658* (A, K, NSW 37333); Wellington, 20 Oct. 1880, *Betche* (NSW 33592); "Merrot," Curriecabark, 30 miles NW. of Barrington, Feb. 1949, *Hyem* (NSW 33594); 6 miles SW. of Scone, 16 March 1960, *Story 7071* (CANB 80160, K); Mt. Wambo, 5 miles NW. of Bulga, 600 m. alt., 30 Aug. 1957, *Constable* (NSW 42865).

Cultivated. Botanic Gardens, Brisbane, 31 Oct. 1930, *Hubbard 4740* (A, K) & 8 Nov. 1963, *Green 1530* (A).

Notelaea microcarpa is one of the two most widespread species in this genus (MAP 3). To judge from its distribution, and from the annotations on the herbarium covers at Sydney, it is characteristic of an area of moderately dry, distinctly continental climate with a summer maximum rainfall. It is an "inland" species of the "western slopes country" and although it approaches the coast in parts of Queensland, e.g. around Rockhampton, it does so in comparatively dry areas. At its southern limit it stops "at the Wellington-Hunter Valley latitude, i.e. where the summer rainfall zone begins to pass into the transitional zone."

At its southern limit the distribution of *Notelaea microcarpa* approaches most closely to *N. neglecta*, perhaps the most nearly related species, and the one under which their differences and affinities are discussed. *N. neglecta* is found to the south and east with a damper and often cooler climate.

Notelaea microcarpa, as its name suggests, is characterized by small fruits, a character it shares with *N. neglecta* and *N. linearis*, both of which have narrow leaves. From *N. longifolia* it may be distinguished by the relative obscurity of the veins on the underside of the leaf (reticulate in *N. longifolia*) and also by the narrow angle at which the primary veins join the midrib, approximately 15°–30° in *N. microcarpa* and 40°–70° in *N. longifolia*.

However, exceptionally narrow leaves may occur rarely on adult plants, for example, a specimen from Sarina (Port Curtis District) Queensland (CANB 136113) exhibits linear leaves, (3–)4.5–7(–9) cm. long by (0.25–) 0.35–0.6(–0.8) cm. broad; the notes on the label say "very narrow leaf form, extreme dry conditions." The venation is obscure as well and it might easily be mistaken for *N. neglecta* were it not from far outside the geographical range of that species.

Using herbarium material alone it is very difficult to evaluate juvenile characters but it is suspected that four herbarium sheets bearing specimens with much larger leaves than usual were gathered from juvenile plants. Three of these are from the Yarraman Forestry Reservation, Moreton District, Queensland, Aug. 1944, coll. *M. S. Clemens* (A). Two sheets have notably juvenile, long narrow leaves 10–27 cm. long and 0.3–1.2 cm. broad exhibiting up to about 20 primary veins on each side of the midrib. The third sheet, annotated as a slender sapling, is in flower and has broader leaves than usual, up to 11 cm. long and 3.5 cm. broad. The fourth, from St. Roman's Station, Mt. Garnet, N. Kennedy District of Queensland, has leaves 20 cm. long and 2 cm. wide. Large juvenile foliage is similarly found in *Notelaea longifolia* and *N. ovata* and particularly in the more distantly related New Zealand species of *Nestegis*.

Notelaea microcarpa is believed to hybridize with both *N. longifolia* and *N. ovata* and more detailed mention of this has been made under these species.

Var. **velutina** (F. M. Bailey) P. S. Green, comb. nov.

N. longifolia Vent. var. *velutina* F. M. Bailey, Comprehensive Cat. Queensl. Pl. 311, 319 & 839. *fig. 293.* 1913; White, Queensl. Agric. Jour. II. **22:** 241. *pl. 77, 78.* 1924 & *op. cit.* **23:** 435, 436. *pls. 80, 81.* 1925; Domin, Bibliot. Bot. **22**(89) (Beitr. Fl. Pflanzengeogr. Austral. **1**(3): 514): 1068. 1929.

Leaves densely velutinous, especially on the undersurface.

Queensland. DARLING DOWNS DISTRICT: Silverwood, Sept. 1922, *White 1764* (A, BRI 7941, K, NSW 33530); Killarney, *Bailey* (? *Wedd*) (BRI 9358, holotype; K, isotype); Wilson's Peak, *Michael 1983 p.p.* (NSW 33532); Stanthorpe, July 1904, *Boorman* (NSW 33531), about 1000 m. alt., June 1924, *Tryon* (BRI 7942, K) & *Perkins* (BRI 7943, K); Eabey, via Stanthorpe, Nov. 1944, *Clemens* (BRI 7923); Granite National Park, Wyberba, Nov. 1944, *Clemens 44738* (K).

New South Wales. Macpherson Range, May 1907, *Dunn 335* (NSW 33533); Rivertree, 5 Sept. 1911, *Cambage 2852* (NSW 33534); head of Wylie Gorge, Liston, 17 Nov. 1943, *Clemens* (A); Nymboida River, near Dorrigo, 5 Nov. 1963, *Green 1519 a, c, e, g, & j–l* (A); Bald Nobbs, Armidale, 28 Sept. 1912, *Stopford 45* (BM); Castle Doyle Road, about 7 miles SE. of Armidale, Feb. 1928, *McKie 93* (NSW 33536); Wollomombi, 4 March 1933, *McKie* (NSW 33537); Apsley Falls, about 900 m. alt., 25 May 1957, *Johnson* (NSW 46142); Tia Falls (E. of Walcha), Dec. 1898, *Betche* (NSW 33538) & Oct. 1900, *Forsyth & Cheel* (NSW 33539).

Although this variety was attributed by F. M. Bailey to *Notelaea longifolia*, it really belongs to *N. microcarpa*. Most specimens are in flower or immature fruit but the collection from Stanthorpe, Queensland, by F. A. Perkins in June 1924 has mature fruits of the typical small size, 8–9 mm. long by 7–8 mm. broad. Furthermore, the angle the primary veins make with the midrib of the leaf, the relative obscurity of the veins beneath (although this is masked by the velutinous covering), the general proportions of the leaf and the length of the individual inflorescences, all indicate *N. microcarpa*. Velutinous forms of *N. longifolia* exist but are found in the southern parts of range for that species, so that all *N. longifolia* in the northern areas of New South Wales or in Queensland are glabrous, or, at the most, glabrate. *Cambage 2702* from the central tablelands region of N.S.W. (from Baerami to Denman, 15 May 1911, NSW 33540) was examined carefully because of its narrow and velutinous foliage and it is believed that it represents the result of hybridization between this species and *N. longifolia* f. *longifolia*.

The distribution of this variety is restricted to the southeastern part of the Darling Downs district of Queensland and the Northern Tablelands of New South Wales. I have seen material from the northernmost areas of New South Wales and again in the southern parts of the New England Ranges but it may well occur in between.

Typical *Notelaea microcarpa* occurs near at hand in parts of the variety's range, e.g. *White 1763* from Silverwood, Queensland, which was presumably collected near to *White 1764* a specimen of the densely velutinous variety, while collections with slight pubescence are found scattered throughout the range of the species. In November 1963 I was fortunate to be taken to a population of *Notelaea* near Dorrigo through the kindness of Alex G. Floyd and Harold C. Hayes, and there took samples from 12 bushes and small trees scattered over a small area near the Nymboida River (*P. S. Green 1519 a–l*). At the time I was struck by the variation in the breadth and pubescence of the leaves, but it is now apparent to me that this variation is due to introgression which has occurred between *N. longifolia* and *N. microcarpa* var. *velutina*. The area, like much of that part of New South Wales, is one where considerable felling has taken place and the velutinous upland plant may well have come into contact with the more lowland *N. longifolia* due to man's activities. In the citation of the population sample I have placed those parts which seem nearer to *N. microcarpa* var. *velutina* above and those nearer to *N. longifolia* under that species. *Turner 29*, cited under *N. longifolia*, from Paddys Land State Forest, a little distance to the northwest, also shows intermediate characteristics and some of the gatherings cited above as var. *velutina* possess leaves which are slightly wider in proportion to their length than is usual for the species, and may perhaps show the influence of *N. longifolia*, for example the Clemens collection from the head of Wylie Gorge, Liston, New South Wales.

6. **Notelaea linearis** Bentham, Fl. Austral. **4**: 300. 1868; F. Mueller,

Syst. Census Austral. Pl. 92. 1882; F. M. Bailey, Synop. Queensl. Fl. 303. 1883 & Cat. Queensl. Fl. 29. 1890; C. Moore, Handb. Fl. New S. Wales, 321. 1893; F. M. Bailey, Queensl. Fl. 3: 973. 1900; Dixon, Pl. New S. Wales 215. 1906; F. M. Bailey, Comprehensive Cat. Queensl. Pl. 311. 1913; Maiden & Betche, Census of New S. Wales Pl. 172. 1916; Anderson, Trees New S. Wales ed. 2. 132. 1947; M. Gray, Contr. New S. Wales Natl. Herb. 3: 59. 1961.

Evergreen shrub 1–2 m. high, branches glabrous or minutely puberulous at first, soon glabrous. *Leaves* glabrous; petiole 1–3(–4) mm. long, glabrous or minutely puberulous above when young; lamina thick, linear or occasionally very narrowly lanceolate or elliptic (? juvenile condition), (2–)3–6(–11.5) cm. long by (0.15–)0.2–0.5(–0.7) cm. broad (? up to 1 cm. broad in juvenile state), punctate, especially below, margin entire, somewhat thickened; apex very acute; base narrowly attenuate into the petiole; venation completely obscure above and below, or rarely (? juvenile state) with primary veins just visible above and below, about 7 per side joining to form a submarginal nerve. *Inflorescence* axillary, 1 per axil, decussate or subumbellate, 0.4–1 cm. long, (3–)5(–7)-flowered, glabrous or puberulous, often only very slightly so; upper bracts 0.5–1 mm. long, thin, triangular-ovate, early deciduous, basal pair thick, persistent, glabrous or puberulous-ciliolate, 1 mm. long, acute. *Flowers* hermaphrodite (Fig. 2), pale yellow (*fide* White & Williams); pedicels 1–4 mm. long. *Calyx* 0.5–0.7(–1) mm. long, lobes 4, irregularly triangular, 0.2–0.5 mm. long, glabrous, margins sometimes slightly ciliolate. *Corolla* induplicate-valvate, lobes 4, (1.5–)2 mm. long, concave, in pairs, joined above the base of filaments for 0.3–0.6 mm. *Stamens* 2, (1–)1.5 mm. long, more or less enclosed within the concave petals, on filaments 0.2–0.3 mm. long with a broad connective and well developed blunt terminal appendage 0.2–0.3 mm. long. *Ovary* 1–1.4 mm. long with 2 stigmatic lobes 0.2–0.4 mm. long on style 0.2 mm. long. *Drupe* ovoid, 5–7 mm. long by 4–5 mm.

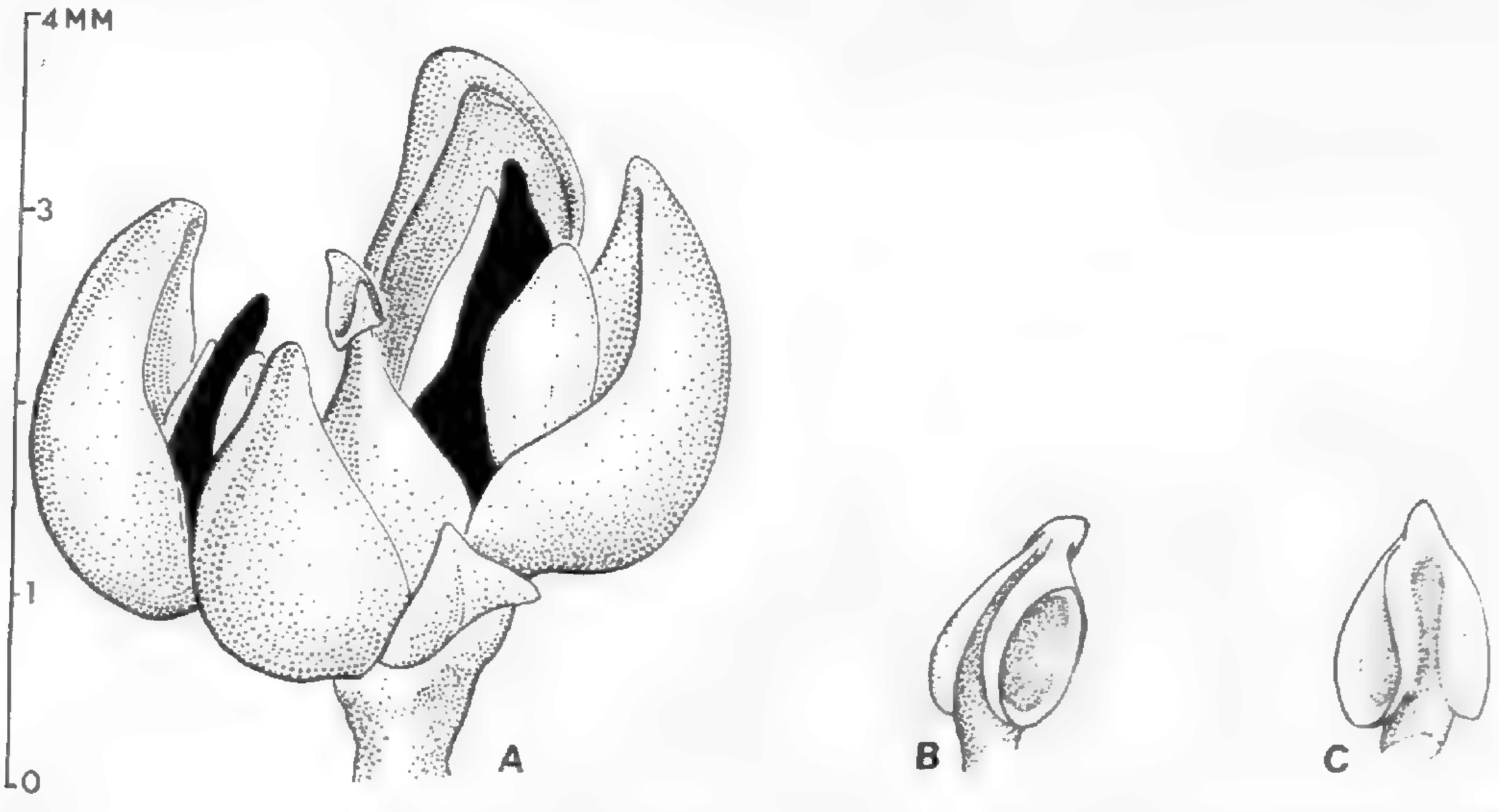


Fig. 2. *Notelaea linearis*. A, flower; B & C, stamen. (Drawn from *Hubbard 3961*).

broad, "white and translucent" (*fide* Galbraith, BRI 49151) and "rich blue with a thin bloom" (*fide* Galbraith, BRI 49152); endocarp hard, 0.2 mm. thick.

Queensland. MORETON DISTRICT: Crow's Nest, Sept. 1920, *Kenny* (BRI 7904), Oct. 1921, *White* (A, NSW 33423); Pearson's Falls, Helidon, *Bailey* (BRI 7905, K). DARLING DOWNS DISTRICT: Thulimbah, *Schindler 3* (BRI 7901); *Messines*, near Stanthorpe, approx. 900 m. alt., 13 Sept. 1930, *Hubbard 3961* (BRI 7906, K); Stanthorpe, *Bailey* (BRI 7903) & July 1904, *Boorman* (NSW 33424); Glen Aplin, 9 Sept. 1933, *White 9253* (A, BRI 7902); Wyberba, Feb. 1964, *Galbraith* (BRI 49151–2); Wallangarra, Nov. 1904 & Jan. 1906, *Boorman* (NSW 33427 & 33428).

New South Wales. Wallangarra area, 16 March 1954, *Jessup & Gray 2554* (CANB 126268); Richmond River, *Beckler* (Z); Wilson's Downfall, 3 Sept. 1911, *Cambage 2809* (NSW 33425); Boonoo Boonoo, Nov. 1904, *Boorman* (NSW 33426); Jennings, Oct. 1901, *Boorman* (NSW 33429); near Tenterfield, *Stuart* (K, syntype); Torrington, Oct. 1911, *Boorman* (NSW 33431); Bismuth, via Deepwater, Aug. 1913, *McNutt* (NSW 33430); Gibraltar Range, NE. of Glen Innes, Apr. 1958, *Williams* (NSW 44089); 27 miles E. of Glen Innes, 1000 m. alt., 4 Oct. 1958, *Williams 625* (NSW 46450); Mount Mitchell, *Beckler* (K, lectotype); top of range near Backwater, 30 Oct. 1929, *Blakely, McKie & Youman* (NSW 33432). Without locality: New England, *F. Mueller* (BM).

Apart from *Notelaea neglecta*, described below, *N. linearis* can be distinguished at a glance from all other species in the genus by its extremely narrow leaves. In juvenile plants it is suspected that they are a little broader perhaps, but one cannot be certain without adequate observations based on living plants. In *N. neglecta* the leaves are a little broader but the two species differ from one another not only by their leaf venation, which is obscure in *N. linearis*, but in the inflorescence length, which is longer in *N. neglecta* (in fact the inflorescence is shorter than in any other species except possibly some representatives of *N. microcarpa*). *N. linearis* is found on siliceous soils in eucalypt forest and is ecologically distinct from *N. neglecta*. *N. linearis* is confined to an area in northern New South Wales and southernmost Queensland, with *N. neglecta* in an even more limited area about 250 miles further south in the Blue Mountains in central New South Wales (MAP 2).

From the type material in the Kew Herbarium I have selected the specimen collected by Beckler and sent to Kew by von Mueller in 1868 as the lectotype because it exhibits both flowers and fruit, whereas the other collection cited in the protologue, the Stuart specimen from near Tenterfield, whilst mounted on the same sheet, bears only one or two young flower buds.

7. **Notelaea neglecta** P. S. Green, sp. nov.

Species foliis angustis (2.5–)4–7(–11) cm. longis, (0.2–)0.3–0.8(–1.4) cm. latis, venatione obscura sed manifesta, inflorescentiis 1–2 cm. longis, drupis parvis 5–6 mm. × 4–5 mm. distincta. A *N. lineari* foliis plerumque longioribus et latioribus, inflorescentiis longioribus (10–20 mm. longis) differt. A *N. microcarpa* foliis angustis, venatione minore prominente, venis primariis sub angulo circiter 40° e nervo mediano exortis, inflorescentiis glabris differt.

Evergreen, probably a shrub; stem minutely puberulous when young, sometimes becoming glabrous. *Leaves* thickish, glabrous, or minutely puberulous above and below at first when young, finely punctate; petiole 1–5(–8) mm. long, minutely puberulent, especially above, often becoming glabrous; lamina very narrowly elliptic or narrowly lanceolate to linear, (2.5–)4–7(–11) cm. long by (0.2–)0.3–0.8(–1.4) cm. broad; margin entire, somewhat thickened; apex elongated, very acute; base acute, long attenuate into the petiole; venation more or less obscure except for the slightly visible primary veins, especially above, often not visible below, (6–)7–10 (–11) per side, making an angle of about 40° with the midrib. *Inflorescence* axillary, 1–2 per axil, decussate, glabrous; 1–2 cm. long, (3–)7–9-flowered; upper bracts early deciduous, broadly ovate to lanceolate, pointed, 1–2 mm. long, somewhat puberulent, especially towards the tip; basal bracts thickish, 1–2 mm. long, acute or acuminate, puberulent, fused bases persistent. *Flowers* hermaphrodite, yellow (?); pedicels (1–)3–5 mm. long. *Calyx* 0.5–1 mm. long with 4 irregularly triangular, more or less erose lobes, 0.3–0.6 mm. long. *Corolla* induplicate-valvate, 1.5–2.25 mm. long, 4 lobes joined in pairs at the filament 0.3–0.5 mm. from their base, concave. *Stamens 2*, 1.25–1.5 mm. long, included within the concave corolla lobes; filament short and broad, 0.2 mm. long. *Ovary* flask-shaped, 1–1.5 mm. long, tapering into an imperceptible style with a bifid stigma 0.2 mm. long. *Drupe* ovoid, globular, 5–6 mm. long by 4–5 mm. broad (NSW 33635).

New South Wales. Capertee, Sept. 1915, *Boorman* (NSW 33618); Jenolan Caves, Sept. 1899, *Blakely* (NSW 33620, holotype; A, K, & NSW 33621, isotypes), 5 Sept. 1923, *Cheel* (NSW 33623), 29 Oct. 1940, *Blakely & Ludowici* (A, K, NSW 33619); Colong-Yerranderie, 5 Oct. 1909, *Cambage 2268* (NSW 33624); Wombeyan Caves, Oct. 1905, *Maiden* (A, BRI 8263, K, NSW 33629–31), 1 Oct. 1905, *Cambage 1345* (NSW 33632); Bullio to Wombeyan, Oct. 1905, *Maiden* (NSW 33628); Bowral to Wombeyan, 30 Sept. 1905, *Cambage 1330* (CANB 7610, NSW 33627); Mittagong to Bullio, 28 Nov. 1919, *Cheel* (NSW 33625); Berrima, July 1906, *Boorman* (NSW 33626); Devil's Hole, Tallong, Oct. 1917, *Rumsey* (NSW 33636); Wingello-Tallong, Oct. 1938, *Murphy* (NSW 33633); Tallong (Barber's Creek), Dec. 1897, *Maiden* (NSW 33635), Oct. 1899, *Rumsey* (NSW 33634).

The epithet chosen for this species is intended to reflect the fact that it has been overlooked for many years. L. A. S. Johnson had already recognized it as distinct and segregated the material in the Sydney Herbarium, before it was sent on loan, and I am greatly indebted to him for his helpful notes.

To judge from the names already on the herbarium sheets, this species has previously been confused with *Notelaea linearis* and *N. microcarpa*, presumably because of the general characters of the leaf, which lie roughly between the two. The typical leaf is neither as narrow as that of *N. linearis* nor as broad as that of *N. microcarpa*. The venation is somewhat intermediate as well, more distinct than that in the former and more obscure than the latter. All three are small fruited and undoubtedly closely allied but, although it is possible that they arose from a common stock, or that at some stage *N. neglecta* developed as a stabilized hybrid between the other two, they are distinct today.

Geographically each has its own area of distribution and, to judge from field notes, their edaphic and climatic adaptations are different. *Notelaea neglecta* grows on limestone, and possibly a variety of rocks, but never on the most siliceous. *N. linearis*, on the other hand, is a species of siliceous soils, including "acid granite." *N. microcarpa* occurs on a variety of rocks and, like *N. neglecta*, never on the most highly siliceous, but climatically it is restricted to the "western slopes country" although, at its southern limit, the two species approach one another (MAPS 2 & 3).

Notelaea sect. **Ligustrina** P. S. Green, sect. nov.

A sectione *Notelaea* corollae aestivatione imbricata differt. Flores parvi, hermaphroditi; corollae lobi 4, leviter imbricati, per paria connati vel ope baseos filamenti conjuncti; corollae tubus perbrevis vel nullus. Drupa parva, vel nigra vel purpurea vel rubra vel rosea vel alba.

TYPE SPECIES: *Notelaea ligustrina* Vent.

The separation of this section and the relationships of its single and type species, *Notelaea ligustrina*, are discussed below under that species.

8. **Notelaea ligustrina** Ventenat, Choix de Pl. sub *t.25*. 1804; R. Brown, Prodr. 524. 1810; Sprengel, Syst. Veg. **1**: 35. 1824; Loudon, Arb. Frut. Brit. **4**: 2579. 1838; A. DC. in DC. Prodr. **8**: 291. 1844; Hooker f. Fl. Tasman. **1**: 268. 1857; Meredith, Bush Friends Tasman. *t.2*. 1860; F. Mueller, Pl. Colony Vict. Lithograms, *t.54*. 1864–65; Bentham, Fl. Austral. **4**: 300. 1868; F. Mueller, Fragm. Phytogr. Austral. **8**: 43. 1873 & 142. 1874; Spicer, Handb. Pl. Tasman. 125. 1878; F. Mueller, Syst. Census Austral. Pl. 92. 1882, Key Syst. Vict. Pl. **2**: 39. *fig. 100*. 1885 & **1**: 357. 1887–8, & Second Census Austral. Pl. 156. 1889; Maiden, Useful Native Pl. Austral. 579. 1889; C. Moore, Handb. Fl. New S. Wales 321. 1893; Rodway, Tasman. Fl. 128. 1903; Dixon, Pl. New S. Wales 215. 1906; Maiden & Betche, Census New S. Wales Pl. 172. 1916; Ewart, Handb. Forest Trees Vict. Foresters 406. 1925, & Fl. Vict. 941. 1930; Anderson, Trees New S. Wales ed. 2. 132, 338. 1947; Audas, Native Trees of Austral. 242 [1935]; Bean in Chittenden, Dict. Gard. **3**: 1379. 1951; Curtis, Students' Fl. Tasman. 470. *fig. 108*. 1967.

Gymnelaea ligustrina (Vent.) L. Johnson, Contr. New S. Wales Natl. Herb. **2**: 414. 1957.

Nestegis ligustrina (Vent.) L. Johnson in Degener, New Ill. Fl. Hawaiian Is. 300, Nestegis. 1958.

Tall evergreen shrub or small tree to 6 or even 12 m. high; young stems minutely puberulous, often densely so, at least when young, or rarely almost glabrous. *Leaves* glabrous, petiole 2–7(–12) mm. long, glabrous or minutely puberulous when young, especially above; lamina thick or thickish, coriaceous, narrowly lanceolate or lanceolate (rarely narrowly ovate) (2–)3–6(–8.5) cm. long by (0.4–)0.7–1.2(–2.5) cm. broad, scattered punctate above and below; margin entire, flat; apex acute, tip acute or obtuse; base acute or subcuneate, attenuate into the petiole; venation obscure above and below, rarely with (4–)5(–6) primary veins per side just visible. *Inflorescence* axillary, 1–2(–3) per axil, decussate, 1.5–2.5 (–3.5) cm. long, (7–)9–11(–13)-flowered (rarely 3–4 flowers at each node), glabrous, sometimes minutely and scattered puberulous, especially towards the base; upper bracts narrowly lanceolate, early deciduous, 1–1.3(–2) mm. long, ciliolate; basal bracts thickish, 1–1.5 mm. long, glabrous or minutely puberulous, acute, relatively early deciduous, fused bases of basal pair persistent. *Flowers* small, hermaphrodite (Fig. 3), yellowish to greenish-white; pedicels 2–6(–7) mm. long (4–10 mm. long in fruit). *Calyx* glabrous, very short tube 0.1–0.4 mm. long with 4 acute, triangular or ovate-triangular lobes 0.4–1 mm. long, usually entire. *Corolla* with 4 ovate, acute, slightly imbricate lobes, tube very short or nil, lobes paired, bases joined for 0.5–0.7 mm. at base of stamen, joined or adnate for 0–0.2 mm. between pairs, free portion of lobes 0.8–1.5 mm. long. *Stamens* 2, anthers 1.3–1.5 mm. long, elliptic or broadly elliptic with scarcely discernible terminal appendage; filament 0.1–0.4 mm. long. *Ovary* bottle-shaped, 0.8–1.5(–2) mm. long including gradually tapered style, 0.5 mm. long, with 2 narrow stigmatic lobes 0.5 mm. long (elongating to 1 mm. after corolla and stamens shed ?). *Drupe* fleshy, black, purple, red, pink or white, ovoid-spherical, 8–12 mm. long by 6–10 mm. diameter; endocarp crustaceous, 0.1 mm. thick.

SELECTED EXSICCATAE. **New South Wales.** Tuross River, Apr. 1933, *Arnold* (NSW 33398); 8 miles W. of Pericoe, WSW. of Eden, about 900 m. alt., 28 May 1952, *Floyd* (NSW 33399).

Victoria. Upper Genoa River, *F. Mueller* (K); Delegate Mt., May 1949, *Costin* (NSW 33400); Bonang, Feb. 1899, *Bäuerlen* (NSW 33402); about 31 miles NNE. of Buchan, Gippsland, 21 Jan. 1953, *Melville 3043* (K); Mt. Buffalo, subalpine, under 1200 m. alt., 11 Jan. 1950, *Stewart* (BRI 7909); 16 Mile Creek, near its confluence with Howqua River, about 730 m. alt., 11 Apr. 1959, *Muir*

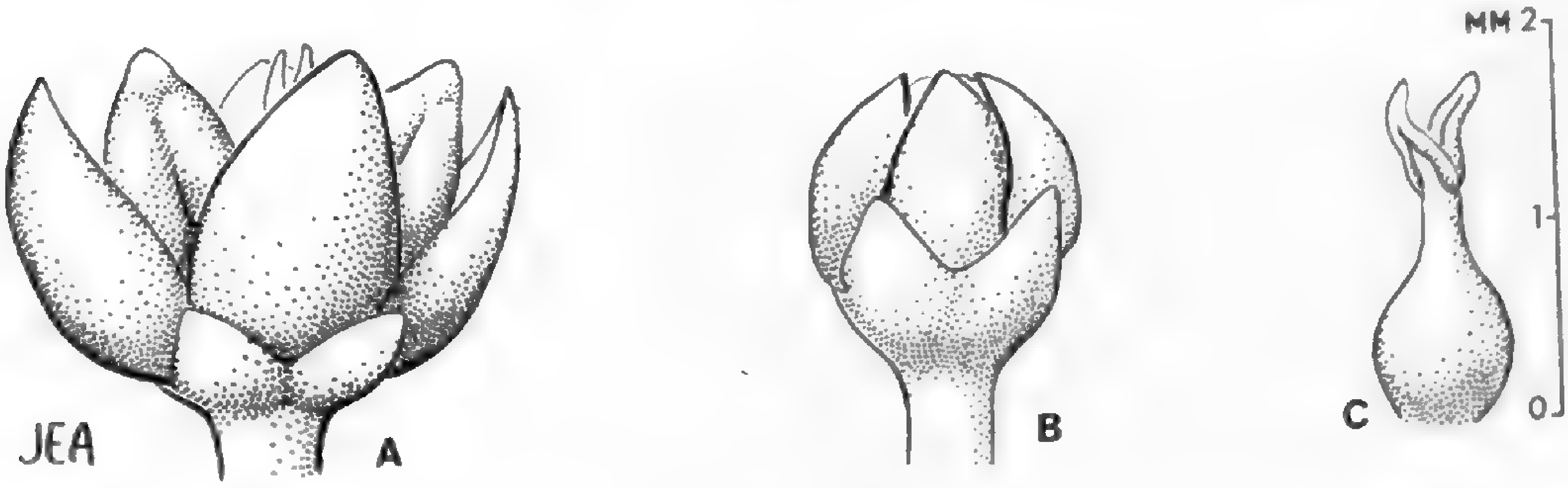


FIG. 3. *Notelaea ligustrina.* A, flower; B, bud; C, ovary. (Drawn from *Comber 2189*).

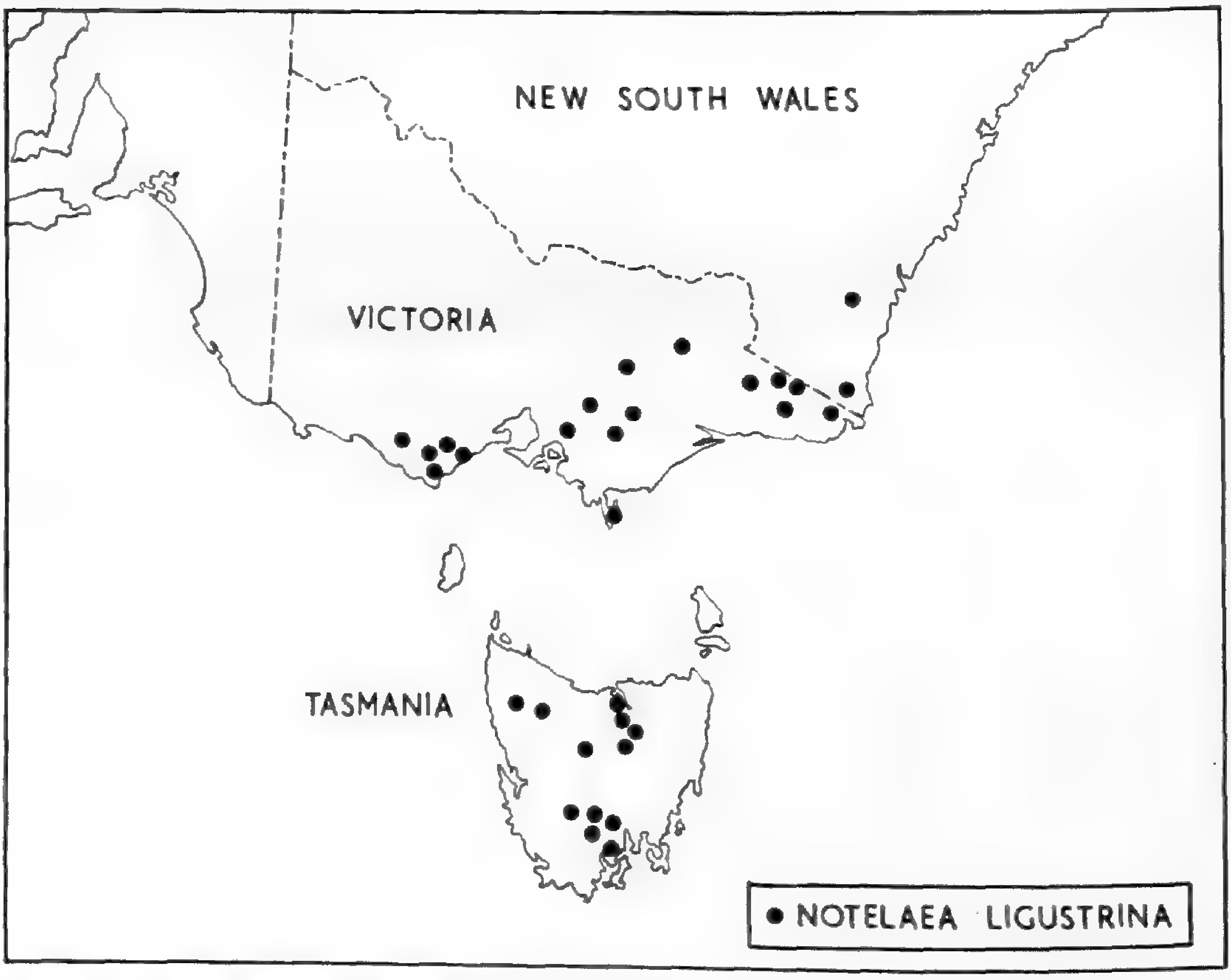
744 (A, K); Upper Yarra, Apr. 1911, *Staer* (NSW 33404); Sherbrooke Forest, Dandenong Ranges, Dec. 1932, *Willis* (K); Sealer's Cove, *Walters* (GH); Lutitt [Loutit] Bay, *F. Mueller* (BM); Cape Otway, *F. Mueller* (GH); Curdie's River, Nov. 1898, *Walter* (Z).

Tasmania. Hazelwood River near Waratah, edge of river, 180 m. alt., 3 March 1930, *Comber 2189* (E, K); Port Dalrymple, *R. Brown* (BM); Cataract, Launceston, 20 Oct. 1880, *Simson 551* (BRI 7908, LE); Launceston, 22 Jan. 1842, *Gunn* (BM, K); Ironstone, Dec. 1899, *Rodway 6224* (NSW 33434); Mt. Field, Nov. 1895, *Rodway 6223* (NSW 33433); Glen Leith, 14 Sept. 1840, *J. D. Hooker* (K) & 18 Dec. 1840, *Gunn* (GH, NSW 41468); River Derwent, 1804, *R. Brown* (BM, E); "ad ripas fluvium, in clima d'Entracasteaux," [1801], *Leschenault*, ex Herb. Jussieu & Ventenat (G, holotype). Without locality: [1804], *R. Brown* (E, G, K, LE, NSW 33406).

Cultivated. TASMANIA. Franklin Square, Hobart, 11 Apr. 1931, *Rodway 6220 & 6221* (NSW 33436). NEW ZEALAND. Botanic Garden, Christchurch, Oct. 1962, Sykes 151/62 (A, CHR 125955).

This species has the southernmost distribution (see MAP 4) and, to judge from various field notes, grows in open sclerophyll forest or scrub dominated by species of *Eucalyptus* and, in Tasmania at least, on river banks throughout the State.

L. A. S. Johnson in his review of the family *Oleaceae* (Contr. New S. Wales Natl. Herb. 2: 395–418. 1957) transferred this species to the resurrected genus *Gymnelaea* (more correctly *Nestegis*) along with the native "olives" of New Zealand and species of *Osmanthus* from New Caledonia



MAP 4. Distribution of *Notelaea ligustrina*.

and Hawaii. The reason for doing this appears to have been the fact that the aestivation of the corolla in this species is different from that of the rest of those from Australia and not typical of *Notelaea*. The corolla in *N. longifolia*, the type species, and in the other species too, is induplicate-valvate in the bud (FIG. 1, A & B), but in *N. ligustrina* the lobes are imbricate (FIG. 3, B). However, the imbrication is not very strong, at least in herbarium specimens, where there appears to be a tendency to induplication, and some adjacent petals are distinctly valvate. Furthermore, when one considers the rest of the corolla structure it is seen to resemble, not that of *Osmanthus*, but other species of *Notelaea*. In *Osmanthus* there is a distinct corolla tube of varying length; in the New Caledonian species the corolla is campanulate with a tube at least 1.2 mm. but usually 1.5 mm. or more long. In *N. ligustrina* the tube is extremely short or nonexistent. At the base of the staminal filaments the adjacent corolla lobes are united for about 0.5 mm. but in the alternate position, where there is no stamen, they may, in some cases, be joined at the base by only 0.2 mm., in other cases they appear to be merely adnate, and in yet others they seem quite separate. This situation, with the petals in separate pairs, joined by the base of the filament, is comparable with that in the rest of *Notelaea*, and, in the family, otherwise found only in *Linociera* and *Chionanthus*.

There is an undoubted strong phytogeographic affinity between Tasmania (and the southeasternmost mainland of Australia) and New Zealand; and it is interesting to speculate how closely the native New Zealand "olives" which, following Johnson (*l.c.*), I have treated in a separate genus *Nestegis* (Jour. Arnold Arb. **44**: 377–389. 1963), are related to *Notelaea ligustrina*. Characters of the corolla are of primary value in the Tribe *Oleeae* yet the New Zealand species are apetalous. However, there are other characters which can be considered. The New Zealand species are almost unique in the family, in the color of their ripe drupes, which is red or orange (although I observed yellow fruits on *Nestegis apetala* on Norfolk Island) and it is interesting to realize that those of *Notelaea ligustrina* are recorded as red, pink, and white, as well as purple and black (presumably very dark bluish purple), the usual color in the tribe. Nevertheless, the ripe fruits in *N. venosa* have been reported to be red or white on occasion and those of *N. punctata* as "varicolored."

It is not without significance, perhaps, to consider the sexuality of the flowers in *Notelaea, Nestegis,* and *Osmanthus* (the genus *Linociera* has not been studied in detail yet but it is suspected that in this respect it is comparable to *Notelaea*). In *Osmanthus* sects. OSMANTHUS and SIPHOSMANTHUS (from temperate and warm temperate Asia) and NOTOSMANTHUS (from New Caledonia) the flowers are androdioecious. In sect. LEIOLEA (tropical and warm temperate North and Central America and warm temperate and tropical Asia and Malesia) they are unisexual or hermaphrodite. In *Notelaea*, including *N. ligustrina*, they appear to be consistently hermaphrodite, but in *Nestegis* (that is the New Zealand species) they are unisexual or hermaphrodite. I am inclined to believe that this latter condition has evolved separately from the basic hermaphrodite condition independently in *Osmanthus* sect. LEIOLEA and *Nestegis*. I also think that *Notelaea* is of Australasian origin and is related on the one hand to *Linociera* and on the other to *Osmanthus* and that just as unisexuality has appeared in sect. LEIOLEA so it has developed from the Australasian stock in the genus *Nestegis* (which has also become apetalous). I feel that *Notelaea ligustrina* stands somewhat between *Notelaea* proper and *Nestegis*, and as a reflection of this have proposed the separate section for its accommodation.

Notelaea ligustrina was described by Ventenat, along with his description of the genus *Notelaea* and its type species *N. longifolia*. His description for *N. ligustrina* was contained in an "observatio" and from it one can assume that the type is a specimen collected by Leschenault along the margins of rivers which open into the "golfe d'Entrecasteaux, près la terre de Dieman" and is to be found in the Jussieu Herbarium. The type might thus be expected to be in Paris but I have seen a specimen, ex herb. Jussieu, from Herb. Ventenat in the Geneva Herbarium, which I believe to be the holotype.

Notelaea sect. **Mischopetala,** P. S. Green, sect. nov.

A sectione NOTELAEA corollae et androecii structura differt. Corolla stamina etiam maturitate valde involvens; antherae parvae, sed connectivum et filamenta magna; corollae lobi geminati et maturitate cum staminibus stipitati.

TYPE SPECIES: *Notelaea johnsonii* P. S. Green.

The remarkable structure of the corolla and androecium of *Notelaea johnsonii*, which is the basis for establishing this monotypic section, is discussed more fully under the species. It appears to represent an independent development from the basic stock, as represented by sect. NOTELAEA.

9. **Notelaea johnsonii** P. S. Green, sp. nov.

Species inflorescentia elongata, staminibus parvis cum anthera parva sed connectivo filamentoque latis, corollae lobis etiam maturitate valde involutis et stipitatis, ab omnibus ceteris speciebus differt.

Evergreen shrub or small tree to 6 m. high; branchlets minutely puberulous to glabrate. *Leaves* glabrous, sometimes more or less punctate; petiole minutely puberulous or glabrate, 2–12 mm. long; lamina thickish, coriaceous, elliptic to narrowly elliptic, sometimes slightly lanceolate, (4–)7–10(–12) cm. long by (1–)1.8–3(–5) cm. broad; margin somewhat thickened, very slightly and extremely shallowly crenulate or entire, sometimes somewhat undulate; apex acute, occasionally slightly acuminate, fine pointed; base acute or obtuse, attenuate into the petiole; venation with primary veins visible above and below, sometimes almost obscure, secondary veins usually obscure, sometimes almost reticulate above and below,

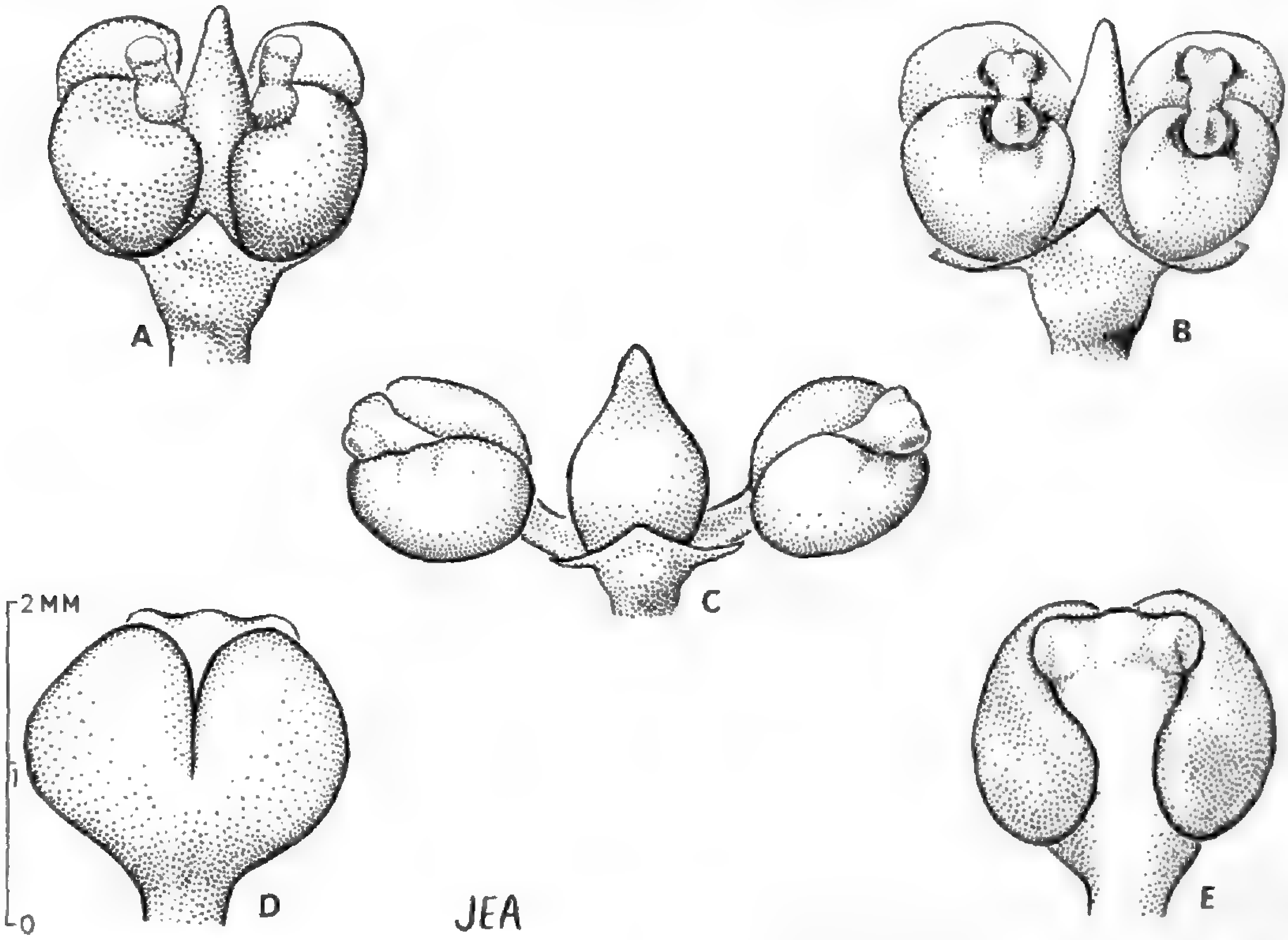


FIG. 4. *Notelaea johnsonii.* A & B, buds; C, flower; D, paired corolla lobes and stamen, dorsal view; E, paired corolla lobes and stamen, ventral view. (Drawn from NSW 42340).

(6–)7–12 primary veins per side. *Inflorescence* axillary, 1(–2) per axil, decussate (4–)5–8 cm. long, 5–11-flowered, occasionally with 3(–4) flowers per node, rachis purplish pink (fide NSW 42340), slender, very minutely and scattered puberulous or with a very few small hairs, at least when young; upper bracts deciduous, unknown; basal pair of bracts thickish 2–3 mm. long, bluntish acute to long acute, glabrous or minutely scattered puberulent, more or less persistent during flowering then deciduous, except for the persistent fused bases. *Flowers* hermaphrodite (FIG. 4), bluish-black (fide NSW 42340); pedicels 3–15 mm. long. *Calyx* 0.75–1 mm. long, with 4 thin, more or less triangular lobes, 0.4–0.5 mm. long, minutely ciliolate, deciduous. *Corolla* of four, fleshy, rounded lobes, joined at the base in pairs 1.25–1.5 mm. long at first, concave and enclosing the stamens, eventually 2 mm. long on a "stalk" 0.5–0.75 mm. long. *Stamens* 2, purplish-pink (fide NSW 42340), 1.25 mm. long, with broad fleshly filament and two small rounded anther lobes 0.3 mm. long borne at the top, with lateral dehiscence. *Ovary* purplish-pink (fide NSW 42340), conical, 1.25–1.5 mm. high, sometimes minutely and scattered puberulent, with a barely perceptible style and very slightly bilobed stigma, 0.1 mm. long. *Drupe* bluish-black, fleshy, obliquely ellipsoid, 1.8–2 cm. long by 0.9–1 cm. diameter.

Queensland. MORETON DISTRICT: Robert's Plateau, Lamington National Park, 900–1200 m. alt., Feb. 1920, *Tryon & White* (BRI 7926, K), & 28 May 1929, *White 6039* (BRI 7916, K); National Park, Macpherson Range, Jan. 1919, *White* (BRI 9694).

New South Wales. Whian Whian State Forest, N. of Lismore, about 600 m. alt., 15 Jan. 1953, *Constable* (NSW 22217); Goonengerry, near Mullumbimby, 7 Nov. 1963, *Hayes* in *Green 1529* (A, K); Bungalow–Byron Bay road, 16 Nov. 1964, *Williams K18* (A, NSW 72725); Wyangarie State Forest, N. of Kyogle, about 900 m. alt., 21 Nov. 1963, *Hayes & Floyd 9* (A); Lismore, Aug. 1906, *Rothwell* (NSW 44053); Wollongbar Experimental Farm, east of Lismore, about 150 m. alt., 11 June 1957, *Johnson & Constable* (NSW 42340, holotype; K, isotype); Rous, 21 July 1925, *Cheel* (NSW 44055); Clarence River, 1868, *Beckler* (BM, K).

This most distinctive species, distinctive at least as far as the flower structure is concerned, is restricted to a relatively small area in northeast New South Wales and adjacent Queensland (MAP 2). Confined to rain-forest, and to judge from the limited field notes to basaltic and basic soils, it is often found surviving today in small patches of rain-forest species left isolated by the spread of cultivation.

The oldest specimen seen for this revision is that gathered by Beckler in the area of the Clarence River and sent to England by Ferdinand von Mueller where it was labelled *Notelaea venosa.* However, most of the material had been determined previously as *N. longifolia,* from which it can be quickly identified by the rather obscure venation of both the upper and lower surfaces of the leaves.

Detailed observations on fresh flowering material would be valuable, but the dried flowers, especially when softened in hot water, show the unusual corolla and stamens. Throughout the other species the petals are joined together in pairs, touch each other laterally and surround the ovary. In this species the pairs are separate even in young flowers (FIG. 4, A & B) and, as they reach maturity, they come to stand on either side of the ovary on a stalk-like structure which is possibly a development of the filament (FIG. 4, C–E). The individual stamens are distinctive too. The anthers are small and completely enclosed in the permanently concave and apparently fleshy corolla, except for the top of the connective and the two small and lateral openings of the pollen sacs (FIG. 4, D & E). Further observations and more collections may well improve our knowledge of this plant and its flower and perhaps show that this species should be distinguished as a separate genus; but for the present its distinctiveness in the genus *Notelaea* is indicated by the provision of a monotypic section.

It is a pleasure to name this plant after Mr. L. A. S. Johnson of the National Herbarium of New South Wales, who has made important contributions to the study of the Oleaceae, has kindly made extensive notes and first-hand field observations on the genus *Notelaea* available to me, and was joint collector of the type material.

EXCLUDED NAMES

Notelaea sect. *Picconia* (DC.) Knobl. in Engler & Prantl. Nat. Pflanzenfam. 4(2): 10. 1892 = **Picconia** DC.

Notelaea austro-caledonica Vieill. Bull. Soc. Linn. Normand. **9:** 345. 1865 = **Osmanthus austro-caledonicus** (Vieill.) Knobl.

N. azorica Tutin, Jour. Bot. **71:** 101. 1933 = **Picconia azorica** (Tutin) Knobl.

N. badula Vieill. ex Panch. & Sebert, Not. Bois Nouv.-Caléd. 184. 1874 = **Osmanthus austro-caledonicus** (Vieill.) Knobl.

N. brachystachys Schltr. Bot. Jahrb. **39:** 228. 1906 = **Linociera brachystachys** (Schltr.) P. S. Green.

N. collina Schltr. Bot. Jahrb. **39:** 229. 1906 = **Osmanthus austro-caledonicus** (Vieill.) Knobl.

N. cymosus Guillaum. Bull. Soc. Bot. France **89:** 232. 1943 = **Osmanthus cymosus** (Guillaum.) P. S. Green.

N. eucleoides Schltr. Bot. Jahrb. **39:** 229. 1906 = **Osmanthus austro-caledonicus** (Vieill.) Knobl.

N. excelsa (Ait.) Webb & Bert. Hist. Nat. Il. Canar. 3(2) (Phyt. Canar. sect. 3): 163. 1845 & *t.186.* 1848 = **Picconia excelsa** (Ait.) DC.

N. flavicans (Vahl) A. Dietr., Linn. Sp. Pl. ed. 6, **1:** 246. 1831; D. Dietr. Synop. Pl. **1:** 38. 1839 = **Noronhia emarginata** (Lam.) Thouars ex Hook.

N. francii Guillaum. Bull. Mus. Hist. Nat. Paris **28:** 198. 1922 = **Linociera brachystachys** (Schltr.) P. S. Green.

N. glandulosa Panch. ex Guillaum. Ann. Mus. Col. Marseille II. **9:** 192. 1911, *nomen in syn.* = **Olea paniculata** R. Br. (*O. thozetii* Panch. & Sebert).

N. lanceolata Teijsm. & Binn. Nat. Tijdschr. Ned. Ind. **27:** 33. 1864 = **Linociera montana** (Bl.) G. Don. TYPE: Java, *M. Binnendyck* (BOG, K).

N. monticola Schltr. Bot. Jahrb. **39:** 229. 1906 = **Osmanthus monticola** (Schltr.) Knobl.

N. ? paniculata Guillaum. Bull. Soc. Bot. France **89:** 233. 1943 = **Linociera paniculata** (Guillaum.) P. S. Green.

N. posua D. Don. Prodr. Fl. Nepal. 107. 1825 = **Osmanthus fragrans** Lour.

N. quadristaminea (F. Muell.) Hemsl. Ann. Bot. **10:** 243. 1896 = **Linociera quadristaminea** (F. Muell.) Knobl.

N. rostrata Teijsm. & Binn. Cat. Hort. Bogor, 122. 1866, *nom. nud.* = **Linociera montana** (Bl.) G. Don. TYPE: Java, *M. Binnendyck* (BOG, K).

N. rostrata Teijsm. & Binn. var. *latifolia* Teijsm. & Binn. *l.c.* 1866, *nom. nud.* = **Linociera montana** (Bl.) G. Don. TYPE: Java, *M. Binnendyck* (K).

N. rostrata Teijsm. & Binn. var. *oblongifolia* Teijsm. & Binn. *l.c.* 1866 = ? **Linociera montana** (Bl.) G. Don. TYPE: not seen.

N. vaccinioides Schltr. Bot. Jahrb. **39:** 230. *fig. 22.* 1906 = **Osmanthus austro-caledonicus** (Vieill.) Knobl.

N. zeylanica Gardner ex Thwaites, Enum. Pl. Zeyl. 188. 1860, *nomen in syn.* = **Olea polygama** Wight.

N. zollingeriana Teijsm. & Binn. Nat. Tijdschr. Ned. Ind. **27:** 33. 1864 = **Olea maritima** Wall. ex G. Don. TYPE: Java, *M. Binnendyck* (K, L).

ROYAL BOTANIC GARDENS, KEW
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GREAT BRITAIN

COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, XVII.

PRELIMINARY OBSERVATIONS ON THE PROBLEM OF TRANSITIONS FROM BROAD TO TERETE LEAVES [1]

† I. W. BAILEY [2]

TWO OF THE MOST significant phenomena in adaptations of the Cactaceae for survival in arid environments are (1) the retention of moisture in abundantly occurring "mucilage" and (2) the reduction of leaves in Opuntioideae and their elimination in Cereoideae *with concomitant transfer of photosynthetic activity to green parts of stems.* Both phenomena merit more extensive and intensive investigation from morphological, ecological, physiological, and biochemical points of view than they have received thus far.

A morphologically and phylogenetically important aspect of the second phenomenon is the question, how many transitions from ancestral broad leaves to terete ones have developed in the Opuntioideae? In my extensive collections of *Pereskia*, *Pereskiopsis*, and *Quiabentia* I have not encountered such transitions up to now. However, they do occur in certain representatives of the Opuntioideae, particularly in *Opuntia subulata* (Muehlenpf.) Engelm.

In my collection of this plant [*Moran 7268*] the leaves are relatively large and persistent. The vasculature in the shorter, broader, less frequently occurring ones closely resembles that which occurs in leaves of comparable forms and sizes of *Quiabentia pereziensis* Backbg. (compare FIGS. 1 and 2). In both cases the venation of the appendages is palmate as in *Pereskiopsis* and *Quiabentia*, rather than dominantly pinnate as in the large, thin leaves of such more primitive pereskias as *P. sacharosa* Griseb., *P. grandifolia* Haw., *P. bleo* DC., and related species. For discussions of variations in the venation of leaves and cotyledons and their phylogenetic significance, see 1960 and 1965.[3]

In *Opuntia subulata* (*Austrocylindropuntia subulata* (Muehlenpf.) Backbg.) none of the abundant more elongated leaves, although relatively slender, are truly terete, i.e., circular in cross section. All of them exhibit

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† This paper was completed by Professor Bailey shortly before his death on May 16, 1967. He had planned the illustrations and discussed them with the artist, Elmer W. Smith, who completed them subsequently.

[1] *Terete* is defined in standard dictionaries as cylindrical and tapering with circular cross section.

[2] This investigation was supported in part by a grant from the National Science Foundation, GB-2935.

[3] Previous papers of this series are listed by their dates of publication.

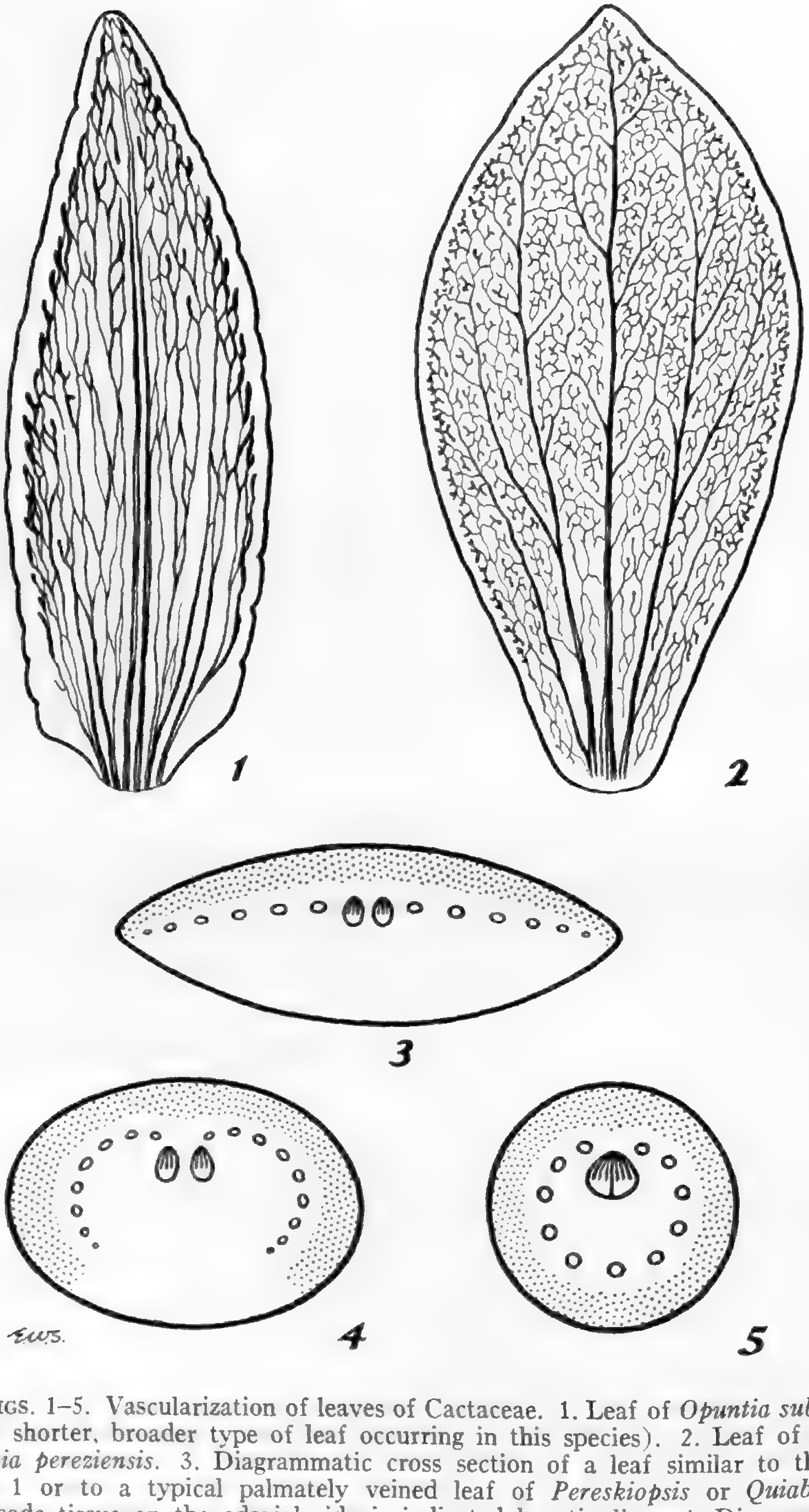
more or less extensive broadening laterally. The two systems of veinlets in opposite sides of the lamina are derived largely from independent vascular strands extending outwardly from the base of palmately veined appendages, except in the upper central parts of the leaves where more or less numerous veinlets may be related to the conspicuous paired vascular traces in the center of the lamina. In such leaves, the two systems of veinlets tend to curve more or less extensively in opposite sides of the lamina toward the abaxial surface (FIG. 4). As they do so, more or less characteristic palisade tissue becomes concomitantly extended laterally, but does not jacket the abaxial surface.

In contrast to this, the evanescent truly terete leaves of such opuntias as *Opuntia ficus-indica* (L.) Mill. and *O. cylindrica* (Lam.) DC., particularly during earlier stages of their development, are jacketed by palisade tissue (FIG. 5). In such tiny terete leaves, the vasculature is much modified. The paired traces in the center of the lamina commonly are massive in appearance and exhibit frequently occurring fusions. Independent vascular strands in the basal part of the lamina tend to be eliminated. The two systems of veinlets in opposite sides of the lamina, although reduced and modified, commonly tend to be conspicuously coarse and related to the two more or less fused mid-veins in the center of the lamina rather than to independently occurring lateral vascular strands as in the large leaves of *O. subulata*.

In my collections of *Opuntia ficus-indica* preserved in FAA the leaves vary from circular to oval and exhibit conspicuous adaxially oriented curvatures which may have been intensified during fixation and dehydration. In some of them the two systems of coarse veinlets coalesce in the abaxial side of the lamina (FIG. 5), whereas in others they fail to do so. According to Dr. Boke (1944, and personal communication) the two systems of veinlets in *O. cylindrica* do not coalesce in the abaxial side of matured leaves.

Thus, in dealing with transitions from broad palmately veined leaves to truly terete ones, there are three trends of phylogenetic specialization which merit detailed consideration. These are (1) changes in the occurrence, structure, and distribution of palisade tissue, (2) alterations in the principal vascular strands that extend outward from the base of palmately veined appendages, and (3) reduction and modification of two systems of veinlets in opposite sides of the lamina.

The large, thin, pinnately vascularized leaves of primitive pereskias do not form typical palisade tissue on their adaxial side. However, there is a more or less conspicuous tendency to do so on the adaxial side in the case of the palmately veined leaves of *Pereskiopsis* and *Quiabentia* (FIG. 3). It is evident in the limited collections available to me that the second and third trends of morphological specializations in terete leaves are not consistently similar in minor details of structure, even in different leaves from the same plant. Therefore, it is essential to obtain and compare leaves from as many representatives of the Opuntioideae as possible in a com-



FIGS. 1–5. Vascularization of leaves of Cactaceae. 1. Leaf of *Opuntia subulata* (the shorter, broader type of leaf occurring in this species). 2. Leaf of *Quiabentia pereziensis*. 3. Diagrammatic cross section of a leaf similar to that in FIG. 1 or to a typical palmately veined leaf of *Pereskiopsis* or *Quiabentia*. Palisade tissue on the adaxial side is indicated by stippling. 4. Diagrammatic cross section of one of the more abundant elongate leaves of *Opuntia subulata*.

prehensive search for additional transitional stages in the development of terete leaves. Such an extensive investigation is being undertaken by Professor Norman Boke and myself.

In comparing the form and vasculature of modified leaves, it is necessary to avoid utilizing the appendages that occur on the uppermost external surface of the invaginated tori of flowering shoots. Such modified leaves in the Pereskioideae and Opuntioideae frequently exhibit conspicuous broadening at their base and patterns of vasculature which simulate those that occur in the first-formed tepals on the inner surface of the invaginated tori. These foliar modifications obviously present an independent phylogenetic problem and one that merits detailed investigation in the future. Therefore, in searching for transitions from broad leaves to terete ones, I have focused attention upon the foliar appendages of vegetative shoots and have avoided those occurring on the uppermost invaginated part of flowering ones.

Although possible variations in the form and major details of vasculature in the leaves of additional representatives of the Opuntioideae merit investigation, there is, even in limited collections now available, cogent evidence of the derivation of terete leaves from broad, palmately veined ones. It should be emphasized in this connection, that without knowledge of significant transitional stages occurring in such opuntias as *Opuntia subulata*, it might be erroneously assumed *a priori* that the highly modified vasculature of terete leaves is developed by transitional modifications of broad pinnately veined appendages.

The only cactus that I know of, exclusive of the Opuntioideae, which forms truly terete leaves is the genus *Maihuenia*. Three collections of *M. poeppigii* (Otto) Weber, obtained from Chile by Hutchison in 1951, are under cultivation at the University of California Botanical Garden in Berkeley, California. These plants have grown well in the open, flowering and fruiting annually. In material kindly sent to me [*Hutchison 306*], the numerous short, slender branchlets in the upper part of a plant bear compact clusters of terete leaves terminally. In such branchlets there is a more copious production of "mucilage" than I have observed in any other cactus. Furthermore, there is a very precocious development of encasing periderm in parts of stems immediately subtending the cluster of terminal terete leaves. Photosynthetic activity appears to be largely confined to these long-persistent appendages. The terete leaves at maturity are jacketed on all sides by very conspicuous palisade tissue which contains much enlarged and elongated mucilage cells. As in terete leaves of opuntias, there is a similar tendency for fusion of the paired traces in the center of the lamina, and the two systems of coarse veinlets coalesce in the abaxial side of the appendages.

Palisade tissue extends laterally but does not cover abaxial surface. 5. Diagrammatic cross section of truly terete leaf of *Opuntia ficus-indica*. Palisade tissue extends all around. (Figures not drawn to scale.)

DISCUSSION

In previous papers of this series, I have emphasized that the Cactaceae provide unusually comprehensive evidence in the study of highly divergent trends of morphological specializations. These are so bizarre and so closely correlated from ecological and physiological points of view with adaptations for survival in excessively arid environments as to leave few uncertainties regarding the major directions in which phylogenetic changes are progressing.

The most primitive surviving representatives of the Cactaceae from both reproductive and vegetative points of view are considered to occur in the genus *Pereskia.* Such better known species as *P. sacharosa* Griseb. (1962), *P. grandifolia* Haw. and *P. bleo* DC. (1963c), with their large, thin leaves have long been recognized by taxonomists as having a habit of growth and absence of conspicuous succulence characteristic of many typically woody dicotyledonous trees and large shrubs. The leaves of these species have dominantly pinnate vasculature, and photosynthetic activity is largely confined to them. In contrast to this, the relatively thick leaves of *Pereskiopsis* and *Quiabentia* (1960) have prevailingly pseudo-palmate and palmate vasculature. Photosynthetic activity occurs both in leaves and in green parts of succulent elongating shoots (1964a).

Incipient stages of transition from pinnate to pseudo-palmate venation occur in some of the morphologically more specialized species of *Pereskia*, particularly in *P. pititache* Karw. and allied taxa (1960). Summations of evidence from leaves and cotyledons demonstrate that the transitions in vasculature of the Cactaceae are from pinnate to palmate, rather than *vice versa* (1965). Furthermore, incipient modifications of that dense, strongly lignified secondary xylem of such primitive pereskias as *P. sacharosa* and *P. grandifolia* (1963c) occur in various morphologically more specialized species (1962, 1963a, 1963b, 1963d).

However, *Pereskiopsis* and *Quiabentia* differ significantly from *Pereskia* in the absence of sclereids in their secondary phloem (1961a) and in the structure of the outer tissues of their succulent stems. In young green stems of *Pereskiopsis* and *Quiabentia*, there is a precocious development of a crystalliferous hypodermis which is subtended by compact collenchymatous layers and in turn by thin-walled chlorenchymatous tissue (1961b and 1964b). The form of the druses in the hypodermal layer is consistently and characteristically compact and rotund, rather than stellate as in the druses of softer tissues in internal parts of the stems. It is of interest in this connection from functional physiological points of view that there are no intercellular spaces in the apparently impervious collenchymatous layers, the only means of gaseous communication between stomata and intercellular spaces in the chlorenchyma being through special channels in the collenchyma which are jacketed by thick unpitted walls and which tend to have a tenuous inner lining of cutin.

Although a crystalliferous hypodermis is absent in pereskias, and a structurally homologous form of hypodermis does not occur in the Cereoideae, it develops in characteristic diagnostic form in *Opuntia* and related genera of the Opuntioideae, being present in representatives having flattened green stems, e.g. *O. ficus-indica,* as well as those with cylindrical green shoots, e.g. *O. cylindrica.* It provides significant evidence of relatively close genetic relationships and supports taxonomists (Backeberg, 1966) who include the broad-leaved genera *Pereskiopsis* and *Quiabentia* in the subfamily Opuntioideae. It strengthens my conclusion that the vasculature of terete leaves in this subfamily develops by modifications of palmately veined appendages.

At present the taxonomic affinities of *Maihuenia* with its terete leaves are obscure and uncertain. To place this genus with its highly specialized stems and xylem in the primitive subfamily Pereskioideae (Backeberg, 1966) appears to be premature and discordant. To include it in the Opuntioideae merely on the basis of its terete leaves would be equally unreliable. Similarities in the vasculature of these terete leaves may be due to parallel or convergent evolution rather than indicative of close genetic relationship. Similarities in its pollen and in the highly modified structure of its secondary xylem are suggestive of possible relationship to the Cereoideae, but other morphological features of the genus raise doubts about such a relationship. It is evident that summations of evidence from all organs of the plant and from all species of the genus must be obtained and harmonized in order to determine, if possible, its taxonomic relationships.

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BOTANICAL NAME OF THE TEA SAGERETIA OF CHINA

MARSHALL C. JOHNSTON

THE PAUPER'S TEA of China was first described by Linnaeus' one-time student and collector, Pehr Osbeck, on page 232 of his "Dagbok öfwer en Ostindisk Resa . . ." published in 1757. The short descriptive paragraph, freely translated from the Swedish, reads as follows:

> *Rhamnus Thea*, or Pauper's Tea, is a fathom-high bush, the leaves of which are similar to those of common tea; but the flowers belong to the first Ordo of the fifth Class, are quite small and are fastened to the far ends of the branches which are again branched. Used as a tea by the poor, but in this place [the Danish Island] it served as a hedge. Called "Tja" [i.e., tea] in Chinese.

Linnaeus himself included some of Osbeck's Chinese plants in the 1753 edition of the *Species plantarum* (William T. Stearn, Introduction to the Ray Society facsimile edition, 1957), but not the pauper's tea. He did not notice the species in print until 1771 when, on page 207 of the *Mantissa*, he re-named it *Rhamnus theezans*. Immediately under his phrase-name, Linnaeus cited as a synonym the "Rhamnus Thea Osb. it. 232," and he followed this with an unusually full description. Linnaeus' epithet has been used for the same species ever since 1771. In 1826 it was combined with the generic name *Sageretia* A. Brongn. The name *Sageretia theezans* has survived in recent years because of the faith placed in the careful bibliographic work of C. Schneider (Pl. Wilson. 2: 227. 1914) and A. Rehder (Bibliogr. of Cult. Trees and Shrubs 436. 1949). Schneider and Rehder both deemed Osbeck's name a "*nomen nudum*" or a "*nomen*." They presumably considered Osbeck's few comments insufficient to constitute a description.

The question must be raised again, however, whether Linnaeus' name can stand under the present code of nomenclature. If Osbeck's name can be clearly typified, Linnaeus' name must be considered a superfluous, unusable synonym, despite the scantiness of Osbeck's description.

Osbeck's collections were turned over to Linnaeus. As far as I can determine through search in various herbaria and through correspondence, the only surviving Osbeck collections from China are those in the Linnaean Herbarium in London. I was able to examine and photograph parts of the Linnaean Herbarium in April, 1967. Two specimens are pertinent here, sheets 262.7 and 262.8 as numbered by Savage (Cat. Linn. Herb. 212. 1945). The latter, 262.8, is a mere fragment pinned to the other. Sheet 262.7 is an excellent flowering specimen, annotated "Rhamnus theezans" by Linnaeus himself. I can find no evidence that Linnaeus received specimens of this species from any other source than Osbeck. In the absence of any information to the contrary, it may be concluded reasonably that 262.7 was prepared in China by Osbeck. I here designate it as the type of both *Rhamnus Thea* and *Rhamnus theezans*. This lectotypification serves to put Linnaeus' synonymy on a firm basis and to make quite clear that his epithet is superfluous and must give way to the prior one of Osbeck. Below, I give the necessary combination and the known and suggested synonymy.

Sageretia Thea (Osbeck) M. C. Johnst., comb. nov.

Rhamnus Thea Osbeck, Dagb. öfwer Ostind. Resa 232. 1757; P. Osbeck, Reise nach Ostindien und China, translated by J. G. Georgi, 210, 302. 1765; P. Osbeck, A voyage to China and the East Indies, transl. and with Faunula and Flora Sinensis by J. R. Forster, **1:** 375. 1771; **2:** 345. 1771.

Rhamnus theezans L. Mant. 207. 1771; J. F. Gmel. Syst. **2:** 398. 1791; Poir. in Lam. Encycl. **4:** 464. 1796; Willd. Sp. Pl. **1:** 1094. 1797; R. & S. Syst. **5:** 281. 1819; HBK. Nov. Gen. et Sp. **7:** 54. 1824; Spreng. Syst. **1:** 767. 1825; DC. Prodr. **2:** 26. 1825.

Sageretia theezans (L.) Brongn. Mém. Fam. Rhamn. 53. 1826; G. Don, Gen. Syst. **2:** 28. 1832; Benth. in Hook. Jour. Bot. **4:** 42. 1852; Benth. Fl. Hongkong. 68. 1861; Maxim. Mém. Acad. St.-Pétersb. ser. 6. **10:** 20. 1866; Miq. Ann. Mus. Bot. Lugd. Bat. **3:** 32. 1867 (as "theesans"); Lawson in Hook. f., Fl. Brit. Ind. I. **1:** 641. 1875; Hemsl. Jour. Linn. Soc. **23:** 131. 1886; Matsamura, Bot. Mag. Tokyo **12:** 22. 1898; C. Schneider, Pl. Wils. **2:** 227. 1914; Rehder, Jour. Arnold Arb. **8:** 166. 1927; Handel-Mazzetti, Symb. Sinicae, **7:** 674. 1933; Rehder, Jour. Arnold Arb. **15:** 13. 1934; Kanehira, Formosan Trees, rev. ed. 428. 1936; Rehder, Bibliogr. Cult. Trees and Shrubs 436. 1949; Li, Woody Fl. of Taiwan 516–518. 1963.

Ampeloplis chinensis Raf. Sylva Telluriana 33. 1838.

Sageretia theezans var. *integra* Dum.-Cours. ex G. Don, Gen. Syst. **2:** 28. 1832, the generic name spelled "Segeretia."

Sageretia theezans var. *diospyrifolia* Lawson in Hook. f. Fl. Brit. Ind. I. **1:** 641. 1875, as "diospiryfolia."

Berchemia Chaneti Léveillé, Repert. Sp. Nov. **10:** 433. 1912.

Sageretia theezans var. *tomentosa* C. Schneider, Pl. Wils. **2:** 228. 1914.

Sageretia Chanetii (Léveillé) C. Schneider, *loc. cit.*, a provisional combination.

Sageretia Hayatae Kanehira, Formosan Trees rev. ed. 426. 1936; this synonymy suggested by Li, Woody Fl. of Taiwan 516–518. 1963.

Sageretia taiwaniana Hosokawa ex Masamune, Trans. Nat. Hist. Soc. Formosa, **28:** 286. 1936; this synonymy suggested by Li, *loc. cit.*

?*Sageretia sikayoensis* Masamune, *loc. cit.*; this synonymy suggested by Li, *loc. cit.*

?*Sageretia theezans* var. *microphylla* Suessenguth ex Suessenguth & Overkott, Repert. Sp. Nov. **50:** 329. 1941; tentative synonymy suggested by Li, *loc. cit.*

Of course, in a genus such as this one, so badly in need of monographic work, the synonymy is tentative at best and subject to much revision. The taxonomy of the Chinese species is particularly chaotic.

It is a pleasure to acknowledge the help of Dr. Illka Kukkonen in translating Osbeck's paragraph, and of Carroll Wood and Bernice G. Schubert in going over the preliminary manuscript and making helpful suggestions. The opportunity to study specimens in the Linnaean herbarium was provided through National Science Foundation grant GB–3138 to the Texas Research Foundation.

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VOLUME 49 NUMBER 4

JOURNAL
OF THE
ARNOLD ARBORETUM
HARVARD UNIVERSITY

Final. [illegible]

OCTOBER, 1968

PUBLISHED BY
THE ARNOLD ARBORETUM OF HARVARD UNIVERSITY
CAMBRIDGE, MASSACHUSETTS

THE JOURNAL OF THE ARNOLD ARBORETUM

Published quarterly by the Arnold Arboretum of Harvard University.

Subscription price $10.00 per year.

Volumes I–XX, reprinted, and back issues of volumes XXI–XLV are available from the KRAUS REPRINT CORPORATION, 16 EAST 46TH STREET, NEW YORK, N.Y. 10017.

Subscriptions and remittances should be addressed to MISS DULCIE A. POWELL, ARNOLD ARBORETUM, 22 DIVINITY AVENUE, CAMBRIDGE, MASSACHUSETTS 02138.

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Volume 49, No. 3, including pages 291–380 was issued July 16, 1968.

Second-class postage paid at Boston, Massachusetts

JOURNAL

OF THE

ARNOLD ARBORETUM

VOL. 49 OCTOBER 1968 NUMBER 4

THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 1. INTRODUCTION AND COMPOSITION STUDIES

RICHARD A. HOWARD

ON THE SUMMITS of mountains in many of the islands of the Antillean archipelago are stunted and dwarfed forests composed of dense stands of contorted shrubs and small trees. The forest floor as well as the stems, branches, and exposed bases of the components of the forest are covered with festoons of bryophytes, almost lined with vascular epiphytes, and intertwined or overburdened with woody and herbaceous twiners. The short vegetation on these mountain tops seems always windswept and bathed in mist and clouds, so that an impression of a wet, cold, nearly impenetrable tangle has led to the appellation of elfin-, mist- or cloud-forest, -woodland, or -thicket. The inaccessibility of these zones, which in most cases involves difficult and uncomfortable travel, has restricted visits by botanists and has resulted in few studies of the biology of such areas.

In the Luquillo Mountains of eastern Puerto Rico, trails and roads to the summit of Pico del Este and El Yunque have made several examples of the dwarfed forest easily accessible. In 1965 a road was constructed to Pico del Este, the easternmost peak of the Sierra del Luquillo where radio and radar facilities were established by the United States government. Access to this road was granted to the Arnold Arboretum staff by personnel of the Institute of Tropical Forestry and the U.S. Navy, and a study site was selected on the undisturbed summit of Pico del Oeste (West Peak) at an elevation of 1050 meters above sea level (FIGS. 1, 2, 3, 4). This peak, on the border of Municipio de Ceiba and Municipio de Naguabo, is located at 18° 16′ 47″ and 65° 45′ 47″; it is but two feet lower than Pico del Este, 50 feet less than El Yunque, and is the third highest peak in the Luquillo range, and fourth highest in Puerto Rico. A small flat-roofed shelter was constructed on the summit to protect instruments, equipment, and personnel and to serve as an observation platform. A study area was marked along a very old and unused foot trail which crossed the summit through the forest. Instruments were secure in this isolated area and individual plants could be marked and studied over an extended time period. The roof of the shelter at the level of the canopy

FIG. 1 (ABOVE). A view of the NE slope of Pico del Oeste from the parking area. Ascent to the trail is made in the grassy area indicated by the figure and arrow. The trail is to the right of the cluster of Prestoea palm.

FIG. 2 (BELOW). A view of the south side of Pico del Oeste, showing the flattened summit. The summit and the observation hut are near the left shoulder on the top. The 10-yard-square transect area is at the right shoulder. The mountain palm appears only in the valleys.

offered a wonderful view of eastern Puerto Rico on rare occasions and permitted close observation of plant and animal activity immediately above the forest. Observations and collections of material were made over a period of nearly three years to determine the answers to three basic but deceptively simple questions: what was present; under what conditions did it live; and what was it doing?

This is the first of a proposed series of papers, to be prepared by the many collaborators, which will describe this dwarfed forest.

This study was supported generously by a grant from the National Science Foundation (GB: 3975) for which I am most deeply indebted. The use of the site within the Luquillo National Forest was made possible by a coöperative agreement with the Forest Service, United States Department of Agriculture, with the endorsement of Dr. Frank Wadsworth, Director of the Institute of Tropical Forestry, Río Piedras. All participants in the field study share my deep and personal indebtedness tó Mr. Joseph B. Martinson, who made available a modern house at a lower elevation which supplied most pleasant living accommodations and a laboratory area for the duration of this project. The continuity of observations was possible only through participation of many members of the staff of the Arnold Arboretum and *pro tempore* associates. I list these individually, for their many contributions are anonymous in the data to follow: Judy Appenzeller, Michael Canoso, Dr. and Mrs. Gordon DeWolf, Jr., Mr. and Mrs. Henry Draper, Mr. and Mrs. Lawrence Evans, Madelon Gauer, William Gensel, William Grime, Thomas Hartley, William McClain, Luis Maldonado, Dulcie Powell, Stephanne Sutton, Robert Wadsworth, Dr. and Mrs. Richard Wagner, Nathaniel Whittier, Carroll E. Wood, Jr., Roy Woodbury, Dr. and Mrs. Donald Wyman.

A special word of appreciation is due to members of my family, my wife, Elizabeth Howard, and my children, Jean, Barbara, and Bruce, for the tedious work of collection and measurement of components of the forest during two summers.

The professional collaborators who took part in this study directly or used material collected by others will present their own observations individually or jointly. Dr. Harold Baynton and his associates at the National Center for Atmospheric Research, Boulder, Colorado, assumed responsibility for the meteorological data compiled from their own equipment installed in the study area. Malcolm Gill and Walter Lyford of the Harvard Forest studied the roots of the plants and the soils, respectively. Margaret Fulford and students from the University of Cincinnati collected the liverworts, which dominate the non-vascular epiphytic flora. John Foerster of the University of Connecticut will report on the algal components of the area. Henry Imshaug and his students have studied the lichen flora. Harvey A. Miller of Miami University and the University of Washington, and his associates, collected mosses and other bryophytes. Georgia Persinos of the Massachusetts College of Pharmacy supervised the analysis of much material for alkaloid and other chemical constituents. Additional studies on the biologically active constituents of certain spe-

FIG. 3 (ABOVE). The ridge of the Luquillo Mountains extending in a southeasterly direction. The radar dome on Pico del Este is evident on the cloudy day. Pico del Oeste, although a bit lower, dominates this picture and is marked by an arrow.

FIG. 4 (BELOW). A view of the uniform canopy of the summit of Pico del Oeste. The observation hut and instrument shelter is to the right of the aluminum tower holding the wind generator. *Tabebuia rigida* and *Ocotea spathulata* dominate the canopy vegetation.

cies have been undertaken by the National Institutes of Health and the laboratory of Dr. Norman Farnsworth of the University of Pittsburgh. Dr. Richard Wagner conducted many studies of the phytochemistry of individual species of the vegetation, and with Mrs. Wagner, was responsible for drying and shipping many hundreds of pounds and numerous packages of study materials. Rolla Tryon of the Gray Herbarium identified the pteridophytes collected by others on Pico del Oeste. David Gates of the Missouri Botanical Garden contributed to our knowledge of the physics and environment of the dwarfed forest. William Theobald of Occidental College is investigating the anatomical structure of the woody species. J. L. Lappuck and his associates at the Waltham Laboratories completed the analysis of a series of water samples. Alfred Fordham, propagator of the Arnold Arboretum, has investigated the germination and rooting of many plants of the area and cared for the many species grown at the greenhouses of the Arnold Arboretum. My colleague and companion on much of the work, Lorin I. Nevling, Jr., has been responsible for studies of the floral biology and phenology, the distribution of airborne particles, and the cytological investigations.

PREVIOUS AND COMPARABLE STUDIES

Mist or cloud forests in which the component plants support an extensive layer of non-vascular epiphytes and therefore could be called a mossy forest have been reported for many tropical countries in Asia, Africa, Australia, Central and South America, and in the West Indies. P. W. Richards' excellent summary *The Tropical Rain Forest* (1964) offers many references to basic papers applying to such areas which should be consulted for detailed descriptions. In a chapter on the tropical rain forest at its altitudinal and latitudinal limits, Richards stated that the tropical rain forest with altitudinal ascent "gives way to a formation-type which it is proposed to call the Submontane Rain forest; this at a still higher altitude is succeeded by another formation-type, the Montane Rain forest. In many places, especially on exposed ridges and isolated peaks, the Montane Rain forest consists of dwarfed crooked trees smothered with an overwhelming abundance of epiphytes, especially hepaticae and mosses; this very characteristic type of vegetation is often called Mossy forest or Elfin woodland."

Asia

Seifriz (1923) describes a mossy forest on Mount Gedeh in Java at 5,500 ft. and near the summit at 8,000 ft. where tree species are few and the plants crooked, "moss-bedecked" and laden with vascular epiphytes.

Van Steenis (1935) recognized in Malaysia five zones of vegetation in which the critical altitudinal limits proved to be 1,000, 2,400, 4,000, and 4,500 meters. His montane zone of 1,000 to 2,400 meters has the formation-type of vegetation of the montane rain forest including the mossy forest or elfin woodland.

Lane-Poole (1925) described a mossy forest for Papua and New Guinea which occurred at an average altitude of 7,500 ft. His description includes some vivid expressions of the area. "I know of no region in the tropics so hard to traverse . . . it is the saturated condition of the atmosphere and the persistent driving Scotch mist that makes life so desperately miserably cold.

". . . As a rule the wet clouds are down all the daytime and the clinging fog and absence of sunlight combine to depress one unutterably.

"There is only one story of trees and that is about 20 feet high. The trunks are grotesquely large in appearance, but this is due to a cloak of moss which converts a 12 inch diameter which is about the maximum over bark to 24 inches or more.

"What is more striking yet is the spring mattress effect of the ground. The trees put out aerial roots, and these lie well above the soil, but are so covered with moss as to deceive one at first, and when walked over the whole network of roots gives to the foot a springy effect which is rather weird. The species are few and are crabbed, gnarled, crooked and bent. They are blanketted in moss, tufted with a thread-leafed orchid, and they put out great elbows of aerial roots."

The classic work of William H. Brown, *Vegetation of Philippine Mountains*, subtitled "The relation between the environment and physical types at different altitudes" contains a description of the northernmost mossy forest at the top of Mt. Maquiling, Luzon, in the Philippines. Brown found the mossy forest zone between 900 meters and the summit at 1,140 meters. His description parallels that for other mossy forests indicating a forest of a single story, many individuals but few species, abundant mist and reduced sunlight, and the overwhelming abundance of epiphytes. Many comparisons with his biological studies will be possible with the data presented in this and later papers concerning Pico del Oeste.

Australia

L. J. Webb (1959) reports the limited occurrence of a similar formation-type which he called a "microphyll mossy thicket." Its characteristics he noted were a level canopy with stunted uneven trees averaging between 6 and 15 meters in height, abundant epiphytes and the persistent mists.

Africa

There are few comparable reports for a mossy forest formation-type in Africa. Richards quotes J. Lebrun (1936) in a paper I have not been able to consult. Lebrun recognized three zones to a montane rain forest with the forest of the upper zone having something of the character of an elfin woodland. The trees did not exceed 10 to 15 meters in height and their trunks and branches were twisted and irregular. Few species and plants have compound leaves in this forest and the leaves in general are small, coriaceous, and entire. A. W. Exell (1944) mentions a mist forest region at 1,400 to 2,024 meters altitude on São Tomé in which the trees are smaller than in lower zones and the epiphytes even more abundant. Richards concludes that the dwarf mountain forest of East Africa seems in many respects comparable with the dwarf mossy type of montane rain forest in Malaysia.

South America

Within continental tropical America the recent work of P. J. Grubb, J. R. Lloyd, T. D. Pennington, and T. C. Whitmore (1963) concerns a montane rain forest in Ecuador. The bibliography indicates the paucity of detailed studies of mist- and mossy forests in this area. The authors suggest a division of Richards' classification of montane rain forest into two units, a "lower montane rain forest" and an "upper montane rain forest." The latter consists of one stratum of trees, 4.5 to 18 meters tall, lacking buttresses, and with leaf size predominantly microphyllous, climbers uncommon, vascular epiphytes common and non-vascular epiphytes abundant. Although they did not study such a forest type they suggest it "certainly occurs in the Andes, as is apparent from the general descriptions of Weberbauer (1911) and Cuatrecasas (1958)."

The Lesser Antilles

John Beard as a resident forester in the Lesser Antilles during the years of World War II visited most of the islands of the Antilles and published a number of papers on the forest- and vegetation-types which culminated in three outstanding works: *Forestry in the Windward Islands* (1944); *The Natural Vegetation of the Windward and Leeward Islands* (1949); and *The Classification of Tropical American Vegetation-Types* (1955). Grubb and his co-workers find Beard's proposed vegetation classification "unsatisfactory because too great emphasis is placed on the criterion of stratification while the criterion of leaf size is not used at all."

Above the montane rain forest, Beard recognizes woody vegetation types as "elfin woodland" and "montane thicket." The elfin woodland according to Beard is a single storied impenetrable tangle whose height varies from 10 meters down to 1 meter in which the trees are predominantly mesophyllous. Grubb and his associates note that elfin woodland is a term which has been used extensively for forests of similar general aspect in the Old World but that these are predominantly microphyllous. They suggest that "depending on locality it may be best to regard the Elfin woodland as a stunted facies of either the Lower or Upper Montane Rain forest," a classification they propose to indicate a more appropriate reclassification of Richards' montane rain forest. The same authors define their "Lower Montane Rain forest" as consisting of two strata of trees which may have buttresses uncommon or small, the Mesophyll leaf size class, the canopy at 15 to 27 meters; the photophytic climbers uncommon and the skiophytic climbers common, and both vascular and non-vascular epiphytes abundant. Beard (1955) previously stated that the terminology of "*Elfin Woodland* or *Mossy Forest*" is not precise for the type of vegetation found on the mountain peaks in tropical America and suggested "we should correctly speak of montane woodland and elfin thicket; 'elfin woodland' is however an old established name."

Grubb and his co-authors objected to Richards' classification "because there is nothing particularly 'Submontane' about Lower Montane Rain forest." As no one has objected to the fact that mosses may be rare in "mossy forests" where hepaticae abound or that "elves" have not been seen recently in "elfin forests" both terms may still be applied as they have been for years to the unusual, dwarfed, high altitude, mist shrouded, vegetation type of the Caribbean.

Beard (1946) found the elfin formation in Trinidad to be represented by a consociation of stilt-rooted trees, *Clusia intertexta*, only on the summit of El Aripo near 3,085 feet. In addition to this dominant tree there were only six other dicotyledonous trees and a total woody flora of but eleven species.

In Grenada the elfin formation is of "low, gnarled growth of small trees and shrubs 4 to 20 feet high, windswept and festooned with moss." The principal species are *Didymopanax attenuatum, Charianthus coccineus, Ilex sideroxyloides, Byrsonima martinicensis, Ternstroemia peduncularis,* and *Stylogyne lateriflora* . Such areas however are few.

On St. Vincent the trees are from 8 to 12 feet tall on some of the higher ridges and peaks, covered with moss and epiphytes. Stunted and gnarled and windswept formations are comprised of *Charianthus*, *Didymopanax, Ilex*, *Ternstroemia* along with *Prestoea montana*, *Ficus*, and *Clusia* species.

St. Lucia has an elfin woodland capping the principal pitons and this is composed of *Clusia venosa*, various Araliaceae, and the same species of *Ternstroemia* and *Charianthus*.

Stehlé (1937) wrote mostly of the vegetation of Guadeloupe where he was employed. He indicates that at 1,000 to 1,484 meters and derived from dense forest one encounters various associations which occur due to the intensity of ecological factors. These he notes to be abundant rain, accentuated slopes of the soil, rigorous temperature and past and present volcanic action. The forest is transitional from dominance of *Clusia venosa* and *Cyrilla racemiflora* to the semi-arboreal savannas of *Lobelia guadalupensis* and *Didymopanax attenuatum*. On Martinique, outside the influence of past volcanic action, he reports *Clusia plukenetii* plays a similar role.

Dominica has been studied intensively by Hodge (1943, 1954). He stated "The vegetation of the elfin forest is perhaps more interesting than that of any other region of the island, but because of its inaccessibility plant collections in the past have been few and incomplete. The flora is distinct. Few of its members occur in other associations on the island; more endemics and species of restricted range are found here. Near the mountain summits the dwarf trees grow close together, forming a single tight canopy; in fact, the crowns are so enmeshed that it seems almost possible to walk across them."

The dominant species of the mossy forest in Dominica is *Clusia venosa* which can form pure thickets in places. Associated in the formation may be *Charianthus*, *Didymopanax*, *Ilex*, *Hibiscus tulipiflorus*, *Prestoea mon-*

tana, *Freziera*, and *Endlicheria sericea*. Vines are few but a thicket-forming bamboo and a scandent *Mikania* are familiar.

Only the islands of St. Kitts and Nevis within the Leeward islands have peaks of sufficient altitude to develop the cloud or mist cover necessary for the development of a mossy forest. However, a fully developed mossy forest is not found. A concurrent but less detailed study of St. Kitts will be reported in a later paper in this series. A small amount of mossy forest type of vegetation is found on the higher peaks of Mt. Misery, Camp's Mountain, and Verchild's Mountain. Here the major components are the woody genera *Didymopanax*, *Weinmannia*, *Coccoloba*, *Ilex*, *Charianthus*, *Bumelia*, *Cyrilla*, and *Podocarpus*. A comparable type is present in restricted areas at the summit of the principal peak on Nevis.

The Greater Antilles

The work of Forrest Shreve on *A Montane Rain-forest* in Jamaica (1914) describes the forest vegetation of the central range. His studies of forest type, soils, rainfall and cloud cover, transpiration, and light characteristics are cited very frequently. Shreve noted that the montane rain forest gave way to thickets at the summit of Blue Mountain Peak and others. He reported on the frequency of the well-known temperate zone genera, *Vaccinium*, *Hypericum*, *Clethra*, *Lycopodium*, and *Viburnum* which in reality have Andean affinities. Throughout Jamaica as well as in Cuba and Hispaniola the "mossy" forest, in contrast to the area being studied in Puerto Rico, is more open and taller and where low the vegetation is less mossy and more frequently interrupted and discontinuous. Asprey and Robbins (1953) in their survey of vegetation types in Jamaica regarded the elfin woodland at the exposed summits of the northern ridges of the Blue Mountains at 5,000 feet and over as a faciation of the montane mist forest. They noted that the branching was rambling and distorted and frequently began close to the ground. The crowns were sheared and sloping due to wind exposure and little emphasis was made of the mossy characteristic. Asprey and Robbins agreed with Shreve that rain forest was a misnomer and suggested the use of the name montane mist forest since the vegetation in such areas is controlled not by rain but by mist and clouds.

Seifriz (1943) related that the summit of Pico Turquino in eastern Cuba "is credited with an altitude of 6,580 ft. This is not high enough for an alpine meadow in the tropics; its place on Turquino is taken by an alpine thicket. Alpine thickets have been referred to but little owing to their absence on temperate mountains and the paucity of ecological studies in the tropics, but they are very characteristic of mountain tops around the equator. . . The thicket which caps Turquino is a tall one, the slender trees averaging 12 to 15 feet in height. The association is very dense, a machete being necessary to cut one's way through."

Seifriz stated "Whether it is in New England, on the summit of Pangerango in Java, or of Turquino in Cuba, the genera are the same: Vaccinium, Myrica, Viburnum, Smilax, Clematis, Rubus, . . . Hypericum, Vernonia, Pilea, Solanum, Eupatorium, Bidens and the sedge Rhynchospora." However he found "Associated with these familiar northern genera on Turquino are many tropical ones, of which several are endemic. The most abundant tree is *Cyrilla racemiflora* . . . A typical minute-leaved alpine thicket tree is *Rapanea microphylla* (Myrsinaceae). But that family of trees which, more than any other, is certain to be found high on tropical American mountains is the Melastomaceae, and among them the genus Miconia predominates . . .

"Though the summit vegetation is a very heterogeneous mixture, several of the trees in the Turquino alpine thicket are far more abundant than others; one of these is *Haenianthus salicifolius*." Seifriz gives a list of 81 species of trees, shrubs, vines, epiphytes, and terrestrial herbs and ferns clearly indicating the heterogeneous nature of the alpine thicket in Cuba.

Ecological studies of Hispaniola are also few in number. The central mountain range is dominated by *Pinus occidentalis* which does not become involved in thicket formation. Even at higher altitudes the occurrence of tropical species of the Myrtaceae, Melastomataceae, Myrsinaceae and similar families is limited to moist valleys and they are not in any formation which could be compared with a "mossy forest." In the Sierra de Bahoruco range a few peaks possess a mossy forest comparable to that of the Blue Mountains of Jamaica where species of *Weinmannia, Hedyosmum, Miconia, Turpinia, Coccoloba, Vitex, Clidemia, Guettarda, Brunellia* and *Gyrotaenia* form the woody components of contorted thickets and are laden with epiphytes both vascular and non-vascular.

The most detailed study of the mossy forest in Puerto Rico is that of H. A. Gleason and M. T. Cook (1927) as part of their ecological survey of the island. They recognized on the slopes of the Luquillo Mountains a succession from a rain forest to a palm forest, to a mossy forest in correlation with the increase in altitude. The area of El Yunque which they visited is today part of an insular national park and is included in the Luquillo Experimental Forest. Although visited by many people who walk the easier trails the area has been little changed in the 40 years which have passed and extracts from their descriptions remain pertinent.

"In the Luquillo Mountains, the habitat of the mossy forest probably receives the highest rainfall and certainly has the highest average atmospheric humidity. Throughout most of the year, even in the dry seasons, the peaks are wrapped in fog or cloud, raising the humidity nearly or quite to the saturation point, causing rainfall almost every day, and reducing the sunshine to short intervals. . . . As a result of the high precipitation and humidity, the soil of the mossy forest is generally water-soaked and frequently quite boggy, and the vegetation is almost constantly dripping with moisture. . . . the trail traverses a sharp ridge, so narrow that one can look down a steep slope on both sides. Even here, with every opportunity for rapid drainage, the soil is muddy and the pedestrian sinks deeply into it at every step. The soil is also usually thin and in many places the forest floor consists merely of irregular rocks separated by masses of wet muck covered with fallen leaves, dead twigs, superficial roots and prostrate stems . . .

"The trade winds blow almost constantly over the peaks of the Luquillo Mountains. They are so moist that they probably do not affect the water-relations of the vegetation seriously but they do have considerable mechanical effect on the plants, so that over the most exposed portions the vegetation is limited to a height of two to three meters (6–9 feet), and the tops of the plants are shorn to a perfectly uniform level . . .

"There are, then, four environmental conditions which may be of considerable importance in determining the peculiar vegetation of the mossy forest, low temperature, great wind exposure, a water-soaked soil, and an atmosphere of high humidity, frequent fog and mist, and heavy precipitation. Of these, it seems probable that wind is the important factor in differentiating the palm forest from the mossy forest, since the former is regularly limited to the most sheltered sites and the latter to the exposed ridges and peaks; wind also determines the general physiognomy of the mossy forest and induces the development of dwarf trees so characteristic of high altitudes. The other three conditions, but more especially the nature of the soil and the humid atmosphere, seem primarily concerned in preventing the development of the normal rain forest and thereby encouraging the dominance of the mossy forest . . .

"Four species constitute the bulk of the arborescent vegetation: *Weinmannia pinnata* L., *Ocotea spathulata* Mez, *Eugenia borinquensis* Britton, and *Tabebuia rigida* Urban, none of which occurs in the rain forest, except possibly as rare and widely isolated individuals. . . . these . . . together constitute probably 75 per cent. of the dominant trees. Associated with them, but of secondary importance are *Ravenia Urbani* Engler, *Calycogonium squamulosum* Cogn., *Miconia pycnoneura* Urban, *Miconia pachyphylla* Cogn., *Miconia foveolata* Cogn., *Ceratostemma portoricensis* (Urban) Hoerold [*Gonocalyx portoricensis*], *Petesioides yunquense* (Urban) Britton [*Wallenia yunquensis*], *Thibaudia Krugii* Urban and Hoerold [*Hornemannia racemosa*], *Ilex Sintenisii* (Urban) Britton, *Clusia Krugiana* Urban [*Clusia grisebachiana*], *Grammadenia Sintenisii* (Urban) Mez, *Mecranium amygdalinum* (Desr.) C. Wright, and *Cordia borinquensis* Urban. . . . *Marcgravia Sintenisii* Urban and *Marcgravia rectiflora* Tr. & Pl., both common in the palm forest and to a lesser extent also in the rain forest, are also very abundant and constitute a striking feature of the vegetation."

At a lower elevation ". . . these species grow into trees eight to twelve meters (25–40 feet) high. They differ from the trees of the rain forest in aspect, having usually crooked trunks and more branches, and even at this altitude the abundance of mosses, Selaginella, and epiphytes is striking. With increase in altitude and especially with full exposure to the wind, the stature of the trees is reduced. . . .

"Toward their lower limits, the larger size and spreading branches of the trees leads to their rather open spacing. At higher altitudes and with decreased stature they are more closely crowded, until at the summit . . . they form a dense thicket of crooked, gnarly, interlaced stems, through which vision can seldom penetrate farther than three to five meters (10–15 feet).

". . . The trees are covered to a height of three or four meters (10–12 feet) with a thin layer of moss, while mosses carpet a considerable portion of the forest floor. The density of this growth increases toward the peak . . . until the ground is completely covered with dense mats of *Selaginella Krugii* Hieron., covering the irregular surface of the ground, hiding the rocks and creeping up the tree trunks to a height of a meter. Above the Selaginella, the trunks of the trees are entirely covered with a dense coat of several species of mosses and hepatics, in which the pendent stems are 10–15 cm. long and give the trunk an apparent diameter far greater than its actual size. This covering extends up the trees and out to the smaller twigs, completely obscuring the bark and making all the trees look precisely alike, except for their leaves, which are also well covered with smaller species of hepatics. In such a condition, the differences between terrestrial and epiphytic habitats become negligible and most species of secondary plants grow indiscriminately either on the ground or on the side of the trees."

In a more recent study of the area by Pierre Dansereau (1966) descriptive material is supplemented by many tabular presentations including pictorial charts.

Dansereau selected several sites in the Luquillo Mountains and his categories, numbering 88 with sub-units, include for El Yunque: a sierra broadleaf forest of *Clusia minor*, *Calycogonium squamulosum*, and *Ocotea leucoxylon*; a sierra palm forest of *Euterpe globosa* (*Prestoea montana*); a sierra moss forest of *Tabebuia rigida*, *Podocarpus coriaceus*, and mosses; an elfin forest of *Micropholis garciniifolia*, *Clusia krugiana*, *Tabebuia haemantha*, and *Rapanea ferruginea*; and a high montane scrub of *Eugenia*, *Tabebuia*, *Thibaudia krugii* (*Hornemannia racemosa*), *Ilex sintenisii*, *Ocotea spathulata*, and *Icacorea luquillensis* (*Ardisia luquillensis*).

Dansereau stated, "At the highest levels, below the outcropping and isolated rocks, the palm drops out almost completely and so-called elfin forest develops . . . This formation is less than eight meters high — therefore a scrub by my present standard . . . Like the elfin forest — or the elfin woodland of Beard (1944) — it may have a moss-line at mid-height. The most sarmentose trees are twisted into a very complex network.

"It is tempting to consider this montane vegetation as temperate instead of tropical. The simplicity of its composition, the well-marked dominance of a few species, the importance of mosses, all liken it to woody formation in Madeira or New Zealand. Several of the genera are widespread temperate rain-forest characteristics: *Podocarpus*, *Ardisia*, *Ocotea*, *Alsophila*, *Cyathea*, *Hemitelia*, *Myrica*, *Magnolia*, *Ilex*, *Symplocos* . . . Another feature is the accumulation of humus. One of these

FIG. 5. A view within the elfin forest giving indication of the density of the vegetation and the abundance of non-vascular epiphytes, vines, and such plants as *Dilomilis* and *Vriesia*. Photo. *H. W. Baynton.*

stands . . . had a great depth (35 cm. or so) of fibrous organic matter, a dry peat of sorts."

The forest at the summit of Pico del Oeste showed many of the characteristics included in the beautiful descriptions of Gleason and Cook, yet detailed examination revealed unexpected information relating to the peculiar forest form. I have difficulty applying Dansereau's pictographs and much of his information to Pico del Oeste. The several studies which follow will, I believe, support some previously published ideas of the cloud environment and will also offer alternate explanations of the form and activity of the component species of the forest. Overall it is apparent that the summit dwarfed forests of the Caribbean islands, being small in extent and occurring on small land masses, are different from the mossy forest, the cloud forests, the upper montane rain forests and similar formations previously described in other parts of the world. Their characteristics, however, are similar and the idea of a selection of species within a microclimate is an appropriate one. This is indeed a special ecological niche. The formation-type on Pico del Oeste does differ slightly from that on the summit of El Yunque as well as from those on islands to the south. The material which follows is descriptive of one variation of the elfin forest of Beard.

THE SUMMIT FOREST OF PICO DEL OESTE (WEST PEAK)

The area selected for study on West Peak occurs along a ridge and across the summit of the peak which is flattened into a small plateau, perhaps an acre in extent (FIGS. 1, 2, 3, 4). The shrubs and trees on the easternmost, windswept face form a very dense tangle often less than 2 meters in height or in valleys or protected lees becoming 4 to 5 meters tall (FIGS. 5, 6). On the summit plateau the canopy is 2.5 to 4 meters above ground level and on the lee side of the ridge rock slides form cirques where *Prestoea*, *Micropholis* and *Magnolia* reach 8 to 10 meters in height. Non-vascular cryptogams, ferns, and filmy ferns and *Selaginella* species cover the forest floor throughout. Herbs are scattered individuals or small seed groupings except in the palm glades where ferns and herbaceous dicotyledons form solid stands of vegetation. The exposed roots, the prop roots, the rhizomes and trailing or leaning branches form ridges or cones or peculiarly shaped mounds where the mosses, liverworts and selaginellas occur in thick layers as an epiphytic growth. The trunks and branches are festooned with hanging liverworts and often exhibit shiny masses of gelatinous colonies of algae. Vascular flowering plants occur as epiphytes in this zone, and nearly every species of flowering plant of the forest is found as an epiphyte at least in the immature stage. Herbaceous and woody climbers such as *Ipomoea, Rajania, Hornemannia,* and *Gonocalyx* scramble and climb throughout the shrubs and often form dominating masses as part of the canopy. Long trailing branches of *Marcgravia* make reticulate patterns on the forest floor. The young climbing

FIG. 6. A view of the more stunted vegetation on the windward side of Pico del Oeste. Dr. Howard is 6 feet 5 inches tall. Plants *Tabebuia rigida*, *Ilex sintenisii*, *Miconia pachyphylla*, *Eugenia borinquensis*, and *Calyptranthes krugii* can be discerned.

shoots are flattened and have adpressed leaves in marked contrast to the terete axillary shoots which stand away from the substrate and bear large, lanceolate leaves. These arching and pendent shoots bear the inflorescences at their apices. *Wallenia yunquensis* and *Gesneria sintenisii* exhibit rhizomatous green growth, from which upright shoots develop and form a sub-layer abundant in places and missing in others.

The branching of many of the taller shrubs is dichotomous, presenting one characteristic appearance, while other species display a peculiar growth pattern, horizontal or candelabra-like in nature due to the occurrence of terminal short shoots and lateral long and often repeated shoots, during their development. Slender stem growth is exhibited by *Ilex sintenisii*, *Trichilia pallida*, and *Symplocos micrantha* so that many specimens appear to be scrambling and dependent for support on the surrounding vegetation. The innumerable rosette-forming epiphytes of the Bromeliaceae, *Vriesia* and *Guzmania*, occur in all size classes and exhibit both red photophytic and green skiophytic growth forms. A cane-like orchid, *Dilomilis* is nearly equally abundant, with long erect stems subtended by pendent masses of whitish, green-tipped roots. Frequently, due to insecure attachment or to top-heaviness, these plants are angled or pendent from the normal upright position. Aërial roots are conspicuous on many species as prop roots or adventitious branched or unbranched growths from horizontal stems, or clustered when developed from broken and injured stems. Especially conspicuous are the glistening gelatinous sheaths on the aërial roots of several species.

In open areas along the trail where light reaches the forest floor the grasses *Ichnanthus* and *Isachne* invade and form dense green mats. *Scleria secans*, presumably another invading species, forms tangles of scrambling branches soon noticed for the sharp marginal serrations on the leaves. Clumps of *Carex polystachya* occur on the forest floor, and tangles of the low creeping bamboo-like grass *Arthrostylidium* create barriers in other areas. In moist open places along the trail rosettes of *Eleocharis* and masses of *Sphagnum* are present.

A survey of the vegetation on Pico del Oeste revealed the species of vascular plants in the following list. The taxa cited and preceded by an asterisk are the common components of the mossy forest. The analyses we have made of these will be presented in subsequent papers. The unmarked species were of single occurrence or quite rare, excepting only the ferns, which did not lend themselves to phenological studies or to comparison in structural characteristics to the vascular flowering plants.

Lycopodiophyta

LYCOPODIACEAE

Lycopodium cernuum L. Terrestrial or scrambling plant. Locally dominant.

Lycopodium taxifolium Sw. Infrequent epiphyte.

SELAGINELLACEAE

Selaginella krugii Hieron. Most common species with long naked rhizomes; in masses or epiphytic and hanging in festoons.

Selaginella substipitata Spring. Occasional, erect, semi-rigid, terrestrial plants.

Polypodiophyta

CYATHEACEAE

Cyathea borinquena (Maxon) Domin. Rare, small terrestrial tree fern with erect stem less than one foot tall.

Cyathea pubescens Mett. ex Kuhn. Most common small tree fern in elfin woodland and in palm glades. Terrestrial but young plants commonly epiphytic. Under story plant never reaching canopy in forest but occasionally exposed in valleys. Frond with unusual and characteristic pouring-out zone behind circinnate tip.

Lophosoria quadripinnata (Gmel.) C. Chr. Trunk to 2 feet tall, base of fronds characteristically blue-black. Rare in palm glades.

POLYPODIACEAE

Blechnum divergens (Kunze) Mett. Small, erect-stemmed plant of open forest, to 2 feet tall. Common.

Blechnum lineatum (Sw.) Hieron. Erect plant in more open areas. Abundant.

Blechnum underwoodianum (Broadh.) C. Chr. Climbing or erect plant in open areas forming stem to 4 feet long. Occasional.

Cochlidium minus (Jenm.) Maxon. Occasional epiphytic fern in forest area.

Cochlidium seminudum (Willd.) Maxon. Occasional epiphyte in forest area.

Diplazium centripetale (Baker) Maxon. Small tree fern with trunk to 1 foot tall, in palm glades.

Diplazium grandifolium Sw. Occasional small tree fern in palm glade, trunk to 3 feet tall.

Diplazium l'herminieri Hieron. Small tree fern with trunk to 1 foot tall in palm glades.

Diplazium striatum (L.) Presl. Terrestrial plant rarely developing a short erect stem, rare.

Elaphoglossum firmum (Mett.) Urban. Epiphytic plant occurring mostly in juvenile form.

Grammitis hessii (Maxon) Alain. Epiphytic, very small plant locally abundant.

Grammitis serrulata (Sw.) Sw. Very small epiphyte, locally abundant.

Grammitis taenifolia (Jenm.) Proctor. Epiphyte. Infrequent.

Lindsaea stricta (Sw.) Dryand. Upright terrestrial or epiphytic plant. Rare.

Oleandra articulata (Sw.) Presl. Infrequent terrestrial herb.

Peltapteris peltata (Sw.) Morton. Epiphyte, locally abundant but seen only on trunks of *Prestoea montana.*

Polybotrya cervina (L.) Kaulf. Terrestrial plant mostly in palm glades. Infrequent.

Polypodium chnoodes Spreng. Epiphytic, sometimes climbing plant with pubescent rhizome. Occasional.

Polypodium loriceum L. Epiphyte with characteristic green or silvery ascending rhizomes. Occasional.

Thelypteris decussata (L.) Proctor. Large terrestrial fern of palm glades, young crozier characteristically surrounded by a gelatinous mass.

HYMENOPHYLLACEAE

Hymenophyllum lineare Sw. Abundant epiphyte.

Hymenophyllum macrothecum Fée. Abundant epiphyte.

Trichomanes crispum L. Abundant as a terrestrial or epiphytic plant.

Trichomanes rigidum Sw. Abundant plant, epiphytic or more commonly terrestrial.

Magnoliophyta — Liliatae

GRAMINEAE

Andropogon bicornis L. A single clump of this adventive species was exterminated by travel on the trail.

**Arthrostylidium sarmentosum* Pilger. A trailing terrestrial plant with arching stem; forest floor. Common.

**Ichnanthus pallens* (Sw.) Munro. Terrestrial herb sometimes forming dense stands.

**Isachne angustifolia* Nash. Scrambling terrestrial herb.

CYPERACEAE

**Carex polystachya* Sw. ex Wahlenb. Rosette or clump plant within forest, abundant.

**Eleocharis yunquensis* Britton. Rosette clump plant in trail area. Common.

**Scleria secans* (L.) Urban. Possible adventive into breaks, scrambling. Occasional.

Fimbristylis dichotoma (L.) Vahl. Adventive in area cut over during road construction.

PALMAE

**Prestoea montana* (R. Grah.) Nichols. Tree of valleys, common.

ARACEAE

**Anthurium dominicense* Schott. Epiphyte or terrestrial, herb, common.

BROMELIACEAE

**Guzmania berteroniana* (R. & S.) Mez. Epiphyte, rosette, rare on research site, common at lower altitudes.

**Vriesia sintenisii* (Baker) Smith & Pittend. Epiphyte, rosette, common.

DIOSCOREACEAE

**Rajania cordata* L. Herbaceous twiner, occasional.

ZINGIBERACEAE

**Renealmia antillarum* (R. & S.) Gagnep. Herbaceous, terrestrial, rare and perhaps an invader.

ORCHIDACEAE

**Brachionidium parvum* Cogn. Epiphyte, rare.

**Dilomilis montana* (Sw.) Summerhayes. Epiphyte or terrestrial, common.

Epidendrum nocturnum Jacq. Epiphyte, seen outside transect or trail areas.

Epidendrum pallidiflorum Hook. Epiphyte, seen outside transect and trail areas.

Magnoliophyta — Magnoliatae

PIPERACEAE

**Peperomia emarginella* (Sw.) DC. Delicate, herbaceous, root-climbing epiphyte, common.

**Peperomia hernandiifolia* (Vahl) A. Dietr. Succulent herbaceous root-climbing epiphyte, common.

CHLORANTHACEAE

**Hedyosmum arborescens* Sw. Small shrub never reaching canopy, occasional.

MORACEAE

**Cecropia peltata* L. Tree of disturbed areas; invader of trail.

URTICACEAE

**Pilea krugii* Urban. Terrestrial herb, common.

Pilea obtusata Liebm. Terrestrial herb in palm glades, common.

**Pilea yunquensis* (Urb.) Britt. & Wils. Terrestrial or often epiphytic herb, common.

LAURACEAE

**Ocotea spathulata* Mez. Dominant tree in canopy.

MAGNOLIACEAE

Magnolia splendens Urban. Common tree of lower elevations, single specimen found in transect area on lee side.

CUNONIACEAE

Weinmannia pinnata L. Occasional tree in dwarfed forests on El Yunque, single specimen found on Pico del Oeste but not in transect or trail area.

MELIACEAE

**Trichilia pallida* Sw. Very slender scrambling tree on Pico del Oeste, infrequent.

AQUIFOLIACEAE

**Ilex sintenisii* (Urb.) Britton. Scrambling shrub reaching canopy; occasional.

CELASTRACEAE

**Torralbasia cuneifolia* (C. Wr. ex Griseb.) Krug & Urban ex Seguí. Slender upright shrub with branches reaching canopy in places; occasional.

OCHNACEAE

**Sauvagesia erecta* L. Herbaceous terrestrial, early invader of trail area; common roadside weed at lower elevations.

MARCGRAVIACEAE

**Marcgravia sintenisii* Urban. Abundant heterophyllous woody root-climber terrestrial and reaching canopy.

THEACEAE

**Cleyera albopunctata* (Griseb.) Krug & Urban. Rare as a forest tree, occasional as slender shrub with scrambling branches.

GUTTIFERAE

**Clusia grisebachiana* (Planchon & Triana) Alain. Occasional stalk-rooted scrambling tree.

Clusia gundlachii Stahl. Rare plant in the forest not encountered in transects.

BEGONIACEAE

**Begonia decandra* Pav. ex A. DC. Herb of forest floor; locally abundant.

THYMELAEACEAE

Daphnopsis philippiana Krug & Urban. Rare shrub not encountered in transects; abundant at slightly lower elevations.

MYRTACEAE

**Calyptranthes krugii* Kiaersk. Abundant shrub occasionally reaching canopy.

Eugenia borinquensis Britton. Common tree of canopy.

MELASTOMATACEAE

**Calycogonium squamulosum* Cogn. Common tree of canopy.

**Mecranium amygdalinum* (Desr.) C. Wright ex Sauv. Occasional shrub, never in canopy.

**Miconia foveolata* Cogn. Common shrub, rarely in canopy.

**Miconia pachyphylla* Cogn. Common shrub, occasionally in canopy.
**Miconia pycnoneura* Urban. Infrequent shrub, never in canopy.
**Miconia sintenisii* Cogn. Common shrub at lower elevation, not encountered in transects.

ERICACEAE
**Gonocalyx portoricensis* (Urb.) A. C. Sm. Woody root-climber forming masses in canopy, common.
**Hornemannia racemosa* Vahl. Woody climber forming masses in canopy; common.

MYRSINACEAE
**Ardisia luquillensis* (Britton) Alain. Tree forming portion of canopy, occasional.
**Grammadenia sintenisii* (Urb.) Mez. Slender shrub, never reaching canopy; rare.
**Wallenia yunquensis* (Urb.) Mez. Low shrub, rhizomatous; abundant.

SAPOTACEAE
**Micropholis garciniaefolia* Pierre. Tree forming a portion of canopy, occasional.

SYMPLOCACEAE
**Symplocos micrantha* Krug & Urban. Slender shrub usually scrambling or with scrambling branches; rare.

OLEACEAE
**Haenianthus salicifolius* Griseb. var. *obovatus* (Krug & Urb.) Knobl. Tree forming portion of canopy; rare.

CONVOLVULACEAE
**Ipomoea repanda* Jacq. Herbaceous twiner; rare.

BORAGINACEAE
Cordia borinquensis Urban. Found only outside the transect area as a small tree.

BIGNONIACEAE
**Tabebuia rigida* Urban. Dominant tree.

GESNERIACEAE
**Alloplectus ambiguus* Urban. Epiphytic or terrestrial fleshy herb; occasional.
**Gesneria sintenisii* Urban. Terrestrial wandlike shrub, never reaching canopy; occasional.

ACANTHACEAE
Justicia martinsoniana Howard.[1] Occasional herb of forest floor.

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[1] **Justicia martinsoniana** Howard, nom. nov. FIG. 7.
Rhytiglossa verticillaris Nees in DC. Prodr. **11**: 354. 1847; type *Plée 268* (P).
Justicia verticillaris (Nees) Urb. Symb. Antill. **4**: 579. 1911, non L. f. 1781.
Stethoma verticillaris (Nees) Britton, Sci. Surv. Porto Rico Virgin Is. **6**: 218. 1925.

When Urban transferred the species described by Nees to the genus *Justicia* he made note of the existence of the identical name used by Linnaeus filius for a different plant. A new name is required unless one maintains the species in the poorly defined genus *Stethoma*, as Britton did.

It is a pleasure to name this attractive though small-flowered endemic herb for Joseph B. Martinson whose coöperation and support through the duration of this project made our work possible and our life in Puerto Rico more enjoyable.

FIG. 7, a-d. *Justicia martinsoniana* drawn from fresh material; a, habit, × ½; b, flower, side view, × 5; c, flower, face view, × 5; d, stamen, × 15.

RUBIACEAE

**Hillia parasitica* Jacq. Epiphytic shrub; occasional immature specimens only.

**Psychotria berteriana* DC. Shrub, possible adventive in breaks or landslide areas.

**Psychotria guadalupensis* (DC.) Howard. Small semi-succulent epiphyte, common.

Rondeletia portoricensis Krug & Urban. Occasional at lower elevations; seen only as seedling in transect area.

CAMPANULACEAE

**Lobelia portoricensis* (Vatke) Urban. Herb of forest floor, occasional in open areas.

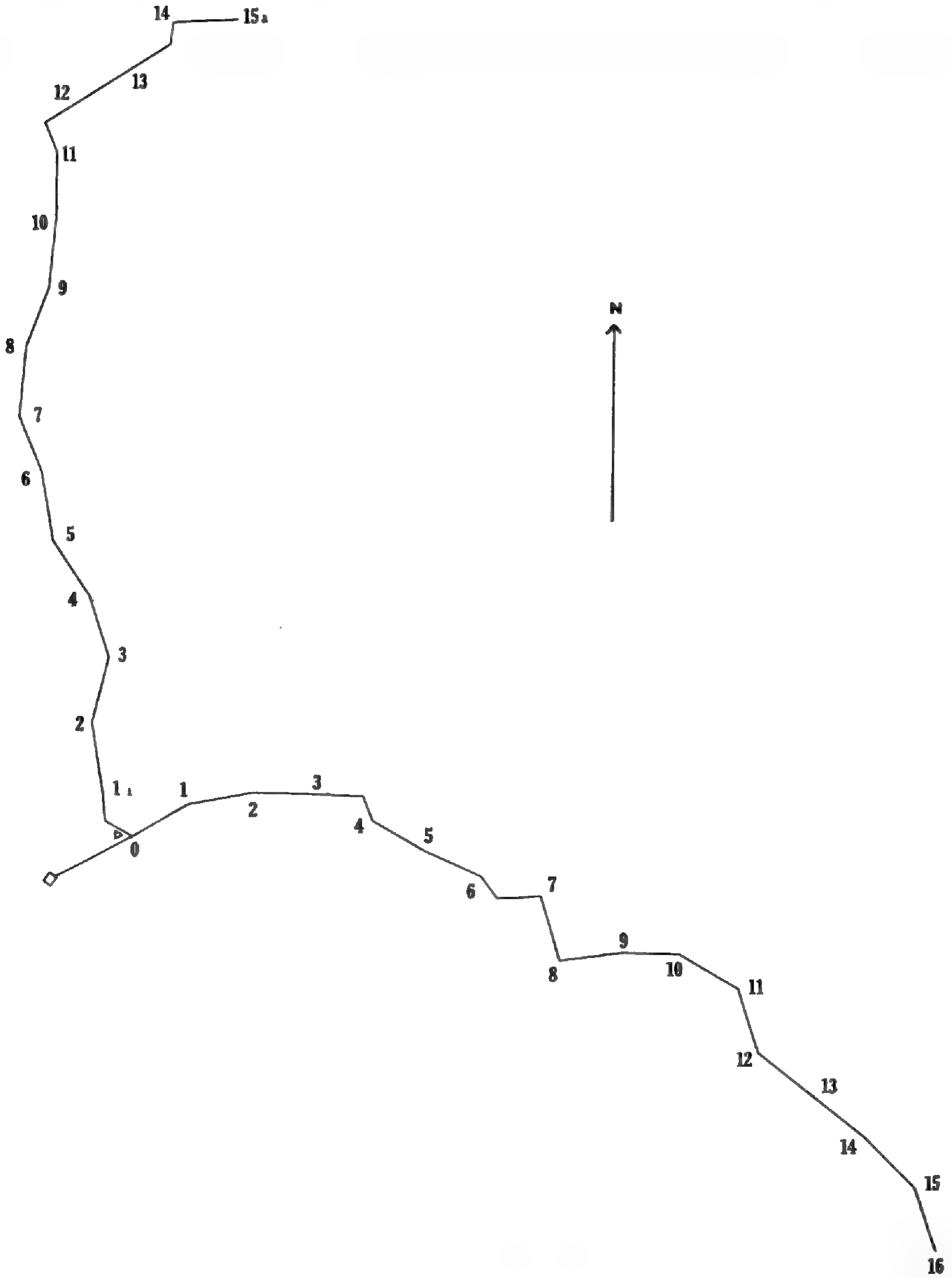

FIG. 8. Map of the study trail on Pico del Oeste.

COMPOSITAE
Clibadium erosum (Sw.) DC. Shrub of lower elevations; juvenile plants only as adventive weeds of trail.
**Mikania pachyphylla* Urban. Herbaceous twiner; occasional.

The composition of the vegetation on the top of Pico del Oeste is unusual for the complete lack of *Cyrilla racemiflora* found commonly at lower elevations. The absence of members of the families of Leguminosae, Rosaceae, Solanaceae, and Verbenaceae also is worthy of note.

The dominant flowering plants selected for further study represent eight families of 14 species of Monocotyledoneae comprising one palm, seven terrestrial herbs, five epiphytic herbs and one herbaceous twiner. Three species of Gramineae and three of Cyperaceae make up the largest families. There are 27 families of Dicotyledoneae in the study selection represented by 40 species. Twenty-four species are trees or shrubs; twelve herbs or herbaceous vines; four woody climbers. Four species occur most commonly as epiphytes. The most common family is the Melastomataceae with three genera and five species, with the genus *Miconia* having three species.

GEOGRAPHIC DISTRIBUTION OF THE VASCULAR FLORA

Many patterns of distribution have been discerned within the flora of the Antilles. The vascular flora of Pico del Oeste consists of 35 principal species which were considered in this study, 31 species of ferns, 14 species of Monocotyledoneae and 40 species of Dicotyledoneae. Of these, 27 or 32% are endemic to Puerto Rico; 17 or 20% are restricted to the Greater Antilles in various patterns of distribution; 17 or 20% are restricted to the Greater Antilles and the Lesser Antilles in various patterns of distribution; 17 or 20% are of widespread distribution in tropical America, occurring in the Greater Antilles, the Lesser Antilles, Mexico and Central America, and in South America; 4 or nearly 5% are found in the Antilles and northern South America but do not occur in Central America; 2 or roughly 2% occur in the Greater Antilles, Central and South America but do not occur in the Lesser Antilles; and one species has a distribution of the Greater and Lesser Antilles and Central America but has not been reported from South America.

Within the systematic classification of the component taxa 55% of the Dicotyledoneae are endemic to Puerto Rico and 87% are restricted to the Greater and Lesser Antilles; 14% of the Monocotyledoneae are endemic to Puerto Rico and 79% restricted to the Antilles, while in the ferns only 9% are endemic to Puerto Rico; 49% are restricted to the Antilles but 38% are known to have a wide distribution in tropical America.

The distribution of species within Puerto Rico remains an unworked problem. Britton and Wilson, in their reports on the vascular plants of Puerto Rico, indicated a very high percentage of endemic species (18%) are found in the Luquillo Mountains. A large number of these are now known to have wider distribution in Puerto Rico through the extensive but unpublished and unreported collection records of resident botanists, while many other taxa have been reduced to synonymy by monographers.

Within the various growth forms of the component species 61% of the epiphytes are restricted to the Antilles but only 5% are endemic to Puerto Rico. All six of the climbing species are restricted to the Antilles. Of the 58 terrestrial species 39% are endemic to Puerto Rico and 69% are restricted in their distribution to the Antilles.

FIG. 9. Profile of the study trail on Pico del Oeste.

THE TRAIL

Once the physical site for the research problem was chosen, a marked trail was laid out so that reference points could be established against which all information could be correlated. A minimum of disturbance in establishing the trail was necessary because it followed the vague outline of an old abandoned trail which led to Pico del Este. The trail is roughly in the shape of an inverted Y with a much abbreviated base. The juncture of trails was designated as point 0 and it was at this point that a tower to hold weather instrumentation was later erected. A small observation structure was constructed at the end of the base of the Y (and at the summit of Pico del Oeste). The two large trails were marked (FIGS. 8, 9) at ten yard intervals with numbering beginning at 0 and running to 160 yards on the one arm and 150 yards on the other (the latter is designated as the A trail and reference numbers all bear an A). The two arms face roughly in a northeasterly direction which proved to be of considerable significance in regard to general wind direction. As primary wind direction was demonstrated to be from the northeast, many points along the trail could be considered as the first wind contacts on Puerto Rico. An additional advantage was that windward and lee positions could be found at many places along the trail. The trail was marked by two-by-four inch × 2 foot posts driven every ten yards with code numbers attached. The upper part of each post was painted bright red for ease of locating.

Along the trail individual specimens of each species were marked and a variety of labels were tested to determine ease of application, durability of label, and durability of the legend applied. The most satisfactory label proved to be a wooden one of the type also used at the Arnold Arboretum (Arnoldia **24**: 9–12. 1964) made of pine strip 1½″ × 4″ × ⅜″ which had been painted with two coats of white enamel. The name of the plant (or pertinent data) was embossed on a plastic tape and through its adhesive affixed to the wood. A copper wire was used to fasten the label to the plant. The paint and the plastic proved to be resistant to the effects of weather, the algae, and spores of hepaticae. The tags were placed on the various species at the beginning of the trail as well as on particular plants selected for long-term observation along the trail and in the canopy of the forest surrounding the observation hut. This method of labeling assured a continuity of observation by the personnel who manned the project and permitted a rapid mastery of the unfamiliar species by visitors to the site. In retrospect, we believe that this labeling of plants

Distribution of Species

DISTRIBUTION	MONOCOTS	DICOTS	FERNS	EPIPHYTES			TERRESTRIAL			CLIMBERS	
				M	D	F	M	D	F	M	D
Endemic to Puerto Rico	2	22	3	1		1	1	19	2	0	3
Greater Antilles	3	1	6	2		3	1	1	3		
Greater Antilles & Lesser Antilles	2	4	4		1	2	1	2	2	1	1
Puerto Rico & Guadeloupe	2		1	1			1		1		
Puerto Rico to Martinique	1			1							
Lesser Antilles to Puerto Rico		1	1			1					1
Greater Antilles except Jamaica	1	3					1	3			
Puerto Rico & Cuba		3						3			
Antilles, N. South America but not Central America		3	1		2	1		1			
Jamaica, Puerto Rico & Lesser Antilles		1						1			
Antilles, Central & South America	3	2	12			5	3	2	7		
Greater Antilles, Central & South America, not Lesser Antilles			2						2		
Antilles & Central America but not South America			1						1		
	14	40	31	5	3	13	8	32	18	1	5

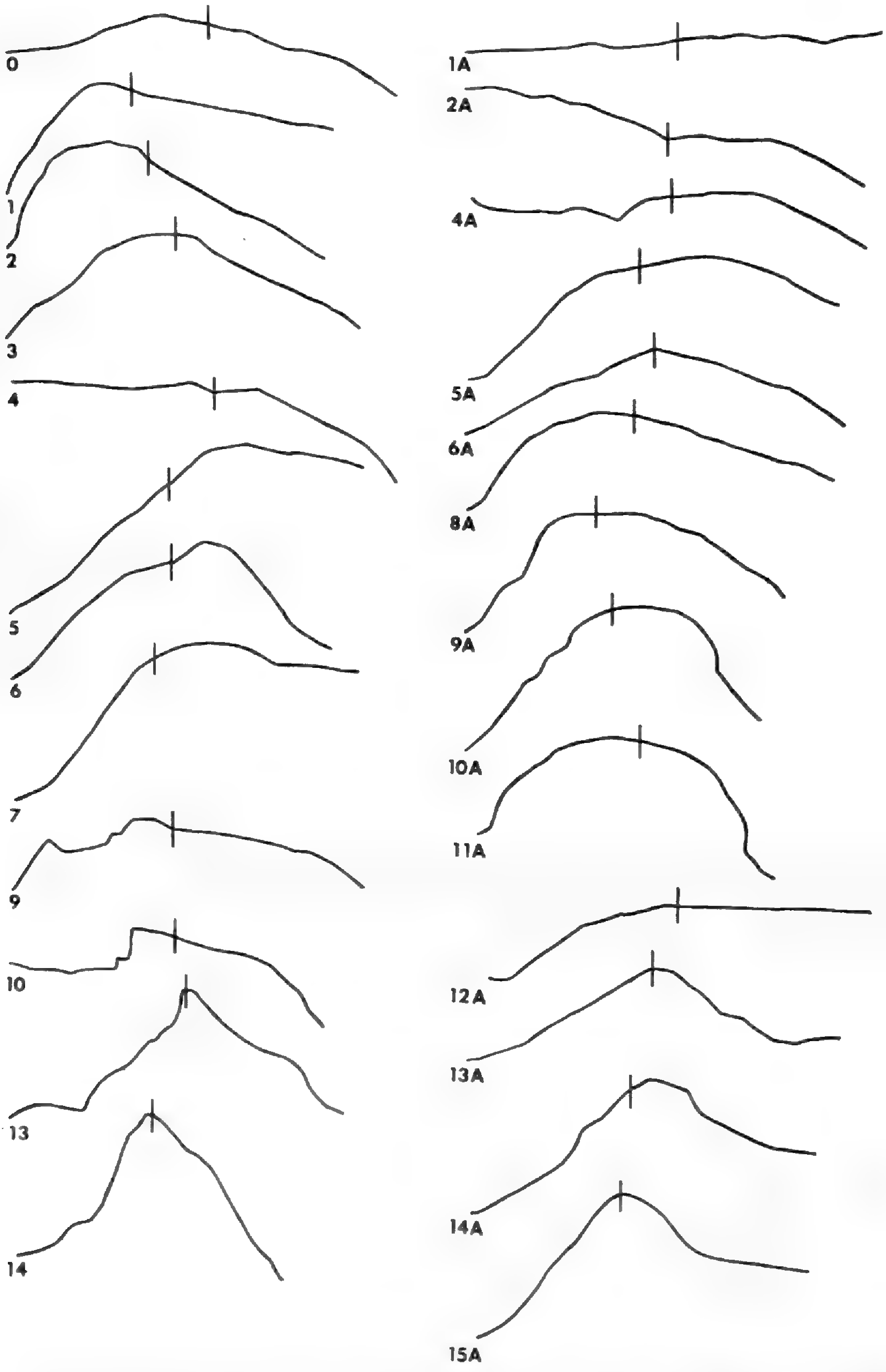

FIG. 10. Profiles of transect lines run for 50 feet at right angles on each side of markers on the West Peak (Pico del Oeste) trail. The vertical lines indicate the location of the trail itself. The left half of the transect at marker 4, and the right half of transects at markers 7, 9, 8A and 12A progress along the steep bank of a land slide zone.

and species contributed materially to the success of the project. Instructions could be given to replacement observers for the location of specific plants between trail markers on a particular side of the trail. Although several types of labels are made of material on which a stylus or pencil can make an impression these proved to be less durable and certainly less satisfactory.

COMPOSITION STUDIES

The vegetation at the sides of the old trail used as a base line had been affected by the former use of the trail, and in attempts to record the frequency of component species it was soon apparent that a false impression was being obtained. For that reason transect lines 50 feet long were established at right angles and in both directions from each of the 10-yard markers along the base trail. Even this short distance, involving the study of an area 3 feet on each side of the line, proved to be a physically difficult and exhausting survey (FIG. 10). The plants within 63 such areas were counted as accurately as possible and at the same time a survey was made to obtain the elevations of each line as well as the base trail, and thus construct the profile diagram of the hill top (FIG. 9). The lines were essentially leeward and windward plots of the vegetation of Pico del Oeste.

The density of the vegetation in many of the areas was due (1) to fallen trees from which lateral branches had grown upright or adventitious shoots had developed; (2) to the rhizomatous habit of some of the undershrubs, where a single rooted plant might produce six to twelve upright shoots with or without secondary rooting; and (3) to the tangle of vines which crossed and recrossed the study area. In all cases we attempted to record only individual plants clearly rooted within the study area, hence even the large figures given in the composition studies do not reveal accurately the tangle and thickets that characterize the vegetation. The very many young plants of *Vriesia sintenisii* also offered a minor problem. The wind-blown seeds of this epiphytic bromeliad found suitable media for germination in the heavy layers of liverworts which formed on all trunks, branches, and on the ground. The number of mature flowering specimens of *Vriesia* suggested a very high mortality of the seedlings, hence only plants 4″ or more in diameter were included in this survey. In one estimate we concluded these represented less than 10% of the total number of plants of that particular species on a single isolated tree. For most of the woody species we tried to record separately the seedlings to which the cotyledons were still attached. Another problem was encountered in *Marcgravia sintenisii*, which formed a tangle of stems on the ground, epiphytically on the trunks of many trees, and in the canopy. Lateral branches of this woody climber could have either the juvenile foliage form or the mature foliage or a successive combination of both foliage types when the stems changed angles or were attached by adventitious roots to other upright stems. The figures given represent individual plants as accurately as possible.

The ten most common species represented in these transect studies were the following, in order of frequency. The second figure given represents the number of seedling plants.

1. *Pilea krugii*	1376	Terrestrial herb
2. *Wallenia yunquensis*	1120–40	Semi-woody, terrestrial
3. *Calycogonium squamulosum*	1063–224	Woody, canopy plant
4. *Vriesia sintenisii*	978	Epiphyte
5. *Ocotea spathulata*	904–297	Woody, canopy plant
6. *Calyptranthes krugii*	807–140	Woody, canopy plant
7. *Pilea obtusata*	731	Herb restricted to palm glades
8. *Dilomilis montana*	717	Epiphyte
9. *Miconia pachyphylla*	433–25	Woody, canopy plant
10. *Cyathea pubescens*	386	Woody, sub-canopy plant

The total distribution is the following:

HERBACEOUS

Pilea krugii	1376	*Ichnanthus pallens*	110
Pilea obtusata	731	*Arthrostylidium sarmentosum*	32
Pilea yunquensis	297	*Scleria secans*	22
Begonia decandra	256	*Renealmia antillarum*	5
Carex polystachya	168	*Justicia martinsoniana*	1

EPIPHYTES

Vriesia sintenisii	978	*Alloplectus ambiguus*	11
Dilomilis montana	717	*Peperomia emarginella*	10
Psychotria guadalupensis	36–2	*Peperomia hernandiifolia*	10
Anthurium dominicense	13	*Hillia parasitica*	9–5
Guzmania berteroniana	11		

WOODY EMERGENTS

Calycogonium squamulosum	1063–224	*Ardisia luquillensis*	40
Ocotea spathulata	904–297	*Clusia grisebachiana*	38–5
Calyptranthes krugii	807–140	*Miconia pycnoneura*	33
Miconia pachyphylla	433–25	*Prestoea montana*	23–192
Tabebuia rigida	294–2	*Micropholis garciniaefolia*	24
Eugenia borinquensis	185–387	*Grammadenia sintenisii*	23
Torralbasia cuneifolia	104	*Symplocos micrantha*	19–3
Ilex sintenisii	98	*Cleyera albopunctata*	11
Miconia foveolata	91–37	*Haenianthus salicifolius*	4
Trichilia pallida	59	*Magnolia splendens*	1
Hedyosmum arborescens	58–1	*Rondeletia portoricensis*	1
Mecranium amygdalinum	46–34	*Miconia pycnoneura*	1

UNDERSHRUBS

Wallenia yunquensis	1120–40	*Diplazium grandifolium*	48
Cyathea pubescens	386	*Psychotria berteriana*	35–2
Gesneria sintenisii	163–26	*Lobelia portoricensis*	12

CLIMBERS

Marcgravia sintenisii	154–117	*Mikania pachyphylla*	73
Ipomoea repanda	82	*Rajania cordata*	21
Gonocalyx portoricensis	82	*Hornemannia racemosa*	19

The total area represented by these 63 transects was 18,900 square feet, approximately 0.4 acres or 0.17 hectares. Within this area there were by count 11,328 mature or adult plants and 1,536 juvenile plants or seedlings, for a conservative total of 12,864 individuals.

The base trail is curved and the transects were run on both the windward and leeward sides of a ridge as well as on the flatter summit area. Lines from trail markers 13, 14, and 15 on the leeward side dropped very sharply and extended across a slight talus slope where *Prestoea montana* was the dominant plant. It was only in this area that *Diplazium grandifolium* and *Pilea obtusata* grew. The palms were all mature plants or individuals over 5 feet tall. Seedling palms all less than a foot tall were encountered in the windward transects but none of the plants appeared to be vigorous. A total of 57 taxa as recorded in the 63 transects, with a high frequency of 28, a low of 17, and an average of 21 taxa on the windward plots, while a high of 27 taxa, a low of 15, and an average of 21 were found in the leeward plots.

A second transect study area was selected on the small plateau (leeward side and between markers 3 and 2) near the summit of Pico del Oeste (FIGS. 11, 12). The site was chosen to be as comparable as possible to the area on El Yunque diagrammed by Dansereau.

The area selected was 10 yards square. Lines a yard apart were laid through the forest to form a grid. Each square yard was then mapped to show the origin of the plants and their place of rooting. The path of each stem was marked, as was the area covered by the crown of each plant. The transect of 900 square feet contained 1,419 mature plants and 153 juvenile specimens for a total of 1,670 individuals with 35 taxa. On a comparative basis with the line transects, the number of individual plants was 2.7 times as many in this plateau study plot. The ten most abundant plants were the following:

1.	*Dilomilis montana*	332	Epiphytic herb
2.	*Vriesia sintenisii*	329	Epiphytic herb
3.	*Wallenia yunquensis*	187	Semi-woody terrestrial shrub
4.	*Ocotea spathulata*	106+76	Woody plant of canopy
5.	*Calyptranthes krugii*	75+6	Woody plant of canopy
6.	*Calycogonium squamulosum*	74+19	Woody plant of canopy
7.	*Carex polystachya*	53	Terrestrial herb
8.	*Gonocalyx portoricensis*	51	Woody liana
9.	*Ipomoea repanda*	41+2	Herbaceous climber
10.	*Marcgravia sintenisii*	38	Woody liana

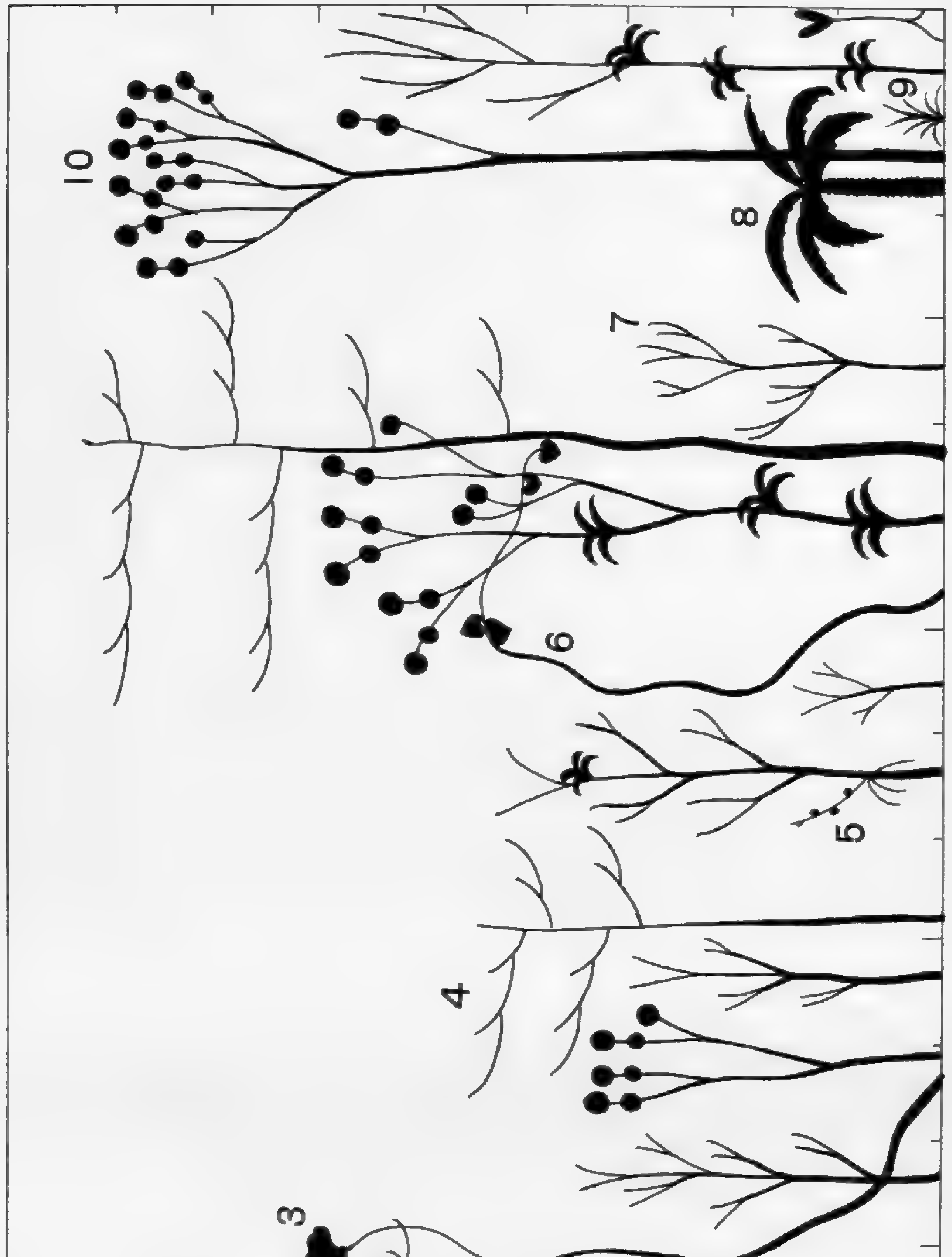

FIG. 11. A representation of the composition of the vegetation along the study trail between markers 2 and 3. Dimension lines represent one foot, i.e. the highest tree, an *Ocotea*, near no. 12 (on FIG. 12) is 9 feet tall and each diagram (FIG. 11 and FIG. 12) represents 15 feet of linear transect. Component species represented are: 1, *Miconia pachyphylla*; 2 *Vriesia sintenisii*; 3, *Marcgravia sintenisii*; 4, *Ocotea spathulata*; 5, *Dilomilis montana*; 6, *Rajania cordata*; 7, *Calyptranthes krugii*; 8, *Cyathea pubescens*; 9, *Carex polystachya*; 10, *Eugenia borinquensis*.

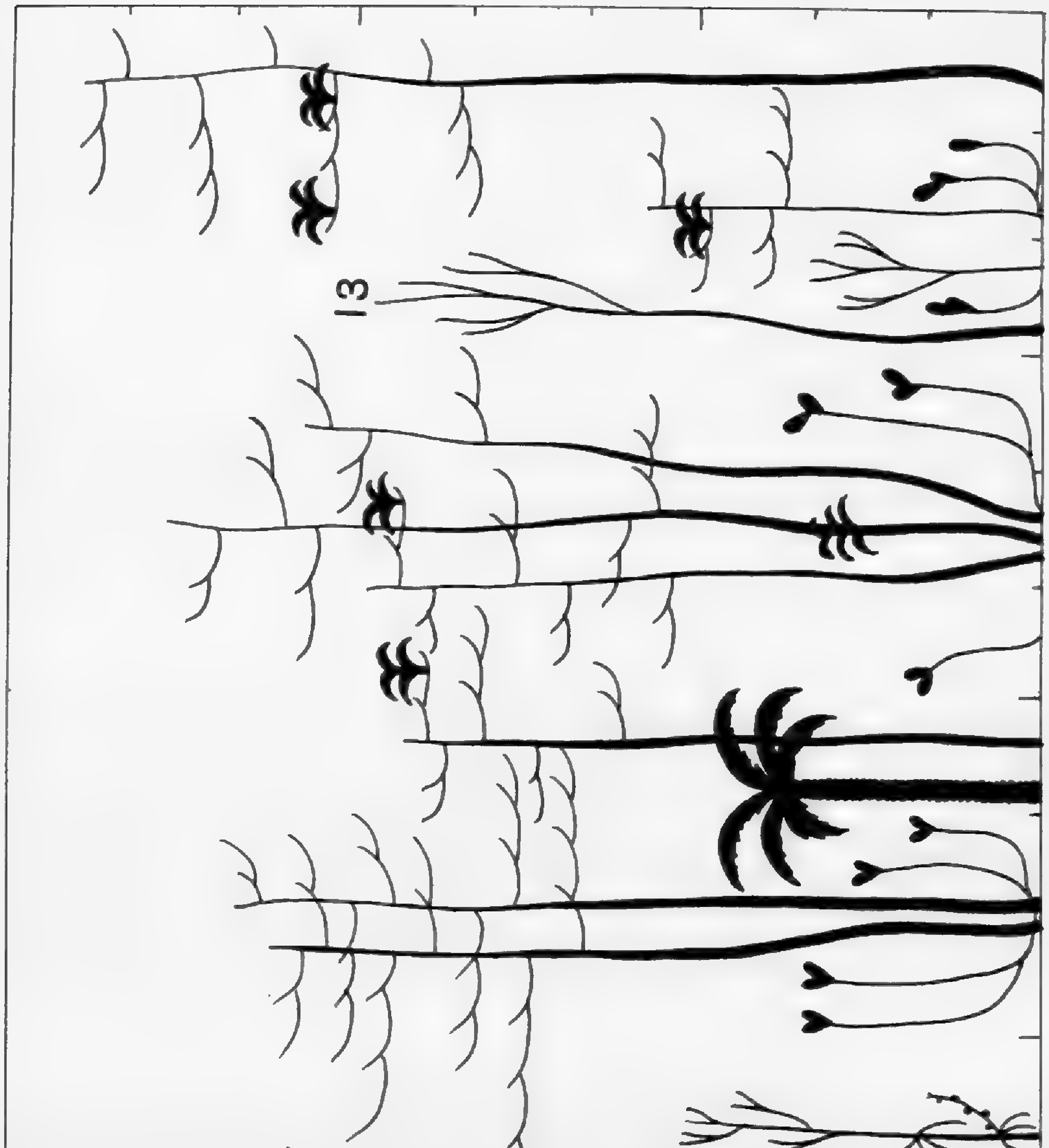

FIG. 12. A representation of the composition of the vegetation along the study trail between markers 2 and 3. Dimension lines represent one foot, i.e. the highest tree, an *Ocotea*, near no. 12 is 9 feet tall and each diagram [FIG. 11 and FIG. 12] represents 15 feet of linear transect. Component species represented here are: 11, *Tabebuia rigida*; 12, *Wallenia yunquensis*; 13, *Ilex sintenisii*.

WOODY COMPONENTS OF CANOPY

Ocotea spathulata	106+76	*Tabebuia rigida*	21
Calycogonium squamulosum	75+19	*Ardisia luquillensis*	21
Calyptranthes krugii	75+6	*Ilex sintenisii*	6
Eugenia borinquensis	21+9	*Hedyosmum arborescens*	2

CLIMBERS AND SCRAMBLERS, MOSTLY IN CANOPY

Gonocalyx portoricensis	51	*Mikania pachyphylla*	32+2
Ipomoea repanda	41+2	*Rajania cordata*	2
Marcgravia sintenisii	38	*Hornemannia racemosa*	2

EPIPHYTES

Dilomilis montana	332	*Peperomia emarginella*	1
Vriesia sintenisii (plus numerous juveniles)	187	*Anthurium dominicense*	1
		Alloplectus ambiguus	1
Psychotria guadalupensis	5		

TERRESTRIALS

Wallenia yunquensis	187	*Miconia foveolata*	4
Carex polystachya	53	*Miconia pycnoneura*	3
Blechnum spp.	42	*Clusia* (seedlings)	3
		Prestoea (seedlings)	2
Hymenophyllum macrothecum	32	*Pilea yunquensis*	1
Miconia pachyphylla	26+4		
Cyathea pubescens	10+16	*Symplocos micrantha* (seedling)	1
Trichilia pallida	8		
Pilea krugii	5	Miscellaneous juvenile ferns	13

A SINGLE LINE TRANSECT OR A PROFILE THROUGH THIS SAME PLOT WOULD SHOW THE FOLLOWING COMPOSITION:

Vriesia sintenisii	15	*Cyathea pubescens*	2
Ocotea spathulata	11	*Calycogonium squamulosum*	1
Calyptranthes krugii	8	*Marcgravia sintenisii*	1
Wallenia yunquensis	8	*Rajania cordata*	1
Dilomilis montana	5	*Miconia pycnoneura*	1
Eugenia borinquensis	3	*Carex polystachya*	1
Tabebuia rigida	2	*Ilex sintenisii*	1

Dansereau's pictogram showed 24 individuals representing 12 taxa. The profile (FIGS. 11, 12) constructed from this line through the plateau plot contains 60 individuals representing 14 taxa.

The roof of the shelter constructed on the summit of Pico del Oeste permitted observations of the canopy from above. It was obvious that the vegetation as seen from above presented a different aspect from that represented by the numerical surveys or by the profile diagrams (FIG. 13). Herbs and undershrubs and some of the epiphytes were not seen in the canopy, so consideration was given to methods of mapping the forest from above. I am grateful to friends and pilots from the U.S. Navy based at Roosevelt Roads for making several attempts to take aërial photographs of the study area on Pico del Oeste. Their photographs, although not of quality for species analysis, did allow additional studies

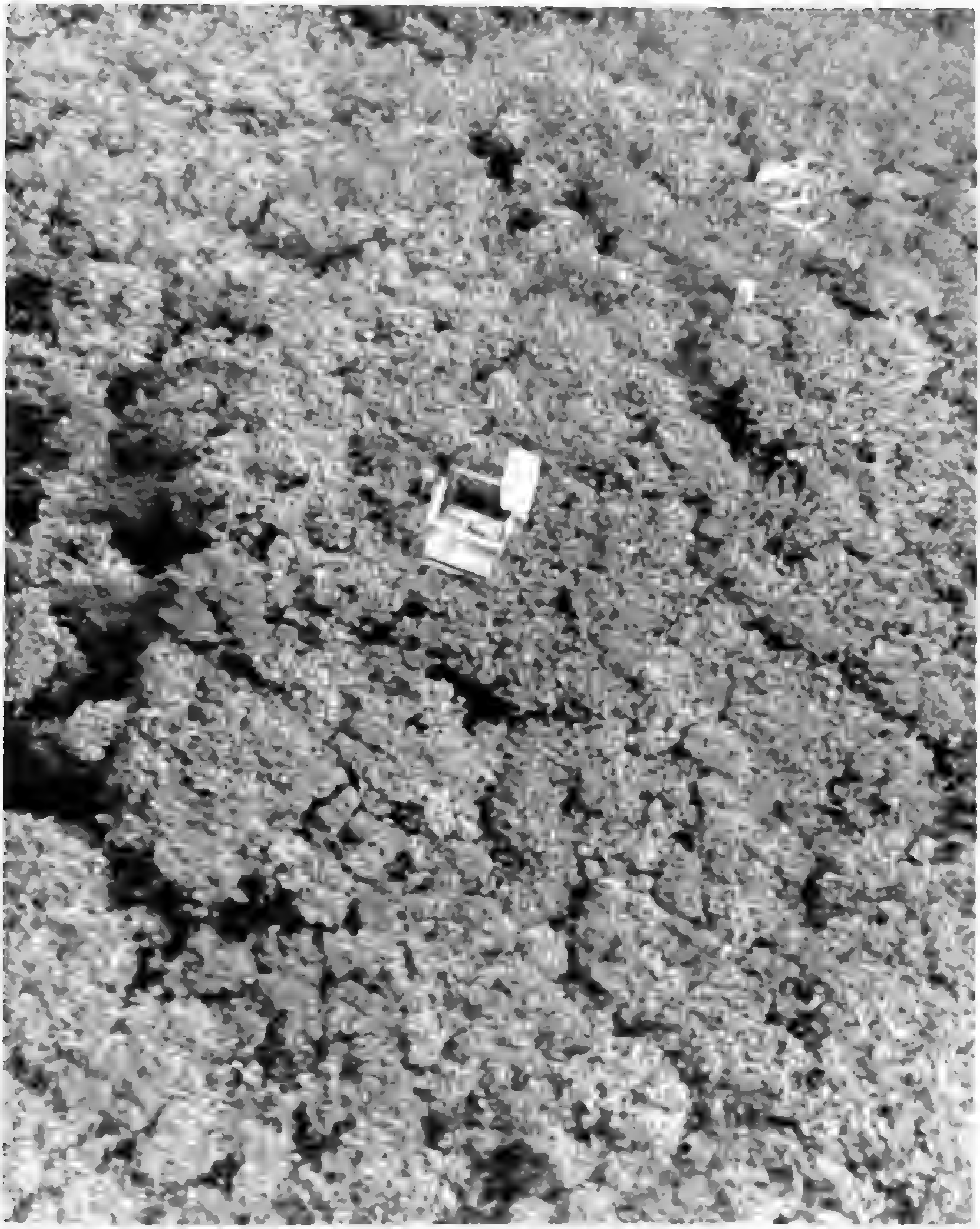

FIG. 15. An aërial view of the study site on the summit of Pico del Oeste. The platform on top of the observation hut holds the instrument shelter. Adjacent are two Durham pollen samplers. The linear board on the floor points due north. The tower holds a wind generator, recording rain gauge, two anemometers and a wind direction indicator. White markers on bamboo poles are visible and were used to correlate ground and canopy studies of the vegetation. Photo reproduced from a color negative, courtesy of the *U. S.* Navy.

of vegetation on the peak by suggesting areas worthy of further study (FIG. 15). Eventually we resorted to the procedure of attaching the camera to a long pole and extending this from the vertical axis of a ladder fastened to the side of the shelter, from the instrument tower built by the staff of NCAR, and from a ladder braced upright in the middle of the

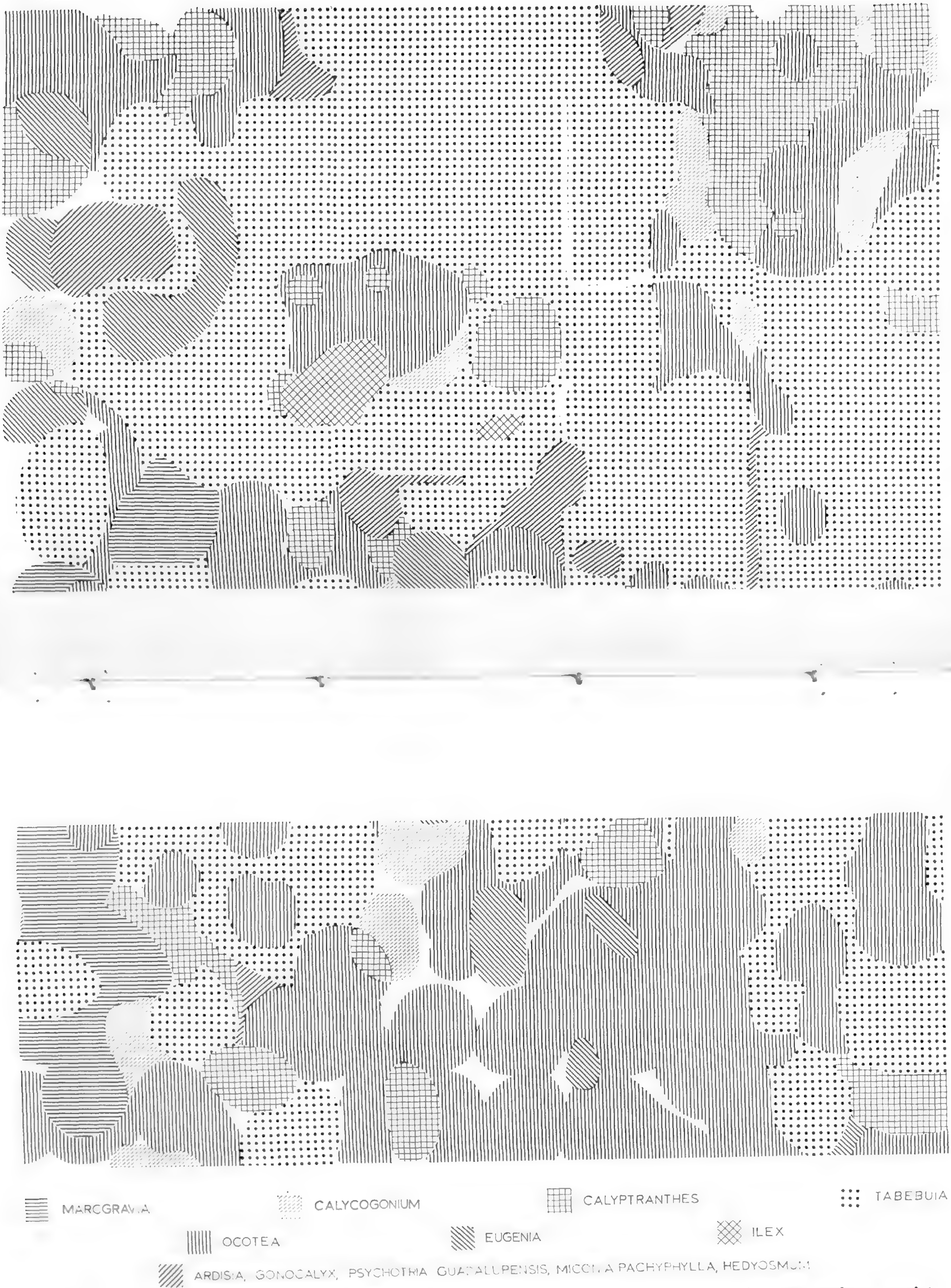

FIG. 14. A reconstruction of the canopy mosaic of the quadrat to the right of the study trail between markers 2 and 3.

10-yard-square transect study at markers 3–2. Photographs were taken in Ektachrome and monochrome film, with a long cable release used to make the exposure. The patience of my son and daughter, Bruce and Barbara, in assisting in this study are again acknowledged, for the combination of bad weather, low clouds or mist, and sporadic winds made this project an extremely exhausting physical experience.

The photographs were used to compare and to verify the mapping done from the ground by looking skyward from each of the yard-square quadrats. A diagrammatic map of the area as revealed by these studies is reproduced as FIGURE 14.

The following species formed the canopy and represented the percentages given here.

	NO. OF PLANTS IN CANOPY	% OF CANOPY
Tabebuia rigida	16	40.7%
Ocotea spathulata	46	30 %
Calyptranthes krugii	26	10.7%
Calycogonium squamulosum	13	4 %
Marcgravia sintenisii	7	4.2%
Eugenia borinquensis	7	4.2%
Ilex sintenisii	2	1 %
Ardisia luquillensis	2	3.9%
Gonocalyx portoricensis	4	
Hedyosmum arborescens	1	
Mikania pachyphylla	1	
Psychotria guadalupensis	1	

Two species, *Tabebuia rigida* and *Ocotea spathulata*, form 70% of the canopy. Scrambling specimens of *Marcgravia sintenisii*, *Gonocalyx portoricensis* and *Mikania pachyphylla* were the uppermost plants in about 5% of the canopy and obscure the supporting woody plant. One large specimen of *Psychotria guadalupensis* was seen on the canopy. No record was made of the surface area covered by the photophytic specimens of *Vriesia sintenisii*, and only a very few specimens of *Dilomilis montana* were evident, covering an insignificant area.

In comparison with the numerical count of specimens within the same plot, it is interesting to note that *Tabebuia*, which would have ranked 16th in frequency, and *Ocotea spathulata* which ranked 4th, dominated the canopy. As viewed from above 46 specimens were seen of the 106 *Ocotea* plants counted, while 16 of the 21 *Tabebuia* plants reached the canopy.

CHANGES IN THE SITE DURING THE STUDY

Although as little disturbance of the vegetation as possible was the working objective of all personnel during the study of Pico del Oeste, some changes did take place. Nearly every participant in the study learned that plants of *Cyathea pubescens* were shallowly rooted and could not be depended upon for support in climbing or descending some of the transect slopes. Many of these plants were uprooted accidentally.

During the initial visit to the study area one clump of *Andropogon bicornis* L. was seen on the trail and a specimen collected from the clump for identification. Subsequently that single clump was trampled into the mud and disappeared. A small wet depression on the downward trail contained many plants of *Sphagnum*. The drainage of this area was altered by repeated crossings of the trail, and the moss also disappeared.

In an open area of trail where it was most narrow and the sides steepest (13), seedlings of *Sauvagesia erecta* appeared within the first year. This pan-tropical weed is common on the roadsides at lower elevations and it it probable that staff members brought in seeds in the mud on their shoes. The plants proved to be perennials which persisted in growth and increased considerably in number during the course of the study. After a period of two years seedlings of *Clibadium erosum* were noticed in the same area. This species, too, occurs along the roadside and was presumably introduced by personnel, on muddy shoes.

At the end of the trail and outside of the study area plants of *Fimbristylis dichotoma* (L.) Vahl appeared in a disturbed area. These do not appear to have been introduced by project personnel.

No major change in the number of specimens along the trail was seen in any species except *Eleocharis yunquensis* Britton. The colonies originally consisted of widely spaced clumps. Near the end of the study the species formed solid mats in areas where the foot traffic was heavy. The plant appears to flourish under adverse conditions of disturbance.

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THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO,
2. THE MICROCLIMATE OF PICO DEL OESTE

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MOUNTAINS PENETRATE the base of trade-wind cumulus on many Caribbean Islands. Topping these mountains is a mossy, bushlike, elfin forest. One such forest is situated on 1050-meter Pico del Oeste in the Luquillo Mountains of eastern Puerto Rico. This forest has recently been the subject of a joint ecological investigation by the Arnold Arboretum and the National Center for Atmospheric Research (NCAR). The objective was to determine the environmental factors responsible for the dwarfed nature of the forest.

One year of meteorological data collected on Pico del Oeste is summarized in this report. In the tropics, as elsewhere, the variability of weather is such that one year does not define a climate. Nevertheless, the microclimate associated with the cloud forest is sufficiently unique that even a single year's data suggest many characteristic weather features. Moreover, more extensive climatologies of Puerto Rico (Briscoe, 1966; Picó, 1950; Wadsworth, 1948) provide a useful standard for evaluating the representativeness of the year reported herein.

Pico del Oeste is at the eastern (i.e. windward) end of Puerto Rico. It is far enough inland to be affected by convective showers produced by the sun's heating of the ground, yet near enough to the coast to receive the full influence of the moist tropical trade winds. Rising to 1050 meters, Pico del Oeste naturally owes much of its rain to the upslope effect. The *Glossary of Meteorology* (1959) specifies 600 to 750 meters as the characteristic base of trade-wind cumulus. It is not surprising that Pico del Oeste is shrouded in cloud most of the time.

Late in September of 1965 a meteorological survey trip was made to Pico del Oeste to aid in determining the variables that should be measured and the instruments that should be used. During February, 1966, the first of the equipment was installed and routine collection of data began. Wind sensors were added during the summer of 1966. Within a year corrosion and electrical failure of equipment had become a chronic problem and later data were too intermittent and unreliable to be included in a climatological survey.

In the following sections the meteorological instruments are described and weather data observed immediately above the canopy are tabulated.

INSTRUMENTATION

The variables that were measured include temperature, humidity, solar radiation, rainfall, wind speed and direction, and soil temperature. A

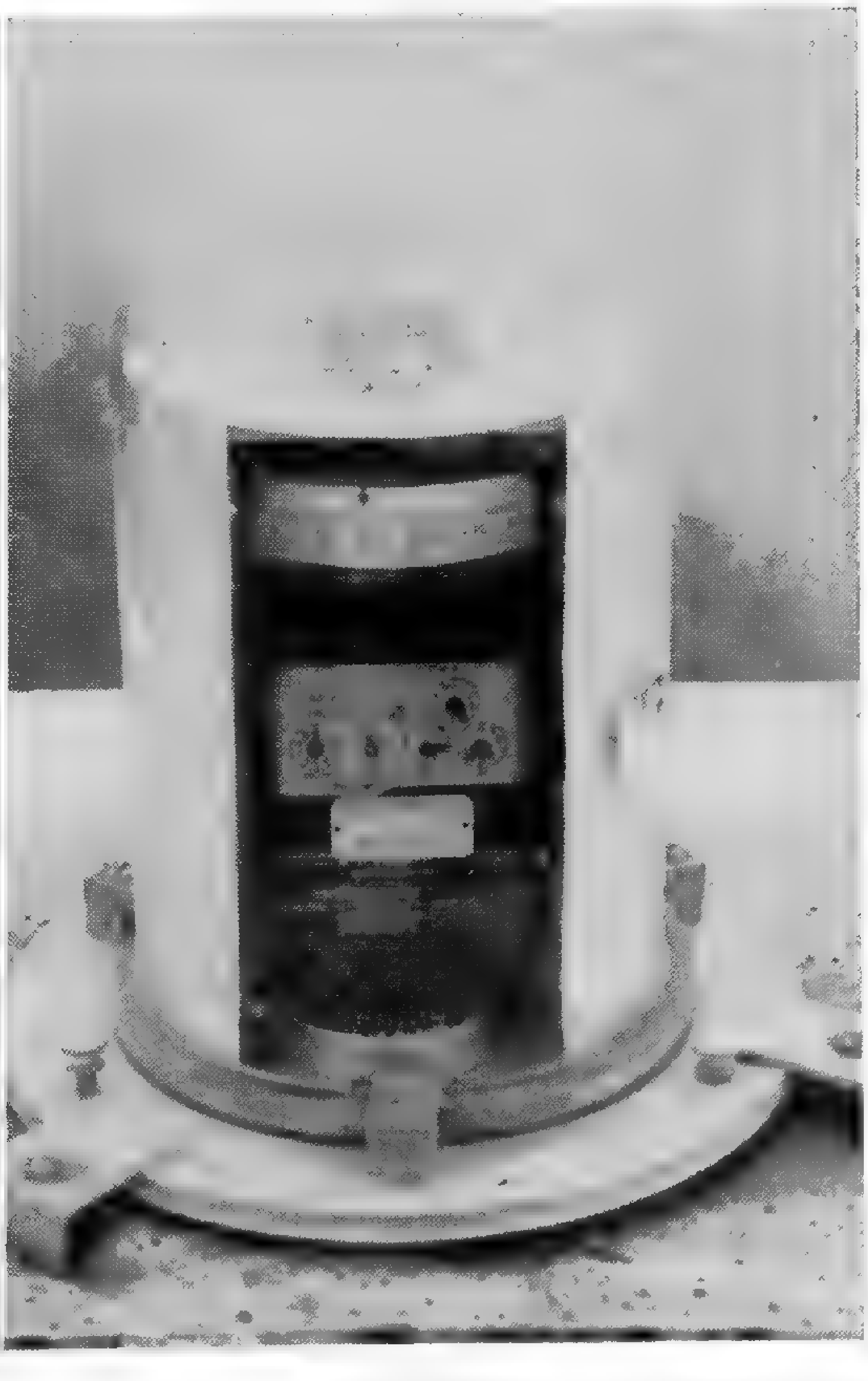
ABOVE: FIG. 1. Thermometer shelter just above canopy.
BELOW: FIG. 2. The 20-foot tower showing tipping-bucket rain gage, 3-cup anemometer, wind vane, and wind-powered generator on top.

relative measure of the amount of water extracted from the impinging cloud was also made. However, since the interpretation to be placed on this measurement is not self evident, the subject will be deferred to a later report.

Temperature and humidity were measured inside a thermometer shelter designed to protect the instrument from direct rain and sun, while assuring adequate ventilation by its louvered structure. The shelter was mounted just above the canopy on the roof of the hut as shown in Fig. 1. Solar radiation was measured on top of the thermometer shelter. Rainfall was measured just at the top of the canopy on a 20-foot tower shown in Fig. 2 and below the canopy. Wind speed and direction were measured at the top of the tower about 8 feet above the canopy, and wind speed was measured below the canopy also.

Because of the lack of commercial electric power, instruments that required little or no power were used. A limited amount of 12-volt direct current was supplied by a wind-powered generator shown atop the tower in Fig. 2.

A standard hygrothermograph, which requires no power, provided continuous records of temperature and relative humidity. The instrument is shown inside the thermometer shelter in Fig. 3. A Bourdon tube and a bundle of hairs were the sensing elements for temperature and humidity



Left: Fig. 3. Hygrothermograph inside thermometer shelter. Cloud-water collector in background, Sol-a-meter on roof.

Right: Fig. 4. Close-up of Sol-a-meter.

respectively. Periodically the calibration of the instrument was checked by a wet and dry bulb psychrometer. A spring-wound 8-day clock permitted weekly chart changes. FIG. 5 is an example of a typical chart. These charts gave daily values of the maximum and minimum temperature, the minimum relative humidity and the duration of less-than-100 percent relative humidity. Experience showed that the latter humidity condition was diagnostic of an absence of cloud on the peak.

Solar radiation was measured by a Sol-a-meter shown in FIG. 4. Four parallel-connected silicon cells generate a current proportional to the incident solar radiation. The output of the cells is connected through a milliammeter that indicates the instantaneous insolation rate, and to an ampere-hour meter that gives a readout of the total solar radiation during any desired period of time. A dessicant of silica gel is changed when a change in its color indicates an accumulation of moisture inside the glass cover. Readings near the beginning and end of the month were used to give an average value of the daily accumulation of solar radiation. The Sol-a-meter also required no power.

The rainfall detector was a tipping-bucket gage, shown in FIG. 2; rain from the collector is funnelled to the tipping-bucket mechanism shown in FIG. 6. Each bucket-tip, resulting from 1/100 inch of rain, closed a magnetic reed switch connected to the 12-volt supply. The switch-closure deflected a pen in an Esterline Angus 20-pen event recorder. Thus the amount of rain in hundredths of an inch is equal to the number of pen deflections. Rate of rainfall was obtained from the elapsed time between bucket-tips as read from the chart, on which 6 inches of chart-travel represented 1 hour.

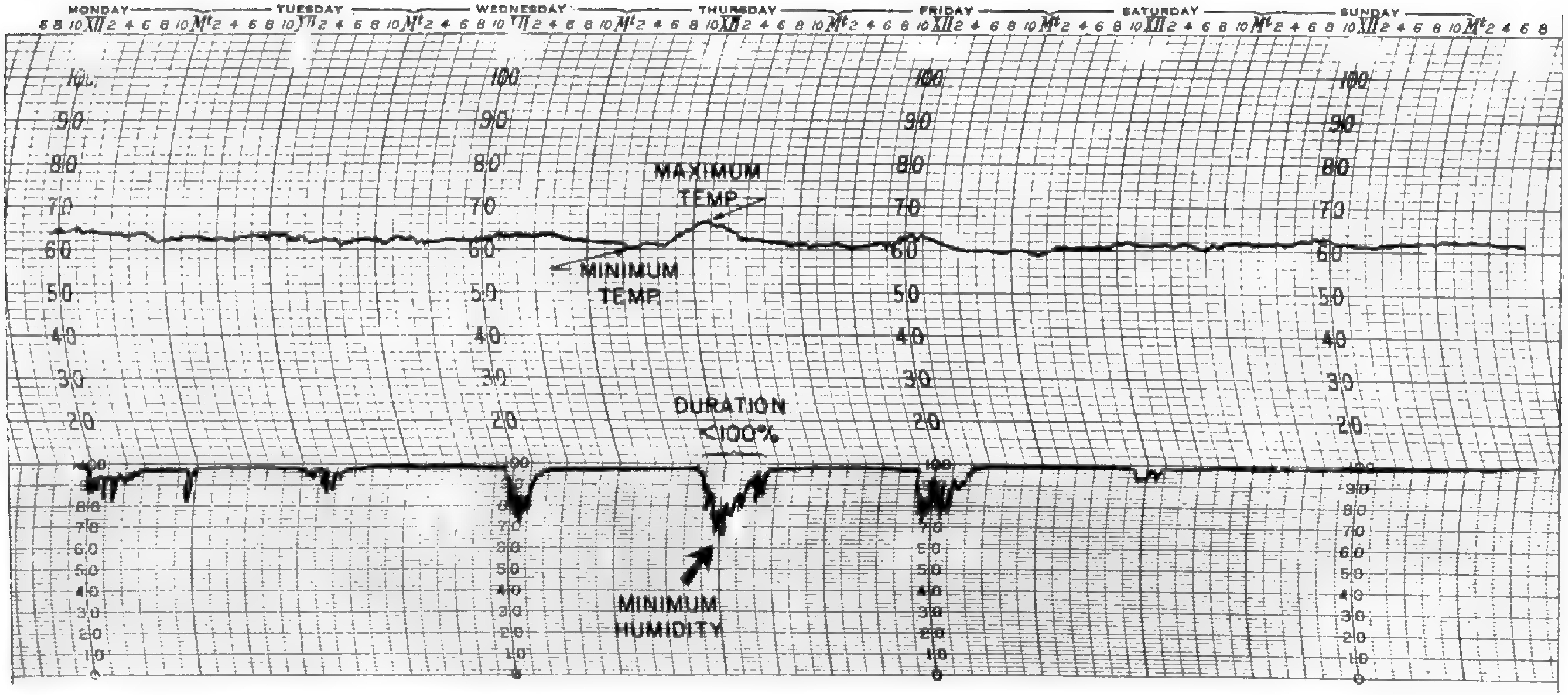
The event recorder was also used to record wind speed and direction. Each mile of wind passage closed a reed-switch inside a 3-cup anemometer, deflecting another pen in the recorder. FIG. 7 shows the below-canopy anemometer. Hourly average winds and the fastest mile of wind were readily obtained. The wind vane, shown in FIG. 8, is attached to a vertical shaft that activates a contacting assembly consisting of eight wiper-type contacts spaced at 22.5 degree intervals. Only one contact is closed at a time. A separate event pen was assigned to each of the eight cardinal directions. By means of a cam switch built into the recorder, once every 3 minutes the circuit was closed and a wind direction was recorded.

Soil temperature at a depth of 8 centimeters was measured by a mercury thermometer. The thermometer was read during the regular visits of the observer.

RESULTS

TABLE 1 contains a summary of mean monthly temperatures, winds, humidity, solar radiation, and total rainfall. Gaps in the record occur when equipment was not operating.

The dominance of the northeast trade winds was almost complete. For the seven months of record the frequency of winds from the north, north-



HYGROTHERMOGRAPH TRACE AT PICO DEL OESTE, JANUARY 2-9, 1967

Fig. 5. Hygrothermograph chart for Pico del Oeste, January 2–9, 1967.

east, and east totalled 81 percent. The fastest mile of wind was 32 mi./hr. on 26 August as a hurricane passed just south of the island.

Rainfall totalling 453 cm. for the year was probably not abnormal. Picó (1950) gives 478 cm. as the 10-year average at La Mina, located about 5 km. northwest of Pico del Oeste at an elevation of 700 m. According to the U.S. Weather Bureau (1965) 402 cm. is the normal annual rainfall at Upper Rio Blanco less than 3 km. southwest of the peak at an elevation of 450 m. The heaviest rate of rainfall during the year occurred in the forenoon of 15 April 1966 when 2.5 mm. fell in just under a minute, a rate of just over 15 cm./hr.

FIG. 6. Tipping bucket mechanism housed inside rain-gage directly under funnel from collector. When one compartment fills bucket tips, closing switch and simultaneously positioning other compartment under funnel.

Solar radiation at Pico del Oeste was compared to Tampa, Florida, and Swan Island, the two nearest stations for which radiation data are available. Normally Swan Island gets about 130 cm. of rainfall annually compared to 153 cm. at San Juan, and since it is at nearly the same latitude as Pico del Oeste it is comparable to the coastal plains of eastern Puerto Rico. Tampa probably gets somewhat less radiation than the coastal plains of Puerto Rico because it is further north. For similar (although not identical) periods in 1966 solar radiation averaged 478 Langleys/day at Tampa and 518 at Swan Island compared to 262 at Pico del Oeste.

This suggests that over 40 percent of the incident radiation is attenuated by the cloud, a plausible value since the peak is enveloped in cloud for about 60 percent of the daylight hours. Based on two years data Briscoe (op. cit.) found that solar radiation on a nearby mountain, 1065-meter El Yunque, was 60 percent of that measured at Cape San Juan on the coastal plain.

Moreover, as pointed out by Szeicz (1966), since the spectral composition of light changes very little with cloudiness, the light energy available for photosynthesis is also attenuated by over 40 percent.

TABLE 2 compares temperatures and rainfall at Pico del Oeste with those for the same period at Roosevelt Roads on the coast about 14 km. to the east southeast and about 1000 meters lower. The differences are readily accounted for by their 1 kilometer (1000 m.) difference in height. During the warmest part of the day temperatures in the first few hundred meters above ground usually decrease at the rate 9.8° C/km. (the dry adiabatic lapse rate). Maximum temperatures were observed to differ by just about this amount. Rainfall at the peak includes a substantial contribution from the orographic process, namely the forced rising, cooling, and resultant condensation within the moist northeast trade winds.

The climate on Pico del Oeste is described further in TABLE 3 in terms of occurrences of meteorological events. The first two columns are events or attributes of unpleasant weather. The last three columns are favorable weather attributes. There are two seasons of favorable weather and two seasons of unfavorable weather. Favorable weather in March and April coincides with the normal dry season over the Caribbean; the favorable weather of October and November may have been an anomaly since these are normally among the wettest months. It is noteworthy that measurable rain fell during 350 days in the year.

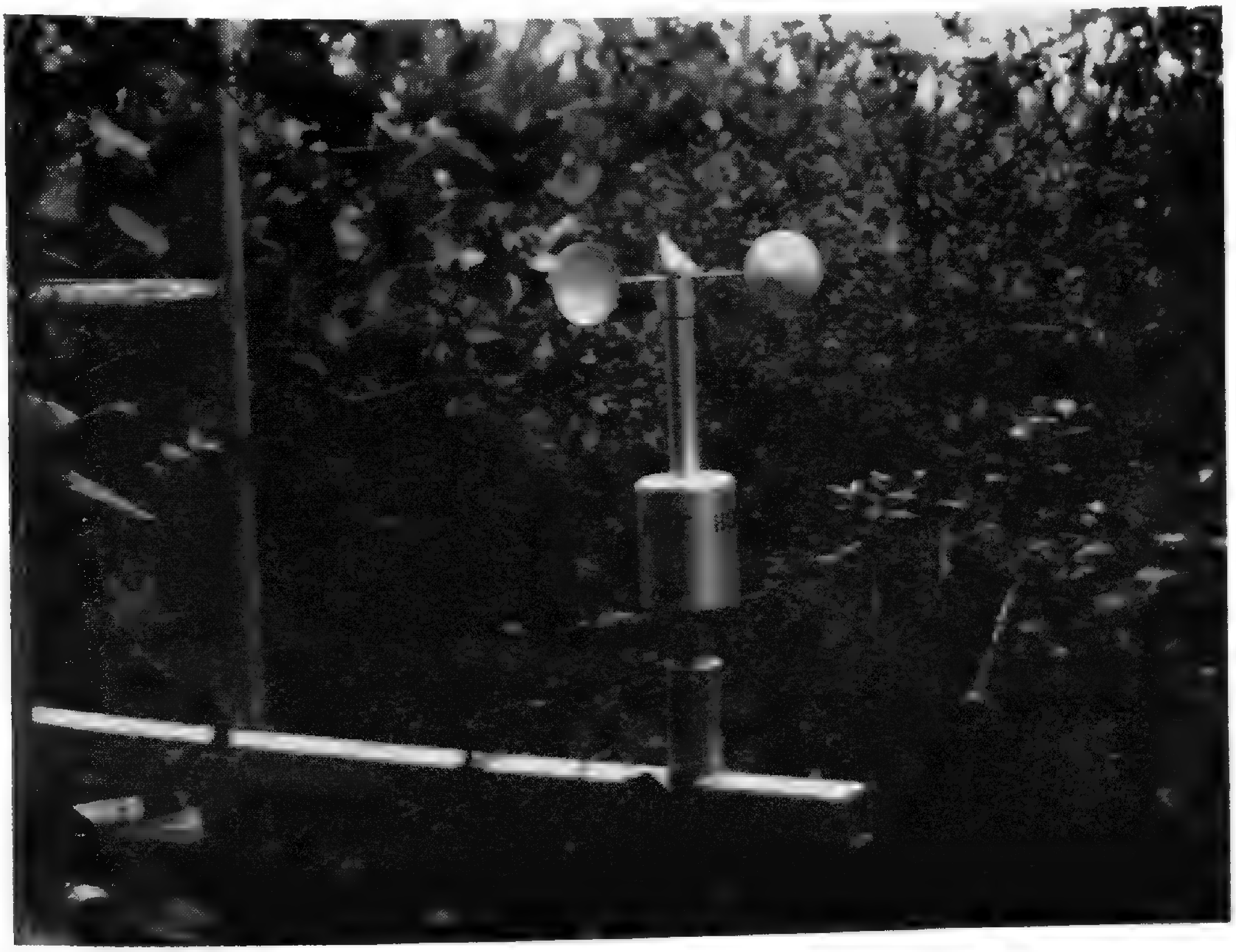


FIG. 7. 3-cup anemometer used for measuring wind speed below the canopy.

The longest spell of fine weather extended from November 8 to 28 or a total of 3 weeks. During this remarkable period there was an average of 15 hours per day of cloud-free weather and radiation averaged 305 Langleys/day. Maximum temperatures averaged 21°C and relative humidity averaged 91 percent. Even so, rain totalled 20 cm.

There were also spells distinguished by their lack of rain. The best example occurred during the normal dry season that generally includes February, March, and April. In the 23 days from March 20 to April 11, 1966, the total rainfall was 6.5 cm., there was an average of 9 hours/day of cloud-free conditions, humidity averaged 95 percent, maximum temperatures averaged 20.5° C, and radiation averaged 360 Langley/day.

There were also two notable spells during which cloud enveloped the peak almost continuously. In the 16 days from June 10 to 25, 1966, there were only 6 hours in which the cloud broke from the peak. On 12 of the days the relative humidity never fell below 100 percent. Maximum temperatures averaged 20.5° C and rainfall totalled 24 cm.

In the 15 days from January 14 to 28, 1967, there were only 7 hours in which the cloud cleared from the peak and on 12 of the days it did not clear at all. This was a cool spell in which maximum temperatures averaged 17.2° C and rainfall totalled 19 cm.

Some additional noteworthy features may be mentioned. The highest and lowest observed screen temperatures during the year were 26° C and 13° C. The diurnal temperature variation is very small. As shown in FIG. 5, it is well defined only on days when the cloud lifts from the peak (i.e. when the humidity falls below 100 percent) for several hours. The peak was enveloped in cloud close to 100 percent of the night hours and 60 percent of the day hours.

SUMMARY

Garnier (1961) defines the humid tropics as "the area where (1) the mean monthly temperature for at least eight months of the year equals or exceeds 68° F (20° C); (2) the vapor pressure and relative humidity for at least six months of the year average at least 20 millibars and 65 percent respectively; and (3) the mean annual rainfall totals at least 40 inches (1000 millimeters), and for at least six months precipitation is 3 inches (75 millimeters) each month." By this definition, Pico del Oeste is clearly not in the humid tropics. During the year reported herein rainfall met the criterion. Although relative humidity more than met the criterion, average vapor pressure exceeded 20 mb. in only 6 of the months. Temperatures were clearly too cold. However the presence of an elfin forest rather than a rain forest tells even more eloquently that Pico del Oeste is not in the humid tropics.

There has been much speculation as to the causes of elfin forests. In discussing this region in Puerto Rico, Cook and Gleason (1928) asserted that high wind exposure is the most important environmental factor in differentiating the mossy forest from the palm forest, although low temperature, water-soaked soil, and high humidity were also considered important. They added that on rocky summits of peaks the trees are bushlike on account of the strong winds and thin and rocky soils. Grubb and Whitmore (1966) suggest that the most important factor in the development of tropical montane forests is the frequency of fog, although they concede that additional exposure to winds and leaching of soils on ridges may contribute to stunting. The first year of data on Pico del Oeste offers little support to the belief that strong winds account for the stunting. Leaching of soils is probably important. The most unusual features of the weather appear to be the high fog incidence and the 40 percent attenuation of solar radiation, tending to support the suggestions of Grubb and Whitmore.

FIG. 8. Wind vane on top of tower.

ACKNOWLEDGMENTS

The contributions of the following individuals are gratefully acknowledged. Mr. Donald Eklund made the original installation of meteorological equipment including the tower and wind-powered generator, and designed and assembled the trough rain-gage for measuring rainfall under the canopy. Later in the year special maintenance and further refinements to the installations were carried out by Dr. Julian Pike. Various members of the staff of the Arnold Arboretum performed the regular chart changes and other routine duties that are essential to a program of continuous data collection.

TABLE 1. **Mean monthly values of temperature, wind, humidity, rainfall and solar radiation, Pico del Oeste, 1 March 1966 to 28 February 1967**

	AVERAGE AIR TEMPERATURE			SOIL TEMP.	WIND				
	Daily Max.	Daily Min.	Daily Mean	8 cm. Depth	Prev. Dir.	Mean Speed	Rel. Hum.	Rain-fall	Solar Radiation Langleys[1] per day
MARCH '66	19.2°C	16.5°C	17.9°C	16.9°C	—	—	98 %	34.8 cm.	245
APRIL	20.0°	16.7°	18.4°	17.0°	—	—	96	38.5	322
MAY	20.0°	18.4°	19.2°	18.3°	—	—	99.9	45.1	203
JUNE	20.4°	18.8°	19.6°	18.9°	—	—	99.8	36.4	260
JULY	20.7°	18.9°	19.8°	19.2°	—	11.0 kt	99.7	43.9	249
AUGUST	20.7°	18.5°	19.6°	19.3°	NE	11.1	99.8	41.8	266
SEPTEMBER	21.1°	18.4°	19.8°	19.7°	NE	9.6	98	39.9	290
OCTOBER	21.6°	18.6°	20.1°	19.4°	NE	8.0	97	25.6	271
NOVEMBER	21.0°	16.8°	19.0°	18.7°	N	—	94	27.4	297
DECEMBER	18.3°	16.3°	17.3°	17.8°	NE	9.3	99	62.0	212
JANUARY '67	17.5°	15.6°	16.6°	17.0°	NE	10.9	99.4	30.3	—
FEBRUARY	17.6°	15.6°	16.6°	17.0°	NE	9.2	99.3	27.6	—
ANNUAL	19.9°	17.4°	18.6°	18.3°	—	—	98.5	453.3	262

[1] One Langley is 1 calorie/square cm.

TABLE 2. **Comparison of monthly mean temperatures and rainfall at Pico del Oeste and Roosevelt Roads, 1 March 1966 to 28 February 1967**

	MAX. TEMP.		MIN. TEMP.		MEAN TEMP.		RAINFALL	
MONTH	Pico	RR	Pico	RR	Pico	RR	Pico	RR
MARCH '66	19.2°C	29.2°C	16.5°C	23.0°C	17.9°C	26.1°C	34.8 cm.	7.5 cm.
APRIL	20.0°	29.6°	16.7°	23.0°	18.4°	26.4°	38.5	11.0
MAY	20.0°	29.8°	18.4°	24.1°	19.2°	26.9°	45.1	9.3
JUNE	20.4°	30.9°	18.8°	25.1°	19.6°	28.0°	36.4	10.0
JULY	20.7°	31.3°	18.9°	25.3°	19.8°	28.3°	43.9	10.5
AUGUST	20.7°	31.1°	18.5°	25.4°	19.6°	28.2°	41.8	10.8
SEPTEMBER	21.1°	31.3°	18.4°	25.1°	19.8°	28.2°	39.9	17.0
OCTOBER	21.6°	31.1°	18.6°	23.9°	20.1°	27.5°	25.6	18.2
NOVEMBER	21.0°	30.0°	16.8°	21.8°	19.0°	25.9°	27.4	17.7
DECEMBER	18.3°	28.4°	16.3°	22.4°	17.3°	25.4°	62.0	12.9
JANUARY '67	17.5°	27.8°	15.6°	21.5°	16.6°	24.7°	30.2	10.0
FEBRUARY	17.6°	28.3°	15.6°	21.8°	16.6°	25.0°	27.6	3.9

Particular mention must be made of the kindness of Mr. J. B. Martinson in providing excellent accommodation close to Pico del Oeste. Both the scope and quality of the research have benefited greatly from this generous support.

TABLE 3. **Occurrences of significant meteorological events by months, Pico del Oeste, 1 March 1966 to 28 February 1967**

	NUMBER OF DAYS				
	In cloud for 24 hrs.	Rain 1 or more cm.	Max. temp. 22°C or more	8 or more hours with Rel. Humid. less than 100%	No Rain
MARCH '66	9	12	3	7	3
APRIL	3	9	4	12	5
MAY	20	17	0	1	0
JUNE	17	14	0	1	0
JULY	14	12	1	2	0
AUGUST	18	13	3	2	0
SEPTEMBER	8	12	4	7	1
OCTOBER	8	7	7	11	1
NOVEMBER	3	9	7	19	4
DECEMBER	10	16	2	8	1
JANUARY '67	15	9	0	3	0
FEBRUARY	13	7	0	6	0
ANNUAL	138	137	31	79	15

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STUDIES OF PACIFIC ISLAND PLANTS, XIX. THE ARALIACEAE OF THE NEW HEBRIDES, FIJI, SAMOA, AND TONGA[1]

ALBERT C. SMITH AND BENJAMIN C. STONE

THIS REGIONAL TREATMENT of the Araliaceae is primarily directed toward an adequate understanding of the species native to Fiji. Although only three genera (*Polyscias, Plerandra,* and *Schefflera*) occur indigenously in that archipelago, an examination of the family in the nearby island groups has proved instructive. In the area of our present concern species of *Polyscias, Brassaia,* and *Dizygotheca* occur as cultivated or adventive plants, and for convenience we also include these records.

Generic limits in the Araliaceae have presented problems to students of the group, and we are well aware that a limited and regional treatment can add little to their solution. In his recent attempt to bring taxonomic order into the family, Hutchinson (Gen. Fl. Pl. **2**: 52–81. 1967) has recognized 84 genera, rearranging them in seven tribes. Harms' treatment of 1894 (in E. & P. Nat. Pflanzenfam. **3**(8): 1–62) had accepted 51 genera in three tribes. Hutchinson has proposed two new tribes (Cussonieae and Anomopanaceae) for taxa that have their flowers singly disposed rather than in umbels. His first 12 genera, removed from the rest of the family on that basis, seem to form an unnatural aggregation. As a single example, the genus *Polyscias* is not amenable to this tribal categorization; its species are usually umbelliferous, but some of them have the flowers individually borne on the ultimate inflorescence-branches, and other species are transitional in this character. We find *Polyscias* to be a satisfactory and coherent genus, as noted in our generic consideration, below, and in our notes under *P. joskei* and *P. reineckei.* By combining *Anomopanax* Harms (the basis of Hutchinson's tribe Anomopanaceae) with *Mackinlaya* F. v. Muell. (the basis of the tribe Mackinlayeae of both Harms and Hutchinson), Philipson (in Bull. Brit. Mus. (Nat. Hist.) Bot. **1**: 3–9. 1951) has also indicated his lack of confidence in the value of umbellate or single flowers as a generic character. Our comments below under *Plerandra insolita* will further illustrate the difficulties of utilizing this character for generic delimitation.

In connection with the present paper the herbarium material of several

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[1] No. XVIII of this series, by the first author, was published in Contr. U.S. Natl. Herb. **37**: 69–106. 1967. The present paper is based on research partially supported by a grant from the National Science Foundation. Our work on the Araliaceae was initiated while both authors were staff members of the Smithsonian Institution, and we take this opportunity of thanking Dr. Wallace R. Ernst, of that organization, for his interest in the problem, his advice, and his aid in handling borrowed material.

institutions has been examined and is cited, with the indicated abbreviations: Arnold Arboretum of Harvard University (A); Bernice P. Bishop Museum (BISH); British Museum (BM); Gray Herbarium of Harvard University (GH); Royal Botanic Gardens, Kew (K); New York Botanical Garden (NY); Department of Agriculture, Suva, Fiji (SUVA); University of California, Berkeley (UC); and U.S. National Herbarium (US). We are indebted to the administrators of these herbaria for the privilege of examining the cited specimens. The accompanying illustrations were prepared by the second author.

KEY TO THE GENERA

Petals imbricate in bud (tribe Aralieae); leaves imparipinnate; flowers in umbels, the pedicels conspicuously articulate at apex; petals and stamens 5; styles and ovary-locules 2 (rarely 3); fruits ellipsoid or obovoid. . . 1. *Delarbrea.*

Petals valvate, broad at base (tribe Schefflereae).

Flowers densely congested in heads, unisexual; fruits sessile, free to firmly concrescent; leaves simple, obovate to oblanceolate. . . . . 2. *Meryta.*

Flowers pedicellate (or, if capitate, the leaves compound); fruits not concrescent.

Leaves pinnately compound or unifoliolate.

Pedicels articulate at apex; petals and stamens (in our species) 5–8 (rarely 4 or 9); styles and ovary-locules (in our species) 2–5; fruits often laterally compressed (sometimes subglobose), the styles often conspicuous and persistent (but sometimes stigmas sessile on a conical stylopodium). . . . . 3. *Polyscias.*

Pedicels not articulate; petals and stamens 8–12; styles and ovary-locules 8–24; fruits subglobose, surmounted by a truncate-conical stylar column with numerous radiating sessile stigmas. . . . . 4. *Reynoldsia.*

Leaves palmately lobed or compound.

Leaves digitately compound, with petiolulate leaflets.

Stamens numerous, 15–500, exceeding the petals in number; petals 4–6; styles, stigmas, and ovary-locules 5–17. . . . . 5. *Plerandra.*

Stamens 4–6, similar to the petals in number; styles, stigmas, and ovary-locules 5–12.

Anthers 2-locular.

Flowers pedicellate. . . . . 6. *Schefflera.*

Flowers sessile in heads borne along the radiating branches of large panicles. . . . . 7. *Brassaia.*

Anthers 4-locular. . . . . 8. *Dizygotheca.*

Leaves palmately lobed, with toothed or incised segments; umbels tripartite, the central radiolus bearing infertile or pseudopistillate flowers, the lateral radioli with hermaphrodite flowers. . . . . 9. *Boerlagiodendron.*

1. **Delarbrea** Vieill. in Bull. Soc. Linn. Norm. **9**: 342. 1865; Harms in E. & P. Nat. Pflanzenfam. 3(8): 61. 1894; Hutchinson, Gen. Fl. Pl. **2**: 63. 1967.

This small genus, of about seven species, is centered in New Caledonia but extends from Timor and New Guinea through the Solomon Islands into the New Hebrides; it is typified by *D. collina*, the only species occurring in our area. Our specific description is based on New Hebridean and New Caledonian material. Both Harms and Hutchinson place *Delarbrea* in the tribe Aralieae, characterized by having the petals broad-based and imbricate in bud.

1. **Delarbrea collina** Vieill. in Bull. Soc. Linn. Norm. **9**: 342. 1865; Guillaumin in Bull. Soc. Bot. France **66**: 270. 1919, in *op. cit.* **74**: 698. 1927, in Jour. Arnold Arb. **12**: 262. 1931, in Jour. Linn. Soc. Bot. **51**: 553. 1938; Philipson in Bull. Brit. Mus. (Nat. Hist.) Bot. **1**: 18. 1951. PL. III, FIGS. 10–13.

A tree, glabrous throughout; leaves imparipinnate, large, up to 85 cm. long, the petiole and rachis subterete, the petiole of mature leaves 12–15 cm. long, swollen to a clasping base and obviously alate in the proximal 1.5–2 cm., the leaflets 11–19, the petiolules slender, of lateral leaflets 3–11 and of terminal leaflet to 40 mm. long, the blades chartaceous, oblong or oblong-lanceolate, 12–20 cm. long and 4–7 cm. broad (basal ones sometimes smaller), unequally subcordate to broadly obtuse at base, acute to sharply short-acuminate at apex, entire at margin, the costa raised above, prominent beneath, the secondary nerves usually 7–10 per side, curved-ascending, with the intricate veinlet-reticulation prominulous on both surfaces; inflorescences racemose-paniculate, up to 45 cm. long and broad, the primary branches to 25 cm. long, all the inflorescence-axes transversely griseo-corticate-lenticillate, the primary bracts oblong, 0.5–1 cm. long or more, caducous, the umbel- and flower-subtending bracts and bracteoles 1.5–3 mm. long, obtuse or subacute; flowers borne in umbels on slender ultimate peduncles (5–) 10–30 mm. long, 15–25 per umbel, the pedicels 1–3 mm. long at anthesis, slightly elongating in fruit, swollen and conspicuously articulate at apex; flowers 3–3.5 mm. long at anthesis, with a narrowly turbinate calyx 2–2.6 mm. long, the tube obconical, the limb subcampanulate, 1.5–2 mm. in apical diameter, the lobes 5, obvious, orbicular-ovate, 0.5–0.7 mm. long, narrowly imbricate in bud; petals 5, oblong-ovate, broad-based, about 1.5 mm. long, imbricate in bud; stamens 5, the filaments slender, eventually about 1.5 mm. long, the anthers oblong, about 0.8 mm. long, versatile; stylopodium hemispheric, 0.5–0.7 mm. high, surmounted by 2 (rarely 3) styles free nearly to base, these elongating to 1.5 mm., eventually recurved and subclavate, with decurrent stigmas; fruits ellipsoid or obovoid, 10–15 mm. long, only slightly compressed laterally, 2- or sometimes 3-locular, each locule containing a marginal pyrene angular-lunulate in cross-section, the fruit thus with an empty central cavity, the sepals persistent, the styles usually caducous.

TYPE LOCALITY: New Caledonia; the type is *Vieillard 625,* from the vicinity of Wagap (isotype at A).

DISTRIBUTION. New Caledonia, Loyalty Islands, Solomon Islands, and New Hebrides, apparently occurring in forest from sea-level to an altitude of 200 meters. Trees up to 12 meters high have been noted, and the fruit is said to be black when mature.

LOCAL NAMES. Reported names in the New Hebrides are *morshmorshalkara* and *nëvarkrab* (Espiritu Santo), *napouiri* (Efate), and *nunginetum* (Eromanga).

New Hebrides. BANKS GROUP: VANUA LAVA: *Kajewski 412* (A, BISH). ESPIRITU SANTO: Hog harbour, *I. & Z. Baker 72* (BM), *295* (BM). EROMANGA: Dillon Bay, *Kajewski 269* (A, US).

The New Caledonian species, with the exception of this one widespread one, appear to be endemic. Among them (according to Guillaumin, Fl. Anal. et Syn. Nouv.-Caléd. 251. 1948), *D. collina* is distinguished by its acute, not falciform, leaflet-blades, and its relatively small flowers and fruits.

2. **Meryta** J. R. & G. Forst. Char. Gen. Pl. 119. 1776; Seem. in Bonplandia **10:** 294. 1862, Fl. Vit. 118. 1865; Harms in E. & P. Nat. Pflanzenfam. 3(8): 34. 1894, in Notizbl. Bot. Gart. Berlin **14:** 315. 1938; Hutchinson, Gen. Fl. Pl. **2:** 74. 1967.

Botryodendrum Endl. Prodr. Fl. Norfolk. 62. 1833.
Neara Sol. ex Seem. Fl. Vit. 118, as synonym. 1865.
Strobilopanax Viguier in Ann. Sci. Nat. IX. Bot. **4:** 148. 1906.

The interesting genus *Meryta*, typified by *M. lanceolata* J. R. & G. Forst., of the Society Islands (cf. Forst. f. Fl. Ins. Austr. Prodr. 92. 1786), is readily distinguished by its large, simple leaves, of which the blades are usually obovate or oblanceolate, and its unisexual, sessile flowers crowded in capitate-paniculate inflorescences. The fruits are either free or firmly concrescent, thus indicating that the character upon which *Strobilopanax* was based is not dependable at the generic level.

Meryta is indicated by Harms (in 1938) to include about 30 species, by Hutchinson (in 1967) to include 16 species. It has its greatest concentration in New Caledonia, but it is now known to extend from New Zealand, Norfolk Island, New Guinea, and the Palau and Marianas Islands eastward through Polynesia to the Austral Islands, the Tuamotus, and the Marquesas. In this vast area, the only major archipelago lacking the genus is Fiji, a very curious fact but one that must now be taken at face value, since Fiji is better known than most Pacific areas and since the genus can scarcely be confused with any other.

The genus is greatly in need of a complete review, since specific characters are evasive. In our area at least one species occurs in the New Hebrides and one or two in Samoa and Tonga. We are able to record little new information, but the following key and pertinent bibliographic and herbarium records will summarize an unsatisfactory situation.

KEY TO THE SPECIES

Fruiting heads composed of fruits firmly concrescent except in the distal portion, or at least united above the middle.

Petioles 1–1.5 cm. long; leaf-blades 28–32 cm. long, obtuse at apex; fruiting heads at apparent maturity about 4 cm. in diameter. . . 1. *M. neo-ebudica.*
Petioles 2–16 cm. long; leaf-blades 40–63 cm. long, acute to acuminate at apex; fruiting heads at apparent maturity 2–3.5 cm. in diameter. . 2. *M. capitata.*
Fruiting heads composed of fruits nearly free or united only below the middle.
Petioles up to 23 cm. long; leaf-blades 40–75 cm. long, cuspidate to short-acuminate at apex. . . . . 3. *M. macrophylla.*
Petioles 4–8 cm. long; leaf-blades 45–120 cm. long, obtuse to acute at apex. . . . . 4. *M. denhamii.*

1. **Meryta neo-ebudica** (Guillaumin) Harms in Notizbl. Bot. Gart. Berlin **14**: 321. 1938.

Strobilopanax neo-ebudicus Guillaumin in Jour. Arnold Arb. **12**: 263. 1931.

As we have seen no additional material of this species, the original description based on the type collection cannot be significantly amplified.

TYPE LOCALITY: Aneityum, New Hebrides; the type is *Kajewski 980* (coll. *J. P. Wilson*), cited below.

DISTRIBUTION. Endemic to the New Hebrides and known definitely only from the type collection, obtained in forest at an altitude of 325 m. and noted as a small tree with white flowers and yellow fruits.

LOCAL NAME. *Nabrouto* was noted by the collector.

New Hebrides. ANEITYUM: Anelgauhat Bay, September 1929, *Kajewski 980* (coll. *J. P. Wilson*) (A type).

Guillaumin notes his novelty as the first record of *Strobilopanax* in the New Hebrides, but he has also indicated the presence of *Meryta* in that archipelago. Earlier (in Bull. Soc. Bot. France **66**: 270. 1919, in *op. cit.* **74**: 698. 1927) he had reported the genus from Efate, with the local name *nafil gnas*; and more recently (in Jour. Linn. Soc. Bot. **51**: 554. 1938) he has reported it from Espiritu Santo, with the local name *nvalval.* The specimens supporting these records have not been examined by us.

2. **Meryta capitata** Christophersen in Bishop Mus. Bull. **128**: 161. *fig. 23.* 1935; Yuncker in Bishop Mus. Bull. **184**: 55. 1945.

Meryta sp. Christophersen in Bishop Mus. Bull. **128**: 164. 1935.
Meryta aff. *macrophylla* sensu Yuncker in Bishop Mus. Bull. **184**: 56. 1945.

In view of our uncertainty of the actual limits of this species or, indeed, of its real distinctness from *M. macrophylla* (see comments below), we refrain from amplifying the original description, which Christophersen seems to have based entirely upon fruiting specimens — his type and his no. *2839.*

TYPE LOCALITY: Near Vaipouli, Savaii, Samoa; the type is *Christophersen & Hume 1913,* cited below.

DISTRIBUTION. Endemic to Samoa, and definitely known from Savaii and the Manua Islands, where it has been collected in forest from near sea-level to 500 m. altitude (with one collection from about 1,400 m. above Matavanu, Savaii) and noted as a tree 4–6 m. high.

LOCAL NAMES. *Fagu fagu* (i.e. *fangu fangu*) is a general name; it has also been recorded on Savaii as *lauma ulu ulu*, and on Olosega as *lau tetali*.

Samoa. SAVAII: Falealupo, *Christophersen 2802* (BISH); Manese plantation, *Christophersen & Hume 2369* (BISH); behind Avao, *Vaupel 135* (BISH); back of Vaipouli, *Christophersen & Hume 1913* (A, BISH type, US); near Vaipouli, *Christophersen & Hume 1837* (A, BISH); above Matavanu, *Christophersen & Hume 2199* (BISH); Taga, *Christophersen 2839* (BISH, US). OFU: Above Ofu village, *Yuncker 9545* (BISH). OLOSEGA: Oloseguata, Piumafua Ridge, *Garber 1079* (BISH). TAU: Amouli trail, *Garber 622* (A, BISH); south of Siufaga, *Yuncker 9162* (BISH).

It may be seriously doubted that more than one species of *Meryta* occurs in Samoa and Tonga. As characters to differentiate his *M. capitata* from *M. macrophylla* Christophersen mentions the subglobose heads of united fruits and the broader leaves. The latter of these is surely of little consequence, as there is substantial variation in leaf-breadth and also in petiole-length in plants that otherwise seem essentially identical.

Fruiting specimens referable to *M. macrophylla* (*U.S. Expl. Exped.*, the type, *Setchell 15667*, *Bryan 99*, *Christophersen 1253*, and *Yuncker 16181*) have the fruits united only in the basal portion or up to the middle. Fruiting specimens referable to *M. capitata* (*Christophersen & Hume 1913*, the type; *Vaupel 135*, *Christophersen 2839*, and *Yuncker 9162*) have the fruits concrescent except in the uppermost portion, which is rounded and obtusely costate when dried. The dividing line between the two conditions is not entirely clear, and indeed is approached in *Vaupel 135*. By matching intangible foliage characters of staminate and sterile specimens with the fruiting collections we have grouped the available material into two taxa, but without much conviction that species are represented. Staminate flowers are quite uniform throughout, as are stylar characters; the petiole seems totally variable in length and diameter and probably reflects conditions of age or habitat.

3. **Meryta macrophylla** (Rich ex A. Gray) Seem. in Bonplandia **10**: 294. 1862, Fl. Vit. 119. 1865; Drake, Ill. Fl. Ins. Mar. Pac. 182. 1890; Hemsl. in Jour. Linn. Soc. Bot. **30**: 180. 1894; Burkill in Jour. Linn. Soc. Bot. **35**: 40. 1901; Christophersen in Bishop Mus. Bull. **128**: 163. 1935; Yuncker in Bishop Mus. Bull. **220**: 206. 1959.

Botryodendrum macrophyllum Rich ex A. Gray, Bot. U.S. Expl. Exped. **1**: 732. 1854, Atlas *pl. 97*. 1857.

A redescription of this species should await a detailed revision of the genus; hopefully a specialist will reach a satisfactory conclusion as to the limits of taxa in Samoa and Tonga.

TYPE LOCALITY: Samoa, without definite locality; the U.S. Exploring Expedition specimen cited below is the type.

DISTRIBUTION. Samoa (known definitely from Upolu and Tutuila) and Tonga, where it occurs in forest at elevations from near sea-level to 700 m. and has been noted as a tree 2.5–8 m. high.

LOCAL NAMES. *Fagu fagu* is the general name in Samoa and *kulukulu* in Tonga; further notations indicate *leva va'u* (Upolu), *lau fagu fagu* (Tutuila), and *kulukulufa* (Vava'u).

Samoa. UPOLU: Malololelei, *Christophersen 304* (BISH), *Setchell 15667* (BISH); above Malololelei, *Christophersen 236* (BISH); Vaea Mt., *Bryan 99* (BISH). TUTUILA: Pago Pago and vicinity, *Christophersen 1253* (BISH), *1254* (BISH), *Garber 929* (BISH); Alava Ridge, *Christophersen 1130* (BISH, US); Papatele Ridge, *Christophersen 1006* (BISH, US). SAMOA, WITHOUT FURTHER LOCALITY: *U.S. Expl. Exped.* (GH, US 62360 & 73912 type).

Tonga. VAVA'U: Northwestern side of island, *Yuncker 16181* (BISH, GH, US); Talau hill, *MacDaniels 1095* (BISH); above Anovai Lake, *Yuncker 16050* (BISH, GH, US). EUA: Above Fuai, *Yuncker 15688* (BISH, US).

As an example of the difficulty of specific delimitation in *Meryta* one may note that Harms (in Notizbl. Bot. Gart. Berlin **14**: 320. 1938) has referred a collection from the Tuamotus to *M. macrophylla*. In spite of a similarity in fruit, this particular specimen (*St. John 14263*, BISH, from Anaa) has leaf-blades rounded at the apex, and we confidently exclude it from the species of Samoa and Tonga.

4. **Meryta denhamii** Seem. in Bonplandia **10**: 295. 1862; Harms in Notizbl. Bot. Gart. Berlin **14**: 318. 1938.

Meryta denhami Seem. Fl. Vit. 119. 1865; Hemsl. in Bot. Mag. **129**: *pl. 7927.* 1903.

As we have not seen material of this species, we cannot add to the above-cited descriptions.

TYPE LOCALITY: New Caledonia: Isle of Pines; the type is from a specimen cultivated at Kew, grown from material obtained by W. G. Milne on Captain Denham's Expedition.

DISTRIBUTION. In addition to the Isle of Pines, the species is attributed by Hemsley (as cited above) to the Banks Islands, New Hebrides, by the statement that ". . . what appears to be the same species has since been collected by Archdeacon Comins. . ." on Santa Maria (i.e. Gaua Island).

The species is listed merely because of Hemsley's note, but its occurrence in the New Hebrides is certainly open to question without re-study of the material and the several species attributed to New Caledonia. The excellent figure cited above clearly indicates the nature of the pistillate plant, which at any rate seems quite distinct from *M. neo-ebudica*, the only species of the genus positively recorded from the New Hebrides to date.

3. **Polyscias** J. R. & G. Forst. Char. Gen. Pl. 63. 1776; Seem. in Jour. Bot. **3**: 179. 1865; Harms in E. & P. Nat. Pflanzenfam. 3(8): 43. 1894, in Bot. Jahrb. **56**: 409. 1921; Hutchinson, Gen. Fl. Pl. **2**: 75. 1967.

Nothopanax Miq. in Bonplandia **4**: 139. May, 1856, Fl. Ind. Bat. **1**(1): 765.

Sept. 1856; Seem. Fl. Vit. 113. 1865, in Jour. Bot. **4**: 293, p. p. 1866. Non sensu Harms in E. & P. Nat. Pflanzenfam. 3(8): 47. 1894, nec Hutchinson, Gen. Fl. Pl. **2**: 76. 1967.

In view of diverse concepts of the delimitation of the genera *Polyscias* and *Nothopanax*, it may be well once again to summarize their typification. *Polyscias*, being based entirely on *P. pinnata* J. R. & G. Forst., presents no problem; its type species has pinnately compound leaves (rarely unifoliolate) and 4 or 5 styles, as understood by the Forsters. Only three species may be considered as typifying *Nothopanax* in Miquel's original sense. These are *N. fruticosum* (based on *Panax fruticosum* L.)[2], *N. cochleatum* (based on *Aralia cochleata* Lam.), and *N. obtusum* (based on *Panax obtusum* Bl.). Two other species (based on *Panax pinnatum* Lam. and *Panax anisum* DC.) were tentatively referred here, prefaced by interrogation marks, and these may be dismissed from consideration as type species.

In his original circumscription of the genus Miquel stated that the styles and ovary-locules were two or three. The only one of the original three species of which the flowers were definitely known to Miquel was *Nothopanax fruticosum*, and it would thus appear imperative to accept that as his type species (cf. Merr. in Philip. Jour. Sci. Bot. **12**: 241. 1912). However, Sprague and Green (in Kew Bull. **1933**: 155. 1933) indicated *N. cochleatum* as Miquel's type species, and in this they have been followed by Fosberg (in Univ. Haw. Occ. Pap. **46**: 9. 1948), Hutchinson (Gen. Fl. Pl. **2**: 76. 1967), and doubtless by other authors.

A misinterpretation of the identity of *Nothopanax cochleatum* Miq. (i.e. *Aralia cochleata* Lam.) has been responsible for the use of the name *Nothopanax* for certain species with digitately compound leaves. These species, as convincingly shown by Philipson (in New Zeal. Jour. Bot. **3**: 333. 1965), should be placed in *Pseudopanax* C. Koch, which appears to have a distribution from China to Tasmania, New Zealand, New Caledonia, and to southern South America. The persistent error of including digitate-leaved species in *Nothopanax* may have originated with Seemann (in Jour. Bot. **4**: 293–296. 1866) and been continued by Harms (in E. & P. Nat. Pflanzenfam. 3(8): 47. 1894), but it is unfortunate that Hutchinson (Gen. Fl. Pl. **2**: 76. 1967) prolongs it and even attributes the generic name to Seemann.

As a matter of fact, indication of *N. cochleatum* as the type species of *Nothopanax*, even if it were acceptable, would not permit confusion of that genus and *Pseudopanax*. *Aralia cochleata* Lam. is based entirely on *Scutellaria prima* Rumph., as pointed out by Merrill (Interpret. Rumph. Herb. Amb. 409. 1917), and hence is a direct synonym of *Polyscias scutellaria* (Burm. f.) Fosberg. Below we point out the specific identity of this concept with *P. pinnata*, the type species of *Polyscias*. Therefore, those who wish to follow Sprague and Green in the typification of *Nothopanax* must equate the genus directly with *Polyscias*.

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[2] We use the neuter termination for these epithets only to retain the usage of original authors in this discussion, although the correct usage is masculine.

Acceptance of *Panax fruticosum* L. as the type species of *Nothopanax* Miq. does raise the question of whether a real discontinuity exists between the species of this complex with 2 (rarely 3) styles and ovary-locules (*Nothopanax*) and those species with 3–5 (rarely 2) styles and ovary-locules (*Polyscias*). That this character is highly unsatisfactory has been indicated by the second author (in Taxon **14**: 284. 1965), and our present study merely supports the conclusion that only one genus is to be maintained, a viewpoint apparently adopted by some other current students of the family (cf. Philipson in Bull. Brit. Mus. (Nat. Hist.) Bot. **1**: 9. 1951).

Another genus of this relationship is *Tieghemopanax* Viguier, which Hutchinson (Gen. Fl. Pl. **2**: 75. 1967) maintains as distinct on the basis of its 4-locular anthers. We are unable to review the New Caledonian and Australian species placed in *Tieghemopanax*, but it seems apparent that the New Hebridean species so referred are properly placed in *Polyscias*, as suggested by the second author in 1965 (in Taxon **14**: 285) and as indicated in the following treatment. However, we refrain from listing this generic name in the synonymy above.

In the area of the present study, *Polyscias* is represented by 12 species, of which 9 are clearly indigenous and an additional one (*P. scutellaria* including *P. pinnata*) is probably indigenous in the New Hebrides. The species of *Polyscias* yield a characteristic acrid fragrance, especially when the leaves are cut or bruised, this being particularly obvious in such cultivated species as *P. guilfoylei*.

KEY TO THE SPECIES

Leaves once pinnate (sometimes unifoliolate in no. 10).
  Styles or stigmas and ovary-locules 2 (very rarely 3); leaves usually with numerous leaflets, only occasionally as few as 7 or 9, very rarely as few as 5; indigenous species.
    Flowers borne singly, alternate or loosely whorled on ultimate inflorescence-branches; leaflet-blades not more than 11 × 5 cm. . . . . . . 1. *P. joskei.*
    Flowers in umbels (or pseudo-umbels in no. 9) or heads; leaflet-blades (except in nos. 3 and 4) consistently larger.
      Inflorescences paniculately capitate, the flowers sessile; leaflets up to 27 × 8 cm., strongly asymmetric and cordate at base. . . . . 2. *P. nusedhul.*
      Inflorescences racemose-paniculate, the flowers pedicellate, in umbels (but pedicels sometimes very short in nos. 7 and 9).
        Petioles slightly swollen at base but not alate; leaflet-blades asymmetric, obviously falcate, usually 4–9 × 1.8–3.5 cm., unequally acute to rounded at base; young vegetative parts and inflorescence-axes with a sparse (and sometimes evanescent) indument of minute 1–several-celled hairs.
          Leaflets (5–) 9–13, the blades coarsely crenulate at margin; petioles 8–14 cm. long on mature leaves; flowers usually 5–12 per umbel, the stylopodium conical, tapering into the slender stylar column. . . . . 3. *P. neo-ebudarum.*

Leaflets 19–23, the blades entire at margin; petioles 5–9 cm. long on mature leaves; flowers usually 11–32 per umbel, the disk concave, the stylar column slender. .... 4. *P. culminicola.*

Petioles alate at base, the wings often obvious; leaflet-blades conspicuously larger, usually much more than 9 × 4 cm. (basal ones occasionally smaller); plants glabrous throughout.

Leaflet-blades ovate-falciform, cordate-auriculate at base. .... 5. *P. excelsa.*

Leaflet-blades not falcate, subequally obtuse to rounded or subcordate (but not auriculate) at base.

Disk concave to slightly elevated, the styles obvious, divaricate in fruit, 1–1.5 mm. long.

Ultimate (umbelliferous) inflorescence-branches very numerous, scattered, irregularly arranged; pedicels comparatively short, not more than 6 mm. long; flowers with a cupuliform calyx not more than 2.5 mm. long.

Petioles inconspicuously alate in the proximal 3–5 cm.; inflorescence-axes griseo-corticate-lenticellate; flowers borne in umbels on ultimate peduncles 10–20 mm. long, 5–15 per umbel, the pedicels 2–6 mm. long. .. 6. *P. corticata.*

Petioles obviously alate in the proximal 7–20 cm.; inflorescence-axes smooth, dark; flowers borne in umbels on ultimate peduncles 1–6 mm. long (or umbels subsessile), (1–) 2–7 per umbel, the pedicels less than 1 mm. long. .... 7. *P. multijuga.*

Ultimate (umbelliferous) inflorescence-branches often aggregated in loose whorls at 2–4 nodes; flowers borne in umbels on ultimate peduncles 12–80 mm. long, 8–15 per umbel, the pedicels conspicuous, 7–15 mm. long (up to 25 mm. in fruit); flowers comparatively long and narrow, the calyx of perfect flowers urceolate, 3–3.5 mm. long. .... 8. *P. samoensis.*

Disk elevated into a broadly conical stylopodium surmounted by two sessile laterally contiguous stigmas, the fruits similarly lacking styles; pedicels short, (0.5–) 1–5 mm. long. .... 9. *P. reineckei.*

Styles and ovary-locules 3–5 (rarely 2); leaves with 1–9 leaflets; cultivated species (no. 10 probably indigenous in the New Hebrides).

Leaflets 1–5, the blades broadly elliptic or orbicular, usually 8–22 cm. long and broad, cordate or broadly concave (rarely truncate) at base, rounded at apex, entire or coarsely crenulate at margin. .... 10. *P. scutellaria.*

Leaflets 5–9, the blades usually elliptic to oblong, usually 6–12 × 4–8 cm. (sometimes larger), obtuse to acute at base and apex, irregularly spinulose-dentate at margin. .... 11. *P. guilfoylei.*

Leaves irregularly pinnate-compound, usually 2 or 3 times divided but rarely simply pinnate (and then with some leaflets pinnatifid or laciniate); cultivated species.

Styles and ovary-locules 3–5; leaflets very variable in shape, some usually elliptic to oblong, the marginal teeth usually 1–3 mm. long. .... 11b. *P. guilfoylei* var. *laciniata.*

Styles and ovary-locules 2 (rarely 3); ultimate leaflet-divisions usually lanceolate and 3–6 times as long as broad, the marginal teeth irregular, some of them usually 5–10 mm. long. .... 12. *P. fruticosa.*

1. **Polyscias joskei** Gibbs in Jour. Linn. Soc. Bot. **39**: 148. 1909; J. W. Parham, Pl. Fiji Isl. 86. 1964. PL. I, FIGS. 1–5.

Botryopanax joskei Hutchinson, Gen. Fl. Pl. **2**: 57. 1967.

A tree, glabrous throughout, the branchlets stout (10–15 mm. in diameter toward apices), copiously cicatricose with large obdeltoid petiolar scars, the leaves and inflorescences congested toward ends of branchlets; leaves imparipinnate, up to 60 × 25 cm., the petiole and rachis comparatively slender, shallowly canaliculate, the petiole 10–18 cm. long on mature leaves, slightly swollen at base, the rachis inconspicuously contracted at bases of petiolules, the leaflets 7–15, the petiolules slender, (2–) 5–20 mm. long, the blades chartaceous to thin-coriaceous, ovate- to elliptic-oblong, 5–11 cm. long, (2–) 3–5 cm. broad (basal ones somewhat shorter and broader than middle ones), unequally obtuse to rounded at base, obtuse to short-acuminate at apex, crenulate at margin, the costa raised on both surfaces, the secondary nerves 8–18 per side, subspreading, usually prominulous on both surfaces, the veinlet-reticulation inconspicuous; inflorescences broadly compound-racemose-paniculate, up to 20 cm. long and 40 cm. broad, the peduncle less than 3 cm. long, the primary branches about 8–12, alternate to subopposite or whorled, each bearing numerous secondary branches 3–8 cm. long, the bracts soon caducous; flowers borne singly, alternate or loosely whorled, subtended by lanceolate-subulate bracteoles 0.8–1.2 mm. long, these soon caducous, the pedicels slender, articulate at apex, scarcely 1 mm. long (or flowers subsessile) at anthesis, about 2 mm. long in fruit; staminate flowers about 3 mm. long at anthesis, the calyx conspicuously stipitate at base, cupuliform distally, about 1 mm. in diameter, obscurely (4- or) 5-lobed; petals (4 or) 5, oblong, 2–2.5 mm. long, unguiculate at apex; stamens (4 or) 5, the filaments slender, about 0.6 mm. long, the anthers oblong, 1.5–1.7 mm. long, versatile; stigmas 2, contiguous, forming a minute conical protuberance on the flat disk; perfect flowers not seen; fruits laterally compressed, bilocular, transversely oblong-ellipsoid, 4–5 mm. long, 5–6 mm. broad, surmounted by the persistent calycular rim and 2 conspicuously divergent styles, these about 1.5 mm. long, the stigmas long-decurrent.

TYPE LOCALITY: Nandarivatu, Mba Province, Viti Levu, Fiji; the type is *Gibbs 748*, cited below. Curiously, this number is not cited by Gibbs, although the label notes of the British Museum specimen agree with the data given in the type description, and although the specimen is labelled by Gibbs and bears a printed label "type specimen." The numbers cited in the description are *893* (staminate) and *750* (fruit). We conclude that these specimens were combined and assigned a new number, *748*; this sheet has both flowering and fruiting branchlets and may be indicated as the holotype.

DISTRIBUTION. Endemic to Fiji, and thus far known from Viti Levu, Ovalau, and Vanua Levu, occurring infrequently at elevations of 575–1,150 meters in forest or in the dense thickets of ridges and crests. It has been noted as a tree 3–10 meters high, often compact, with a thin, pale latex. The distal parts of inflorescence-branches and pedicels are purple, the petals are yellow, and the fruits are purple with yellow styles.

LOCAL NAMES. *Sole yalewa* and *nausasa* have been noted on Viti Levu, and *ndanindani* on Vanua Levu.

Fiji. VITI LEVU: MBA: Mt. Evans Range, *Greenwood 1249* (A, BISH, UC, US); Nandarivatu, *Gibbs 748* (BM type, photo at US), *Degener & Ordonez 13578* (A, BISH, SUVA); slopes of Mt. Nanggaranambuluta, *Gillespie 3197* (BISH, GH, NY, US), *3914* (BISH); ridge between Mt. Nanggaranambuluta and Mt. Namama, *Smith 4975* (A, BISH, K, NY, US); between Nandala and Nukunuku Creeks, along trail from Nandarivatu toward Lewa, *Smith 6161* (A, BISH, US). NAMOSI: Summit of Mt. Naitarandamu, *Gillespie 3151* (BISH, GH, UC, US); Mt. Voma, *Fiji Dept. Agr. 1703* (A, SUVA). RA: Ridge from Mt. Namama toward Mt. Tomanivi, *Smith 5685* (A, BISH, K, NY, US). OVALAU: Summit of Mt. Ndelaiovalau and adjacent ridge, *Smith 7584* (BISH, US). VANUA LEVU: MATHUATA-THAKAUNDROVE BOUNDARY: Crest of Korotini Range, between Navitho Pass and Mt. Ndelaikoro, *Smith 568* (BISH, GH, K, NY, UC, US).

Polyscias joskei is clearly different from the other species of our area in having its flowers borne singly on the ultimate inflorescence-branches rather than in umbels. It may be noted, however, that *P. multijuga* and *P. reineckei* sometimes have a reduced number of flowers per umbel and rarely only one, but there the single-flowered condition is sporadic and never consistent for an entire inflorescence. The other characters of these two species are strikingly different, but the point noted above may suggest the flexibility of the single-flowered condition.

A closer relative of *P. joskei* may be *P. tahitensis* (Nad.) Harms, of the Society Islands, but the leaflet-blades of the latter are oblong-lanceolate, proportionately narrower, and entire. The flowers of *P. tahitensis* appear to be borne in compact, few-flowered umbels; when these are one-flowered, the appearance of racemosely borne flowers is simulated.

In his 1967 review of the family, Hutchinson has proposed a new combination for *P. joskei* in the genus *Botryopanax* Miq., unaccountably accrediting our species to the Philippine Islands, even though the generic distribution of *Botryopanax* is stated as Mauritius and the Mascarenes. We cannot express an opinion as to the limits of *Botryopanax*, but, since it is stated to have 13–16 petals and 8–12 ovary-locules, the reference to it of a species with 5 petals and 2 ovary-locules is in error. If those species of *Polyscias* with solitary (rather than umbellate) flowers are to be segregated, Hutchinson's new genus *Gelibia* (in Gen. Fl. Pl. 2: 57. 1967) seems better suited for them, whether the leaves are simply pinnate or bipinnate seeming of little consequence. Since *Polyscias* includes at least one species with decompound leaves (*P. fruticosa*), the two species of *Gelibia* are hardly separable on that basis. Actually, it is quite evident that *P. joskei* in all its basic characters is well placed in *Polyscias*, and transitional stages between single flowers and few-flowered umbels are apparent in the genus, as noted above.

2. **Polyscias nusedhul** (Guillaumin) B. C. Stone in Taxon **14**: 285. 1965.

Tieghemopanax nusedhul Guillaumin in Jour. Linn. Soc. Bot. **51**: 554. 1938.

Having seen no material of this species, we cannot add to the original description.

TYPE LOCALITY: Hog harbour, Espiritu Santo, New Hebrides; two specimens, *I. & Z. Baker 13a* and *71a*, are cited without designation of a type. These cotypes are deposited in the herbarium of the British Museum.

LOCAL NAME. *Nüsedhul* is apparently used generically in this part of the New Hebrides, since it was also recorded for the species we discuss as *P. excelsa*.

On the basis of the description one may feel sure that a species of *Polyscias* is here concerned; Guillaumin's concept of *Tieghemopanax* includes *T. neo-ebudarum*, which is discussed as our next species of *Polyscias*, as well as *T. fruticosus*, a synonym of *P. fruticosa*. The description indicates that *P. nusedhul* is related to the common and variable *P. multijuga*, of Fiji, Tonga, and Niue, but the New Hebridean plant would appear to have more obviously inequilateral leaflets that are consistently cordate at base, shorter petiolules, a less expansive inflorescence, and strictly sessile flowers about 10 per head. The flowers of *P. multijuga* are 2–7 per umbel (rarely solitary) and short-pedicellate (but rarely essentially sessile).

3. **Polyscias neo-ebudarum** (Guillaumin) B. C. Stone in Taxon **14**: 285, as *P. neo-ebudara*. 1965. PL. I, FIGS. 6–8.

Tieghemopanax neo-ebudarum Guillaumin in Jour. Arnold Arb. **12**: 264. 1931.

A tree, glabrous throughout or the young parts and inflorescence-axes with a sparse indument of 1–3-celled spreading hairs scarcely 0.1 mm. long and evanescent, the branchlets 6–8 mm. in diameter toward apices; leaves imparipinnate, up to 40 cm. long, the petiole and rachis slender, subterete, the petiole 8–14 cm. long on mature leaves, slightly swollen at base, the rachis obscurely contracted at bases of petiolules, the leaflets (5–) 9–13, the petiolules slender, 5–10 mm. long, the blades papyraceous, asymmetric and subfalcate (lateral ones), ovate-lanceolate, 4–9 cm. long, 1.8–3.5 cm. broad, unequally acute at base, acute to obtusely acuminate at apex, coarsely crenulate at margin, the costa raised on both surfaces, the secondary nerves 5–8 per side, subascending, prominulous or plane on both surfaces, the veinlets usually obscure; inflorescences racemose-paniculate, up to 30 cm. long, the peduncle very short, the primary branches few, subascending, the bracts small, caducous; flowers borne in umbels on ultimate peduncles 2–10 mm. long, usually 5–12 per umbel, the flower-subtending bracteoles lanceolate, about 0.5 mm. long, evanescent, the pedicels 1–4 mm. long, articulate at apex; perfect flowers with a narrowly cupuliform calyx about 2 mm. long, the teeth minute (calyx of staminate flowers stipitate at base and smaller); petals 5, oblong, 3–3.5 mm. long, unguiculate at apex; stamens 5, the filaments slender, 1.5–1.7 mm. long, the anthers ovate-oblong, about 2 mm. long, versatile; stylopodium conical, about 2 mm. long including the slender stylar column, this minutely bifid at apex; fruits laterally compressed, bilocular, transversely oblong-ellipsoid, 3–4 mm. long, 4–4.5 mm. broad, surmounted by the narrow calycular rim and the stylar column 0.8–1 mm. long, this bifid at apex with 2 stigmatiferous lobes less than 0.5 mm. long.

TYPE LOCALITY: New Hebrides. Three specimens were cited by Guillaumin without indication of a type, and therefore we herewith indicate *Kajewski 291*, from Eromanga, as the lectotype; the holotype is presumably the specimen in the herbarium of the Arnold Arboretum.

DISTRIBUTION. Endemic to the New Hebrides, and thus far known from Eromanga and Aneityum, where it is indicated as relatively common in rain-forest at elevations of 60–600 meters. Specimens were taken from trees 8–12 meters high; the flowers are noted as purple-brown and the fruit as black at maturity.

LOCAL NAMES AND USES. *Narse* has been noted on Eromanga, and *kiviano* on Aneityum; on the former island the leaves are used as an application for sore ears.

New Hebrides. EROMANGA: Dillon Bay, May 23, 1928, *Kajewski 291* (A type, BISH). ANEITYUM: Anelgauhat Bay, *Kajewski 749* (A, BISH, US), *977* (coll. *J. P. Wilson*) (A, BISH, US).

This species clearly falls into our concept of *Polyscias*, in which genus it is closely related only to the Fijian *P. culminicola*.

4. **Polyscias culminicola** A. C. Sm. in Contr. U.S. Natl. Herb. 37: 85. 1967. PL. I, FIGS. 9–12.

Although no material additional to the type collection is available, examination of isotypes permit a slight amplification of the description.

Plant apparently polygamo-monoecious, the central flowers of umbels sometimes perfect or functionally pistillate (self-fertile?), the ovary enlarging before the corolla opens; immature fruit 2-locular, compressed-oblong-ellipsoid, up to 7 × 5.5 mm.; outer (or sometimes all) flowers of umbels staminate, as originally described.

TYPE LOCALITY: Mba Province, Viti Levu, Fiji; the type is *Smith 4514*, cited below.

DISTRIBUTION. Endemic to Fiji, and thus far known from a single locality in western Viti Levu, where it was found in crest forest on a windswept ridge at an elevation of 750–900 meters. The material is from a tree

8 meters high, with leaves tufted at ends of branchlets and with the inflorescence terminal on branchlets.

LOCAL NAME. *Sawira* was recorded for the type collection, but this usually refers to the family Meliaceae and may be incorrectly applied to a *Polyscias*.

Fiji. VITI LEVU: MBA: Northern slopes of Mt. Namendre, east of Mt. Koromba (Pickering Peak), *Smith 4514* (A, BISH, K, US 1965344 type).

Polyscias culminicola is less closely related to *P. joskei*, with which it was originally compared, than to the New Hebridean *P. neo-ebudarum*, with which it agrees in its umbellate flowers, its comparatively small, falcate leaflets, the indument of its young vegetative parts and inflorescence-axes (although this is evanescent in *P. neo-ebudarum*), and its petioles lacking the basal wings so characteristic of most species of *Polyscias* (but also lacking in *P. joskei*). Foliar and inflorescence characters noted in our key clearly differentiate *P. culminicola* and *P. neo-ebudarum*.

5. **Polyscias excelsa** (Guillaumin) B. C. Stone in Taxon **14**: 285. 1965.

Tieghemopanax excelsa Guillaumin in Jour. Linn. Soc. Bot. **51**: 554. 1938.

As we have not seen material of this species, we cannot add to the original description; however, in view of the other dimensions given it seems probable that ". . . floribus . . . 30 mm. longis" is an error for 3 mm.

TYPE LOCALITY: Hog harbour, Espiritu Santo, New Hebrides; the type is *I. & Z. Baker 13*, deposited in the herbarium of the British Museum.

LOCAL NAME. *Nüsedhul* is recorded with the original description.

It may be noted that one of the Baker numbers referred to *P. nusedhul* is *13a*, collected at the same locality as no. *13* but on a different date. On the basis of the descriptions, the two species are amply distinct and are both clearly referable to *Polyscias*. *Polyscias excelsa* also would appear to be of the relationship of *P. multijuga*, with which it agrees in its large inflorescences and few-flowered, compactly arranged umbels. The flowers of *P. excelsa* are noted as 6–10 per umbel, whereas in the Fijian species they are 2–7 or sometimes single. The ovate-falciform, cordate-auriculate leaflet-blades, from the description, seem to provide a further differentiating character for *P. excelsa*.

6. **Polyscias corticata** Gibbs in Jour. Linn. Soc. Bot. **39**: 149. *pl. 13, figs. 14–17*. 1909; J. W. Parham, Pl. Fiji Isl. 86. 1964.

PL. II, FIGS. 10–14.

A tree or shrub, glabrous throughout; leaves imparipinnate, large, up to 100 cm. long, the petiole and rachis comparatively stout, subterete or obscurely canaliculate, the petiole of mature leaves 20–35 cm. long, conspicuously swollen to a clasping, lenticellate base and inconspicuously alate in the proximal 3–5 cm., the rachis geniculate at bases of petiolules, the leaflets (9–) 13–17, the petiolules slender, diverse in length, of lateral leaflets 2–25 mm. and of terminal leaflet to 45 mm. long, the blades papyraceous, oblong or ovate-elliptic, (9–) 15–30 cm. long, (4–) 6–10 cm. broad, subequally obtuse to rounded or subcordate at base, abruptly caudate-acuminate at apex (acumen 1–2.5 cm. long but fragile), entire or with a few callose-denticulate crenations, the costa sharply raised above, prominent beneath, the secondary nerves 8–18 per side, spreading, usually plane above and prominulous beneath, the veinlet-reticulation coarse, prominulous beneath; inflorescences racemose-paniculate, up to at least 50 cm. long, the primary branches diverse in length, up to 40 cm. long, all the inflorescence-axes griseo-corticate-lenticellate, the primary bracts oblong-lanceolate, 1–2 cm. long (those at base of inflorescence to 4 cm. long), at length caducous, the umbel- and flower-subtending bracts and bracteoles oblong, 1–3 mm. long; flowers borne in umbels on ultimate peduncles 10–20 mm. long, usually 5–15 per umbel, the pedicels 2–6 mm. long, articulate at apex; perfect flowers 5–6 mm. long at anthesis, with a cupuliform calyx 2–2.5 mm. long, the rim undulate or obscurely 5-denticulate; petals 5, deltoid-oblong, 2.5–3.5 mm. long, unguiculate at apex; stamens 5, the filaments slender, about 1 mm. long, the anthers oblong, 1.5–2 mm. long; disk concave or flat, the styles 2, free nearly to base, erect or subspreading, 1–1.5 mm. long, with decurrent stigmas; staminate flowers similar but somewhat smaller; fruits laterally compressed, bilocular, transversely ellipsoid, about 4 × 6.5 mm., substipitate at base, surmounted by the persistent calycular rim and the obviously divaricate styles.

TYPE LOCALITY: Mba Province, Viti Levu, Fiji; the type is *Gibbs 769*, cited below.

DISTRIBUTION. Endemic to Fiji, and thus far known from the largest islands, Viti Levu and Vanua Levu, where it occurs in usually dense forest at elevations of 300–900 meters. Specimens have been indicated as slender trees or shrubs, unbranched or few-branched, and 1.5–4 meters high; the inflorescences are axillary among leaves congested toward apices of branchlets. The calyx is purplish or reddish; the petals green to white, but becoming rich purple without at anthesis; the anthers pale yellow to white; and the styles yellowish.

LOCAL NAMES. *Sole* and *ndravi* have been noted on Viti Levu, and *ndanindani* on Vanua Levu.

Fiji. VITI LEVU: MBA: Nandarivatu and vicinity, *Gibbs 769* (BM type, photo at US), *Degener 14458* (A, BISH, K, NY, UC, US), *14806* (A, BISH, K, NY, UC, US), *14834* (A, BISH, K, NY, UC, US); between Nggaliwana and Nandala Creeks, south of Nauwanga, *Smith 5804* (A, BISH, K, NY, US). VANUA LEVU: THAKAUNDROVE: Southern slopes of Korotini Range, below Navitho Pass, *Smith 510* (BISH, NY); southwestern slope of Mt. Mbatini, *Smith 611* (BISH, GH, K, NY, UC, US).

The Fijian *P. corticata* and *P. multijuga* and the Samoan *P. samoensis* form a group of related species, but differences among them are obvious. *Polyscias corticata* is readily distinguished by having its inflorescence-axes pale and with congested transverse lenticels that provide a curiously flaky appearance. In type of inflorescence *P. corticata* is closer to *P. multijuga* than to *P. samoensis*, but in length of pedicels and of umbel-peduncle it is intermediate between them. The petiolar wings of *P. corticata* are less conspicuous than in either of its two relatives.

7. **Polyscias multijuga** (A. Gray) Harms in E. & P. Nat. Pflanzenfam. 3(8): 45. 1894; Yuncker in Bishop Mus. Bull. **178**: 92. 1943, in *op. cit.* **220**: 207. 1959. PL. II, FIGS. 1–9.

Paratropia multijuga A. Gray, Bot. U.S. Expl. Exped. **1**: 722. 1854.
Nothopanax multijugum Seem. Fl. Vit. 115. *pl. 18, 19.* 1865, in Jour. Bot. **4**: 295. 1866.
Panax multijugus B. & H. f. Gen. Pl. **1**: 938. 1867.
Panax multijugum B. & H. f. ex Drake, Ill. Fl. Ins. Mar. Pac. 181. 1890; Hemsl. in Jour. Linn. Soc. Bot. **30**: 180. 1894.

A tree, glabrous throughout; leaves imparipinnate, large, up to 100 cm. long, the petiole and rachis stout, subterete or slightly flattened above, the petiole of mature leaves 10–35 cm. long, conspicuously swollen to a clasping, often lenticellate base and obviously alate in the proximal 7–20 cm. with subcoriaceous wings, the rachis geniculate at bases of petiolules, the leaflets 13–25 (–29), the petiolules stout, diverse in length, of lateral leaflets 5–50 and of terminal leaflet to 60 mm. long, the blades papyraceous to thin-coriaceous, variable in size and shape, oblong to oblong- or ovate-elliptic, (9–) 12–27 cm. long, (3–) 4–12.5 cm. broad, subequally cordate to rounded or obtuse at base, subacute to cuspidate or acuminate at apex (acumen to 1.5 cm. long), entire and narrowly recurved at margin, the costa sharply raised above, prominent beneath, the secondary nerves 6–18 per side, spreading, prominulous on both surfaces or plane above, the veinlets usually plane on both surfaces; inflorescences compound-racemose-paniculate, up to 150 cm. long, composed of 3–8 panicles arising from a stout central rachis, the primary branches stout, bearing numerous irregularly disposed (alternate or opposite or whorled) secondary branches 5–18 cm. long at maturity, the primary bracts often subcoriaceous, ovate-oblong, 4–20 mm. long, obtuse or acute, the umbel- and flower-subtending bracts and bracteoles 0.5–2 mm. long; flowers borne in umbels on very short ultimate peduncles 1–6 mm. long (or umbels essentially sessile), (1–) 2–7 per umbel, the pedicels 0.5–1 mm. long (or flowers sometimes essentially sessile); perfect (or functionally pistillate) and staminate flowers sometimes occurring in the same umbel, differing only in the slightly smaller calyx of the latter; perfect flowers with a cupuliform calyx 1–1.3 mm. long, the rim undulate or obscurely 5-denticulate; petals 5, oblong-ovate, 2–3 mm. long, unguiculate at apex; stamens 5, the filaments slender, minute, the anthers oblong, 0.8–1.2 mm. long; disk slightly concave, the styles 2 (rarely 3?), suberect and contiguous in flower, usually 1–1.5 mm. long, divergent at least distally in fruit, with decurrent stigmas; fruits laterally compressed, bilocular (rarely trilocular ex Seemann), transversely ellipsoid, up to 5.5 × 6 mm., surmounted by the persistent calycular rim and styles, shallowly costate when dried.

TYPE LOCALITY: Mbua Bay ("Sandalwood Bay"), Mbua Province, Vanua Levu, Fiji; the type is the U.S. Exploring Expedition specimen cited below.

DISTRIBUTION. Fiji, Tonga, and Niue, occurring very abundantly at least in Fiji at elevations from near sea-level to 1,100 meters, and reported as a component of many types of forest or second-growth habitats. Specimens have been obtained from trees 2–15 meters high, usually noted as slender, sometimes unbranched, and with trunks up to 20 centimeters in diameter; the inflorescence is terminally borne on branchlets with a cluster of leaves. Color notes indicate the buds to be dark red, the petals and stamens greenish white to pale yellow, and the fruit purple at maturity.

LOCAL NAMES. In Fiji the names *ndanindani* and *sole* are general for this species (and other araliaceous plants); other names noted on Viti Levu are *sole ngga*, *sole katangane*, and *rau-i-tolu*, and in the Yasawas *wala nimbernggua*. In Tonga the names *tanetane* and *kulukulu* have been recorded, and on Niue *tanetane* and *tanetane vao*.

Fiji (because of abundance only island and province are cited). YASAWAS: WAYA: *St. John 18104* (BISH, US). VITI LEVU: MBA: *Parks 20532* (BISH, UC), *Gillespie 4295* (BISH), *Greenwood 297* (K), *297a* (A, UC), *935* (A, BISH), *Smith 4065* (A, BISH, K, US), *4837* (A, BISH, US). NANDRONGA & NAVOSA: *Degener 15264* (A, BISH, K, NY, UC, US), *Smith 5480* (A, BISH, K, NY, US). SERUA: *Degener 15137* (A, BISH, K, NY, UC, US), *Smith 9178* (BISH, US), *Fiji Dept. Agr. 12453* (BISH, SUVA). NAMOSI: *Seemann 205* (BM, GH, K), *Gillespie 2860* (BISH, UC), *2898* (BISH), *3120* (BISH, GH, UC) *Smith 8509* (BISH, US), *Fiji Dept. Agr. 5902* (SUVA). RA: *Degener 15499* (A, BISH, K, NY, UC, US). NAITASIRI: *Gillespie 3428* (BISH, GH, UC), *St. John 18246* (BISH, US), *Fiji Dept. Agr. 10640* (SUVA). REWA: *Gillespie 2210* (BISH, GH, NY). KANDAVU: *Smith 122* (BISH, GH, K, NY, UC, US). OVALAU: *Graeffe* (K). KORO: *Smith 937* (BISH, GH, K, NY, UC, US). NGAU: *Smith 7743* (BISH, US). VANUA LEVU: MBUA: *U.S. Expl. Exped.* (GH, US 47924 & 47925 type). MATHUATA: *Smith 6339* (A, BISH, K, NY, US), *Fiji Dept. Agr. 11498* (SUVA). THAKAUNDROVE: *Smith 365* (BISH, GH, K, NY, UC, US), *Degener & Ordonez 14019, 14081, 15545* (all A, BISH, K, NY, UC, US). TAVEUNI: *Gillespie 4711* (BISH, UC). MOALA: *Bryan 297* (BISH, UC). VANUA MBALAVU: *Smith 1497* (BISH, GH, K, NY, UC, US). AIWA: *Bryan 525* (A, BISH). KAMBARA: *Smith 1299* (BISH, NY). ONGEA LEVU: *Bryan 427* (BISH, US). FIJI WITHOUT OTHER LOCALITY: *Harvey* (GH, K), *Horne 189* (K).

Tonga. TONGATAPU: Near caves of Anahulu, *Setchell & Parks 15278* (UC); near Hufagalupe, *Setchell & Parks 15625* (UC); near Kologa Point, *Setchell & Parks 15385* (BISH, NY, UC); near Houma, *Yuncker 16227* (BISH, GH, US). 'EUA: *Lister* (K, photos at BISH, US), *Hotta 5434* (BISH).

Niue: Near Alofi, *Yuncker 9791* (BISH), *10062* (BISH, UC); near Mutalau, *Yuncker 9717* (A, BISH).

Polyscias multijuga is one of the most frequent small trees of the Fijian forests, and at one time it was probably equally abundant in Tonga and Niue. It is characterized by large, coarse leaves and inflorescences, of which the umbels are few-flowered and short-pedunculate. The stout petiole of *P. multijuga* bears obvious, subcoriaceous wings that extend upward from the base 7–20 centimeters.

8. **Polyscias samoensis** (A. Gray) Harms in E. & P. Nat. Pflanzenfam. 3(8): 45. 1894, in Bot. Jahrb. **25**: 663. 1898; Rechinger in Denkschr. Akad. Wiss. Wien **85**: 323. 1910; Setchell in Carnegie Inst. Publ. **341**: 61. 1924; Christophersen in Bishop Mus. Bull. **128**: 165. 1935. PL. I. FIGS. 15–17.

Panax samoense A. Gray, Bot. U.S. Expl. Exped. **1**: 717. 1854; Drake, Ill. Fl. Ins. Mar. Pac. 182. 1890.

Nothopanax samoense Seem. Fl. Vit. 116. 1865, in Jour. Bot. **4**: 295. 1866; Powell in Jour. Bot. **6**: 366. 1868.

A shrub or tree, glabrous throughout; leaves imparipinnate, large, perhaps up to 100 cm. long, the petiole and rachis comparatively slender, subterete, the petiole of mature leaves up to 20 cm. long, swollen to a clasping base and narrowly alate in the proximal 5–8 cm., the rachis geniculate at bases of petiolules, the leaflets 11–17, the petiolules slender, of lateral leaflets 8–30 mm. and of terminal leaflet to 35 mm. long, the blades papyraceous, oblong- to ovate-elliptic, (7–) 9–21 cm. long, 4–8.5 cm. broad, subequally subcordate to rounded or obtuse at base, gradually attenuate to a slender acumen 1–2 cm. long, entire or undulate and recurved at margin, the costa slightly raised above, prominent beneath, the secondary nerves 6–10 per side, curved-ascending, with the intricate veinlet-reticulation prominulous on both surfaces; inflorescences compound-paniculate, ample, up to at least 50 × 25 cm., the axes comparatively slender, the peduncle up to 18 cm. long, the primary branches numerous, spreading, irregularly disposed on the rachis, sometimes alternate but more often aggregated in loose whorls at 2–4 nodes including a terminal one, each primary branch bearing umbels at apex or again divided like the rachis, the primary bracts caducous (presumably small), the umbel- and flower-subtending bracts and bracteoles lanceolate, 1–3 mm. long; flowers borne in umbels on conspicuous slender ultimate peduncles 12–80 mm. long, 8–15 per umbel (sometimes mixed with additional umbels), the pedicels slender, 7–15 mm. long at anthesis and inconspicuously articulate at apex, elongating to 25 mm. in fruit; flowers (apparently uniformly hermaphrodite) slender, 6–7 mm. long at anthesis, the calyx urceolate, 3–3.5 mm. long including the obvious undulate or 5-denticulate rim; petals 5, lanceolate-ovate, 3–3.5 mm. long, unguiculate at apex; stamens 5, the filaments slender, less than 0.5 mm. long, the anthers oblong, 1.5–1.7 mm. long; disk flat, the styles 2, erect and contiguous in flower, spreading nearly from base in fruit and strongly recurved, elongating to 1.5 mm., with decurrent stigmas; fruits laterally compressed, bilocular, suborbicular, 7–8 mm. long and broad, conspicuously nerved, surmounted by the obvious calycular rim and styles.

TYPE LOCALITY: Samoa, indicated as Savaii and Tutuila; the type is the U.S. Exploring Expedition collection cited below.

DISTRIBUTION. Endemic to Samoa, and known from the three largest islands, occurring at elevations up to about 400 meters, presumably in forest. Specimens have been taken from trees or shrubs up to 7 meters high; the flowers and fruits are reported as dark purple in color, and the fruits have conspicuous reddish or purplish veins.

LOCAL NAMES AND USES. *Tanitani* is probably the name in general use, but Setchell notes *afia* as the name on Tutuila and indicates that oil from the plant is used on the hair. It is interesting to note that Powell (in Jour. Bot. 6: 278. 1868) lists *afia* as the name for *Ascarina lanceolata*, but indicates *afia-vao* for an unidentified shrub that, from his brief note, could represent *Polyscias*.

Samoa. "SAVAII AND TUTUILA": *U.S. Expl. Exped.* (GH, US 47923 type). UPOLU: (No material seen but reported by Harms and Rechinger). TUTUILA: Leone, *Wilder 87* (BISH); Pago Pago, *Wilder 44* (or *244*) (BISH); above Pago Pago, near wireless station, *Setchell 255* (coll. *Sutupe*) (GH, UC, US); between Fagaalu and Fatimafutu, *Setchell 374* (BISH, UC). SAMOA WITHOUT OTHER LOCALITY: *Powell 21* (K), *36* (K), *47* (K, photos at BISH, US), *159* (K, photos at BISH, US), *265* (K, photos at BISH, US), *s.n.* (K, photos at BISH, US), *Whitmee 97* (K), *197* (K, photos at BISH, US).

We have also seen a specimen from Aneityum, New Hebrides, obtained by an unknown collector in February 1859 (BM), which suggests this species. However, it is a very incomplete specimen, suggesting *P. samoensis* in its flowers but with smaller and strongly cordate leaflet-blades. It is noted here as a possibly undescribed relative of *P. samoensis*, which may safely be inferred to be a Samoan endemic.

From its relatives, *P. corticata* and *P. multijuga*, *P. samoensis* differs in its much more lax and open inflorescences, of which the comparatively few branches are whorled at a few nodes and umbellately aggregated apically. The flowers, borne on conspicuous pedicels in long-pedunculate umbels, are longer than those of the related species, with a conspicuously urceolate calyx, and the fruits are larger and very conspicuously nerved.

9. **Polyscias reineckei** Harms in Bot. Jahrb. **25**: 663. 1898; Rechinger in Denkschr. Akad. Wiss. Wien **85**: 323. 1910; Christophersen, Bishop Mus. Bull. **128**: 165. 1935; (?) Yuncker in Bishop Mus. Bull. **184**: 56. 1945. PL. III, FIGS. 1–6.

A tree, glabrous throughout; leaves imparipinnate, large, perhaps up to 100 cm. long, the petiole comparatively stout, of mature leaves 15–25 cm. long, swollen to a clasping base and narrowly alate in the proximal 10–14 cm., the rachis more slender, subterete, geniculate at bases of petiolules, the leaflets (9–) 11 or 13, the petiolules slender, of lateral leaflets 5–40 and of terminal leaflet to 60 mm. long, the blades papyraceous, oblong- to ovate-elliptic, (5–) 10–25 cm. long, (3–) 4–11 cm. broad, unequally rounded to obtuse at base, gradually attenuate to a slender sharp acumen 1–2 cm. long, entire or remotely spinulose-denticulate and narrowly recurved at margin, the costa plane or shallowly canaliculate above, prominent beneath, the secondary nerves 7–10 per side, curved-ascending, prominulous on both surfaces, the veinlet-reticulation intricate, plane or prominulous; inflorescences compound-paniculate, ample, sometimes exceeding 100 cm. in length, composed of a few (2–4?) elongate primary branches arising from a comparatively short peduncle and rachis, the branches pendent, long-pedunculate, each bearing about 6–12 elongate alternate lax secondary branches, the primary bracts lanceolate, 15–30 mm. long, soon caducous, the secondary bracts 3–10 mm. long, the umbel- and flower-subtending bracts and bracteoles 0.5–2 mm. long; flowers borne in (sometimes imperfect) umbels on slender ultimate peduncles (of diverse length) 1–20 (–40) mm. long, (1–) 3–8 per umbel, the pedicels slender, (0.5–) 1–3 mm. long at anthesis and inconspicuously articulate at apex, scarcely elongating (1–5 mm.) in fruit; flowers (apparently uniformly hermaphrodite) 4–4.5 mm. long at anthesis, the calyx cupuliform, 1.5–2 mm. long, the rim short, inconspicuously 5-denticulate; petals 5, deltoid-ovate, 2–3 mm. long, unguiculate at apex; stamens 5, the filaments ligulate, less than 1 mm. long, the anthers oblong, about 1.5 mm. long; stylopodium broadly conical, surmounted by 2 sessile laterally contiguous stigmas; fruits laterally compressed (or triquetrous?), bilocular (sometimes trilocular ex Harms), suborbicular or transversely ellipsoid, 5–6 × 6–8 mm., surmounted by the calycular rim, the stylopodium projecting less than 1 mm. and terminated by strictly sessile stigmas.

TYPE LOCALITY: Letogo Ridge, Upolu, Samoa; the type is *Reinecke 136*, collected in February 1894, and presumably destroyed in the Berlin herbarium.

DISTRIBUTION. Endemic to Samoa, and thus far known definitely only from Savaii and Upolu, where it occurs at elevations of near sea-level to 700 meters in open forest, coastal forest, etc. Plants of the species are reported as trees 4–12 meters high; no color notes are available. Four additional specimens from Upolu were listed by Rechinger in 1910.

LOCAL NAME. *Afia* has been noted on Savaii.

Samoa. SAVAII: Salailua, *Christophersen & Hume 2616* (A, BISH, US); between Salailua and Lataitai, *Christophersen 3010* (A, BISH); between Falelima and Samata, *Christophersen 2764* (A, BISH); Matavanu, near crater, *Christophersen & Hume 1951* (BISH, NY, US); above Sili, *Christophersen 3280* (BISH, US). UPOLU: *Graeffe* (BM).

An additional record of *P. reineckei,* on the island of Tau, Manua Islands, was noted by Yuncker in 1945, but this record was based on an observation by Paul L. Guest and is not supported by herbarium material. In view of the superficial similarity of this species and *P. samoensis,* the record must be questioned, especially as the latter is known from nearby Tutuila and the former is not.

Although in foliage *P. reineckei* is not easily distinguished from *P. samoensis,* there are excellent inflorescence-differences between these two Samoan endemics. The primary inflorescence-branches of *P. reineckei* bear alternate, elongate branches with racemosely disposed umbels, whereas the inflorescence-branches of *P. samoensis* are usually whorled and often again branched in a pseudo-umbellate manner. In both species the peduncles of the ultimate umbels are very diverse in length, but in *P. reineckei* they are usually the shorter. The flowers of *P. reineckei* are uniformly short-pedicellate, the pedicels not exceeding 3 mm. in length at anthesis and 5 mm. in fruit, whereas *P. samoensis* has pedicels 7–25 mm. long. The flowers of *P. samoensis* are notably longer, and the stylar difference is particularly noteworthy, *P. samoensis* having obvious styles strongly recurved in fruit, and *P. reineckei* having its stigmas sessile on a broadly conical stylopodium even in mature fruit.

It may be noted that in *P. reineckei* (e. g. in *Christophersen & Hume 2616*) the flowers may sometimes be only pseudo-umbellate, actually racemosely arranged toward the apices of the ultimate peduncles, which are freely bracteolate along much of their length. Thus we have another type of transition between umbellate and individually borne flowers, indicating that this character is not dependable even at the specific level with exactitude, and certainly not at the generic or tribal level.

10. **Polyscias scutellaria** (Burm. f.) Fosberg in Univ. Haw. Occ. Pap. **46**: 9. 1948; B. C. Stone in Taxon **14**: 284. 1965.

PL. I, FIGS. 13, 14.

Scutellaria prima Rumph. Herb. Amb. **4**: 75. *pl. 31.* 1743.

Crassula scutellaria Burm. f. Fl. Ind. 78. 1768.

Polyscias pinnata J. R. & G. Forst. Char. Gen. Pl. 64. *pl. 32.* 1776; Forst. f. Fl. Ins. Austr. Prodr. 90. 1786; Seem. in Jour. Bot. **3**: 180. 1865; Guillaumin in Bull. Soc. Bot. France **66**: 270. 1919; Harms in Bot. Jahrb. **56**: 409. 1921; Guillaumin in Bull. Soc. Bot. France **74**: 698. 1927, in Bull. Mus. Hist. Nat. II. **9**: 289. 1937, in Jour. Linn. Soc. Bot. **51**: 554. 1938; B. C. Stone in Taxon **14**: 282. 1965.

Aralia cochleata Lam. Encycl. Méth. **1**: 224. 1783.

Panax conchifolium Roxb. Hort. Beng. 21, *nomen.* 1814, Fl. Ind. ed. 2. **2**: 77. 1832.

Panax scutellaroides Reinw. in Bl. Bijdr. 880. 1826.

Panax cochleatum DC. Prodr. **4**: 253. 1830.

Panax heyneanum Wall. Cat. n. 4927, *nomen.* 1832; G. Don, Gen. Syst. **3**: 385. 1835; Walp. Rep. **2**: 429. 1843.

Panax forsteri Dec. & Pl. in Rev. Hort. IV. **3**: 105. 1854.

Nothopanax cochleatum Miq. in Bonplandia **4**: 139. May, 1856, Fl. Ind. Bat. **1**(1): 766. Sept. 1856.

Nothopanax tricochleatum Miq. Fl. Ind. Bat. Suppl. **1**: 340. 1861; Merr. Interpret. Rumph. Herb. Amb. 409. 1917.

Panax rumphii Hassk. in Abh. Naturf. Gesellsch. Halle **9**: 220. 1866.

Panax pinnata Baill. Hist. Pl. **7**: 197. *fig. 205.* 1879. Non Lam. (1788) nec A. Rich. (1847).

Nothopanax scutellarium Merr. Interpret. Rumph. Herb. Amb. 409. 1917.

Polyscias tricochleata Fosberg in Phytologia **5**: 290. 1955.

A shrub or small tree, glabrous throughout; leaves imparipinnate (often unifoliolate), the petiole usually 10–30 cm. long, swollen to a clasping base and narrowly alate in the proximal 1–5 cm., the rachis geniculate at bases of petiolules (or usually jointed in unifoliolate leaves), the leaflets 1, 3, or 5 (less often 2 or 4), the petiolules slender, of lateral leaflets (0.5–) 1–5 and of terminal leaflet to 6 cm. long, the blades papyraceous to subcoriaceous, normally green but often with white margins or areoles, broadly elliptic or orbicular, usually 8–22 (–26) cm. long and broad (but often smaller in cultivated plants), cordate or broadly concave (rarely truncate) at base, rounded at apex, subentire or coarsely crenulate at margin (crenations 1–2 cm. distant and sometimes conspicuously spinulose, or the leaflets sometimes subpalmately lobed), the costa raised above and prominent beneath, the secondary nerves 5–8 per side, spreading, prominulous on both surfaces or prominent beneath, the veinlet-reticulation intricate, plane or slightly prominulous on both surfaces; inflorescences compound-paniculate, up to 60 cm. long, the peduncle short, to 3 cm. long, the primary branches numerous, up to 45 cm. long, alternate toward base of inflorescence but often opposite or verticillate distally, the secondary branches similarly arranged, the primary bracts ovate, acute, to 1 cm. long, soon caducous, the umbel- and flower-subtending bracts and bracteoles ovate to lanceolate, 0.5–1.5 mm. long; flowers borne in umbels on slender ultimate peduncles 4–15 mm. long, 8–26 per umbel, the pedicels slender, 1.5–6 mm. long, articulate at apex; flowers 3–3.5 mm. long at anthesis, the calyx cupuliform, 1–1.5 mm. long and about 2 mm. in diameter at anthesis, the rim short, inconspicuously denticulate with 5–8 (rarely 9) teeth; petals 5–7 (sometimes 8, rarely 4 or 9), narrowly ovate-elliptic, 1.8–2.5 mm. long, unguiculate at apex; stamens as many as petals, the filaments slender, 0.5–1 mm. long, the anthers oblong, 1.3–1.7 mm. long; disk concave, the styles 3–5 (rarely 2), contiguous in an oblong-subconical column but free, 0.4–0.8 mm. long, rounded at apex, ventrally sulcate; fruits subglobose, costate, up to 5 mm. long and broad, surmounted by the persistent calycular rim and the eventually divaricate styles.

TYPE LOCALITY: Amboina; the basis for *Crassula scutellaria* Burm. f. is the Rumphian *pl. 31.* Merrill in his 1917 work points out that this was cited as *pl. 30* by Burman, as it also is by Fosberg in 1948. Of the complex synonymy cited above, most combinations are based either on Burman's name or on *Aralia cochleata* Lam. (also based on the Rumphian plate) and have been elucidated by Merrill, Fosberg, and Stone. The other basic synonym is *Polyscias pinnata* J. R. & G. Forst., typified by material collected in Tanna, New Hebrides, on Cook's second voyage. This material was labelled as collected by Forster and by Anderson, although the specimens may well have come from the same plant. Since the specimen with Anderson's name bears flowers and immature fruits as well as leaves, it is herewith indicated as the lectotype and is so cited below.

DISTRIBUTION. Widespread in cultivation, but presumably indigenous in the New Hebrides and the Solomon Islands, where it occurs in forest from near sea-level to about 300 meters. The available specimens are from shrubs or trees up to 5 meters high, but in cultivation the plants are often pruned into hedges, in which condition they flower infrequently. Such flowers as are available are indicated as pale yellow-green.

LOCAL NAMES AND USES. On Espiritu Santo, New Hebrides, the names *nëwesi* and *nüesi* have been noted, and on Efate *nanlass*, in Samoa *tagitagi*, and in Tonga *tanitani*. It is recorded that on Malekula, New Hebrides, the leaves of this plant are used to rub the gums with the intent of numbing the nerves prior to the extraction of teeth.

New Hebrides. ESPIRITU SANTO: Hog harbour, *I. & Z. Baker 64* (BM), *261* (BM). MALEKULA: Northwestern part, *Cheesman 27* (K, photos at BISH, US); without further locality, *Herre 69b* (NY). EFATE: Onesua, *Stone 2251* (BISH). TANNA: *Anderson* (BM lectotype, photo at US), *Forster* (K, photos at BISH, US). **Samoa.** UPOLU: Mulinu'u, near Apia, *McKee 3024* (BISH).

In 1965 (in Taxon **14**: 281–285) the second author discussed the typification of *Polyscias* and the identity of its type species, *P. pinnata* J. R. & G. Forst., indicating that several widely distributed horticultural forms are closely related to and perhaps derived from *P. pinnata*. One of these, *P. scutellaria*, was discussed in detail because of the tenuous nature of characters that separate it from *P. pinnata*. It was concluded that *P. pinnata* could be maintained as distinct on the basis of having its leaves generally 3- or 5-foliolate rather than 1-foliolate, its petals and stamens 7 or 8 rather than 4 or 5, and its styles 4 or 5 (whereas the styles of *P. scutellaria* are sometimes only 3, but also often 4 or 5). A factor in a decision to maintain both concepts as species was the fact that *P. scutellaria*, based on a binomial of 1768, would have priority if the taxa were merged.

However, on reconsideration and examination of more ample material, we are unable to recognize any morphological discontinuities that are in any sense usable to divide this complex into species. Individual plants often have the leaflets either 1, 3, or 5, and the correlation of number of petals and stamens with number of styles is haphazard. The most common numbers of petals and stamens are 5, 6, and 7, and of styles 3 or 4. One specimen from Bougainville, Solomon Islands (*Kajewski 1965*, A, BISH), has the petals and stamens 5 or 6 and the styles only 2; its leaves are 1- or 3-foliolate. The Kajewski specimen came from a rainforest tree and was apparently indigenous, and only its reduced number of styles separate it from the presumably indigenous New Hebridean specimens cited above.

We must conclude, therefore, that the forest species of the Solomons and New Hebrides, *P. pinnata*, is not separable from the widely cultivated *P. scutellaria* at any rank. It is unfortunate that the epithet of the type species of the genus is the later one.

The above description is drawn from available specimens, both from within and outside our area. It may be noted that specimens cultivated in Samoa and Hawaii are usually inclined to resemble the wild form suggested by the type of *P. pinnata*, with 3 or 5 leaflets; Micronesian and Philippine specimens usually resemble the typical and presumably cultivated form of *P. scutellaria*, with unifoliolate leaves. Fosberg, however, in making the appropriate combination in 1948, pointed out that various specimens cultivated in Hawaii show all variations from pinnate to unifoliolate leaves.

In his consideration of the Micronesian species of *Polyscias* in 1965 (in Micronesica **2**: 51–59), the second author again stressed the close relationship of *P. pinnata* and *P. scutellaria*. In the same paper he described a chimaeric variation of *P. tricochleata* that is essentially indistinguishable from *P. pinnata*, and therefore concluded that *Nothopanax tricochleatum* Miq. is merely a cultivated form of *P. pinnata*. This conclusion is herewith reinforced, but in view of our reduction of the Forsters' binomial to synonymy the correct designation of this particular form is *P. scutellaria* cv. Tricochleata. The cultivar is frequent in Micronesia and doubtless other tropical areas and is characterized by having leaves smaller than those of the indigenous form (of *P. pinnata*) or the normal cultivated form (of *P. scutellaria*), usually variegated and 3- or 5-foliolate, each leaflet being often further 3-divided and with coarsely crenate or spinulose-serrate margins. In our area this cultivar was reported by Yuncker (in Bishop Mus. Bull. **178**: 92. 1943, in *op. cit.* **184**: 56. 1945) as a presumable variety of *P. guilfoylei*. We note *P. scutellaria* cv. Trichochleata from our area as follows:

Fiji. VITI LEVU: REWA: Vicinity of Suva, *Degener & Ordonez 13542* (A).

Samoa. TUTUILA: Pago Pago, *Bryan 1002* (BISH). TAU: Siufaga Village, *Yuncker 9212* (BISH).

Niue. Alofi, *Yuncker 10051* (BISH).

11. **Polyscias guilfoylei** (Bull) L. H. Bailey in Rhodora **18**: 153. 1916.

A shrub or small tree, glabrous throughout, usually with suberect virgate branches; leaves imparipinnate, up to 50 cm. long, the petiole slender, 10–17 cm. long on mature leaves, clasping at base and inconspicuously alate in the proximal 1–2 cm., the rachis often shallowly canaliculate, geniculate at bases of petiolules, the leaflets 5–9, the petiolules slender, of various length, the blades papyraceous, green or variegated with white margins or areolae, variously shaped and incised; inflorescences compound-paniculate to verticillate-umbellate, the primary branches 5–10, up to 60 cm. long, spreading from the very short peduncle and rachis, the secondary branches numerous, alternate or opposite or often verticillate, the primary bracts deltoid-lanceolate, acute, about 1 cm. long, soon caducous, the umbel- and flower-subtending bracts and bracteoles ovate, 0.5–2 mm. long; flowers borne in umbels on slender ultimate peduncles 5–50 mm. long (these often bracteolate and geniculate at 1 or 2 nodes), 10–25 per umbel, the pedicels slender, 3–10 mm. long, articulate at apex; flowers with a cupuliform calyx 1.2–2 mm. long and 2–2.5 mm. in diameter at apex, the rim short, undulate, denticulate with 5 or 6 inconspicuous teeth; petals 5 or 6, deltoid-oblong, 2–2.5 mm. long, unguiculate at apex; stamens as many as petals, the filaments slender, 0.5–1 mm. long, the anthers oblong, 1–1.3 mm. long; disk concave, the styles 3–5, at first contiguous in a conspicuous column 0.8–1 mm. long, soon spreading and elongating to 1.5 mm., the stigmas shortly decurrent; mature fruits not seen.

Our description of the species and of the varieties is based on many available specimens, from both within and outside our area. The immediate relationship of *P. guilfoylei* is open to conjecture, and indeed it may have originated as a sport. Among Pacific species it is suggestive of *P. scutellaria* (including *P. pinnata*) in inflorescence characters, but the differences in foliage are striking and are summarized in our key to species.

Polyscias guilfoylei is perhaps the most widely cultivated taxon in the genus, as plants may readily be pruned into vigorous hedges. Several horticultural forms have been discussed, characterized by degree of leaf-division, variegation, etc. Three such forms are treated as botanical varieties by L. H. Bailey (Stand. Cycl. Hort. 2747–2748. 1925 and later editions). It is doubtful whether these forms merit any designation other than "cultivar," but a definitive review of *Polyscias* in cultivation is outside the scope of this treatment. An additional cultivated form was recently discussed but not named by the second author (in Micronesica **2**: 57. *fig. 4.* 1965); this has dark green, crumpled, bullate, nearly orbicular leaflets. Specimens of it have been noted from Hawaii as well as Micronesia, but not in the area of the present treatment.

For the time being we retain Bailey's varietal concept for a form often grown in the Pacific and elsewhere, with deeply laciniate leaflets. The two forms occurring in our area may be thus distinguished:

Leaflets elliptic to oblong, spinulose-dentate at margin. . . . . var. *guilfoylei.*
Leaflets deeply and irregularly divided or decompound, the ultimate parts variously incised and laciniate. . . . . var. *laciniata.*

11a. **Polyscias guilfoylei** var. **guiloylei.**

Aralia guilfoylei Bull, Cat. 1873; Cogn. & March. Pl. Ornament. **2:** *pl. 58.* 1874.

Nothopanax guilfoylei Merr. in Philip. Jour. Sci. Bot. **7:** 242. 1912; Christophersen in Bishop Mus. Bull. **128:** 165. 1935; Yuncker in Bishop Mus. Bull. **220:** 207. 1959; J. W. Parham, Pl. Fiji Isl. 83. 1964.

Polyscias guilfoylei L. H. Bailey in Rhodora **18:** 153. 1916; Setchell in Carnegie Inst. Publ. **341:** 61. 1924; Yuncker in Bishop Mus. Bull. **178:** 91. 1943.

The type-including variety; leaflets with petiolules (6–) 10–20 mm. long (up to 50 mm. on terminal leaflet), the blades variable in shape but most often elliptic to oblong, (5–) 6–12 (–17) cm. long, (2.5–) 4–8 (–14) cm. broad, obtuse to acute at base, obtuse to mucronately acute at apex, conspicuously and often irregularly spinulose-denate at margin (teeth 1–3 per centimeter), the costa sharply raised on both surfaces, the secondary nerves 5–9 per side, subascending, nearly straight, prominulous on both sides, the veinlet-reticulation intricate, prominulous on both surfaces or plane above.

Type locality: Unknown, but indicated in Bull's Catalogue as "South Sea Islands." It is quite possible that Bull received his material from W. R. Guilfoyle, whose interesting account of "A botanical tour among the South Sea Islands" (in Jour. Bot. **7**: 117–136. 1869) indicates that Samoa, Tonga, Fiji, the New Hebrides, and New Caledonia were visited by Guilfoyle on H.M.S. *Challenger* in 1868. It is mentioned that cultivated plants of "*Aralia*" were observed in Samoa (p. 119) and the New Hebrides (p. 133). That plants of horticultural interest were brought back is indicated by Guilfoyle's final sentence: ". . . I have been successful enough to bring with me in good condition, I have no hesitation in saying, the largest collection of choice and beautiful plants ever yet collected in the islands of the South Pacific." It is doubtful that any type specimen has been preserved.

Distribution. Widely cultivated throughout the Pacific and American tropics, and probably in all warmer areas. Plants grow very readily from cuttings. Although comparatively few flowering specimens are available, inflorescences will probably mature if the plants are not severely pruned. When not cut back, plants develop into shrubs or small trees with ascending virgate branches, up to 6 or 7 meters in height. It is probable that the species has become naturalized in thickets near settlements in parts of its cultivated range.

Local names and uses. *Tanitani* and many variant spellings have been recorded in Samoa, Niue, and Tonga, and *ndanindani* in Fiji; these names are more or less generic but apply especially to the cultivated forms. As elsewhere noted, this species is widely cultivated as a hedge plant, the abundance of the typical variety not being suggested by the few available collections.

Samoa. Tutuila: *Setchell 297* (coll. *Sutupe*) (uc).
Niue: Near Alofi, *Yuncker 9933* (bish).

11b. **Polyscias guilfoylei** var. **laciniata** (Hort.) L. H. Bailey in Rhodora **18**: 153. 1916; Christophersen in Bishop Mus. Bull. **128**: 165. 1935; Yuncker in Bishop Mus. Bull. **178**: 92. 1943.

Panax laciniatus Hort. in Gard. Chron. **1876**: 735. 1876, in *op. cit.* **1880**: 759. 1880.

A variety differing from var. *guilfoylei* in its more finely divided leaves, the petiolules often to 60 mm. long, some of the blades deeply lobed or decompound into irregular divisions, the ultimate leaflets variously incised and laciniate with numerous teeth up to 5 mm. long.

Type locality: Unknown; the original material brought into cultivation may have come from the Pacific area together with that of the typical form.

Distribution. Widespread in cultivation; in our area it seems to be more abundant than var. *guilfoylei*.

LOCAL NAMES AND USES. Not distinguished from the typical form in these respects. Seemann (Fl. Vit. 115. 1865) indicates that in Fiji a juice from the bark was used as a remedy for ulcerated tongue and throat.

Fiji. Without further locality, *Seemann 204* (BM, GH, K, photos at BISH, US), *Horne 588* (K, photos at BISH, US).

Wallis Islands. UVEA: *E. Home* in 1866 (BM).

Samoa. AUNUU ISLAND (east of Tutuila): *Diefenderfer 1239* (BISH). SAMOA, without further locality: *U.S. Expl. Exped.* (GH); *Powell 36* (K, photos at BISH, US), *211* (K, photos at BISH, US).

Niue: Alofi, *Yuncker 10002* (BISH).

Tonga. TONGATAPU: *Setchell & Parks 15418* (UC).

It should be noted that Seemann cited his own and the Home specimen listed above as *Nothopanax fruticosum*; his other comments, however, appear to refer to the following species in our treatment, where his reference is listed in the synonymy.

Although in inflorescence and basic foliage characters this variety clearly belongs in *P. guilfoylei*, we have keyed it with *P. fruticosa* because its variable leaves are often decompound. Dissected leaflets usually occur on the same plants (or even in the same leaves) as simple leaflets, and the texture and margins of the leaflets are obviously suggestive of those of typical *P. guilfoylei.*

12. **Polyscias fruticosa** (L.) Harms in E. & P. Nat. Pflanzenfam. 3(8): 45. 1894; Rechinger in Denkschr. Akad. Wiss. Wien **85**: 323. 1910; Harms in Nova Guinea Bot. **8**: 275. 1910, in Bot. Jahrb. **56**: 412. 1921. PL. III, FIGS. 7–9.

Scutellaria tertia Rumph. Herb. Amb. **4**: 78. *pl. 33.* 1743.

Panax fruticosum L. Sp. Pl. ed. 2. 1513. 1763; A. Gray, Bot. U.S. Expl. Exped. **1**: 716. 1854; Drake, Ill. Fl. Ins. Mar. Pac. 181. 1890; Warburg in Bot. Jahrb. **13**: 396. 1891; Hemsl. in Jour. Linn. Soc. Bot. **30**: 180. 1894; Guillaumin in Bull. Soc. Bot. France **66**: 270. 1919, in *op. cit.* **74**: 698. 1927.

Nothopanax fruticosum Miq. in Bonplandia **4**: 139. May, 1856, Fl. Ind. Bat. 1(1): 765. Sept. 1856; Seem. Fl. Vit. 115. 1865, in Jour. Bot. **4**: 294. 1866; Merr. Interpret. Rumph. Herb. Amb. 410. 1917; Yuncker in Bishop Mus. Bull. **220**: 207. 1959; J. W. Parham, Pl. Fiji Isl. 83. 1964.

Tieghemopanax fruticosus Viguier in Ann. Sci. Nat. IX. Bot. **4**: 61. 1906; Guillaumin in Jour. Arnold Arb. **12**: 263. 1931, in Jour. Linn. Soc. Bot. **51**: 554. 1938; J. W. Parham, Pl. Fiji Isl. 86. 1964.

A shrub or perhaps a small tree, glabrous throughout; leaves irregularly pinnate-compound, usually 2 or 3 times divided but sometimes simply pinnate, up to 50 cm. long, the petiole slender, 5–14 cm. long on mature leaves, clasping at base and inconspicuously alate in the proximal 1–3 cm., the rachis subterete, obscurely geniculate at bases of petiolules, the primary leaflets usually 9–13, with slender petiolules 1–6 cm. long and usually imparipinnately once or twice divided, rarely merely pinnatifid or laciniate or deeply serrate, the ultimate leaflet-divisions papyraceous, usually lanceolate and 3–11 × 0.5–3 cm. (rarely to 20 × 5 cm.), narrowed to an attenuate base, long-acuminate at apex, irregularly lobed or laciniate or spinulose-dentate at margin, the costa prominulous on both surfaces, the secondary nerves short, spreading, with the veinlet-reticulation essentially plane; inflorescences compound-paniculate to verticillate-umbellate, the primary branches 5–12, up to 30 cm. long, spreading or ascending from a short, stout peduncle and rachis, the secondary and tertiary branches often irregularly verticillate, the primary bracts lanceolate-oblong, 0.5–4 cm. long, soon caducous, the umbel-subtending bracts ovate, 1–2 mm. long, the flower-subtending bracteoles minute; flowers borne in umbels on slender ultimate peduncles 10–20 mm. long, 8–30 (–40) per umbel, the pedicels slender, 1–5 mm. long, articulate at apex; flowers 3–4 mm. long at anthesis, the calyx cupuliform, 1–1.7 mm. long and 1.5–2 mm. in diameter at the minutely 5-denticulate rim; petals 5, obovate-oblong, 2–3 mm. long, acute; stamens 5, the filaments slender, 1–1.2 mm. long, the anthers oblong, 1.5–2 mm. long, versatile; disk concave, the styles 2 (rarely 3), at first contiguous into a slender conical column 1–1.2 mm. long; fruits compressed and bilocular (rarely trigonous and trilocular), 4–5 × 5–6 mm., surmounted by the obscure calycular rim and divergent styles, these to 1.5 mm. long and with long-decurrent stigmas.

TYPE LOCALITY: Amboina; the basis for *Panax fruticosum* is the Rumphian *pl. 33,* doubtless drawn from a cultivated plant.

DISTRIBUTION. Widely cultivated throughout the Pacific and American tropics, and probably elsewhere; also popular for greenhouse cultivation. The species is commonly grown as an ornamental shrub or in hedges, attaining a height of 1–3 meters if not pruned. It flowers frequently and has white petals and styles. It may be noted that *Kajewski 931,* cited below, from the New Hebrides, is said to have been taken from a rain-forest tree 8 meters high; this could possibly be an indication of a native habitat, or it could merely represent a naturalization, since the species is freely cultivated in the New Hebrides.

LOCAL NAMES AND USES. *Tanitani* or a variant is applied in Polynesian areas; *ndanindani* in Fiji. Names noted in the New Hebrides are *nüluh* (Espiritu Santo) and *taconerecott* (Efate, ex Guillaumin). Kajewski notes that the leaves are boiled and eaten on Aneityum. The species is, of course, a popular ornamental.

New Hebrides. ESPIRITU SANTO: Tungwi, *I. & Z. Baker 156* (BM). TANNA: Lenakel, *Kajewski 63* (A, NY). ANEITYUM: Anelgauhat Bay, *Kajewski 931* (A, BISH, NY, US).

Fiji: VITI LEVU: MBA: Tumbenasolo, valley of Namosi Creek, *Smith 4724* (A, BISH, K, US). OVALAU: Lovoni village, *Smith 7496* (BISH, US).

Tonga. TONGATAPU: *Graeffe 1518* (K, photos at BISH, US).

Our description is based on many specimens from other parts of the cultivated range as well as those cited. We have not seen the Samoan specimens cited by Rechinger. It should be noted that a form with much smaller leaves, not flowering in our observation, has been collected in Micronesia and in Hawaii, but not within our area. This form and others doubtless have horticultural designations.

The true relationship of *P. fruticosa* is not obvious. It is quite probably a horticultural variant of one of the species of *Polyscias* with two styles and ovary-locules, but its derivation from any such species in our area (species 1 to 9 in the key) seems very unlikely. Although *P. fruticosa* is not immediately related to *P. guilfoylei*, having 2 (rarely 3) rather than 3–5 styles and ovary-locules, the finely divided forms of *P. guilfoylei*, such as var. *laciniata*, may not be readily distinguished from *P. fruticosa* in sterile condition. As a rule, the leaflets of *P. guilfoylei* var. *laciniata* are even more variable and irregular than those of *P. fruticosa*, but they are usually accompanied by at least a few leaflets suggestive of the typical form (elliptic to oblong), and the marginal teeth are comparatively short.

4. **Reynoldsia** A. Gray, Bot. U.S. Expl. Exped. **1**: 723. 1854, in Ann. Sci. Nat. IV. Bot. **4**: 177. 1855, in Proc. Am. Acad. Arts Sci. **3**: 128. 1857; Seem. in Jour. Bot. **2**: 244. 1864; Harms in E. & P. Nat. Pflanzenfam. 3(8): 30. 1894; Hutchinson, Gen. Fl. Pl. **2**: 58. 1967.

Reynoldsia was based on two original species, *R. sandwicensis* A. Gray, of Hawaii, and *R. pleiosperma* A. Gray, of Samoa. Both species are illustrated and the generic description would appear to have been based on both. We are not aware of an earlier designation of a lectotype species than that of Hutchinson (in 1967), who so denotes *R. sandwicensis*. *Reynoldsia* is a genus of at least 7 and perhaps 17 or more species, occurring in Samoa, the Societies, the Marquesas, and Hawaii. In the latter archipelago Sherff (Bot. Leafl. **6**: 7–19. 1952) recognizes 8 species, which we do not attempt to evaluate.

In Samoa three species were recognized by Christophersen in his 1935 treatment, and we herewith add a fourth. The species are probably endemic to various islands: to Savaii 2, to Upolu 1, and to the Manua Islands 1. It must be acknowledged that none of the Samoan species are adequately known and that comparably mature parts are not available for all of them. Nevertheless, good differentiating characters are evident in the shape and margin of leaflet-blades, the inflorescence-type (as to complexity of branching and arrangement of flowers), the length of umbel-peduncles and pedicels, and the size of inflorescence-bracts.

KEY TO THE SPECIES

Inflorescences paniculate, not umbelliferous, the ultimate branches bearing flowers (and fruits) irregularly or in whorls of 2–5 in a few clusters and apically; leaflet-blades lanceolate, subentire, inconspicuously undulate-denticulate at margin. . . . . 1. *R. pleiosperma*.

Inflorescences umbelliferous, the flowers 5–12 in umbels, not borne singly.

  Leaflet-blades conspicuously dentate at margin with widely spaced callose-obtuse teeth; umbel-peduncles 1.5–3 cm. long, subtended by bracts 2–4 mm. long, the pedicels 7–9 mm. long. . . . . 2. *R. lanutoensis*.

Leaflet-blades inconspicuously undulate and rarely remotely and minutely callose-denticulate at margin.

Inflorescences racemose-umbellate, the umbels few, borne singly on the upper part of the inflorescence, the umbel-peduncles about 7 cm. long, simply umbelliferous at apex, the pedicels 15–20 mm. long; leaflet-blades broadly ovate, 12–14.5 × 6–8 cm. . . . . 3. *R. grayana.*

Inflorescences racemose-verticillate, the umbels laxly verticillate at 2 or 3 nodes, the umbel-peduncles, 1.5–3 cm. long, sometimes with a secondary whorl of flowers below the ultimate umbel; umbel-subtending bracts of proximal nodes conspicuous, 5–15 mm. long; leaflet-blades ovate-lanceolate, 7–12 × 3–5 cm. . . . . 4. *R. tauensis.*

1. **Reynoldsia pleiosperma** A. Gray, Bot. U.S. Expl. Exped. **1**: 725. 1854, Atlas *pl. 93*, pro parte fructifera. 1857, in Ann. Sci. Nat. IV. Bot. **4**: 178. 1855, in Proc. Am. Acad. Arts Sci. **3**: 129. 1857; Seem. in Jour. Bot. **2**: 245. 1864; Harms in Bot. Jahrb. **25**: 664. 1898; Christophersen in Bishop Mus. Bull. **128**: 160. 1935.

Eschweileria pleiosperma Dur. ex Drake, Ill. Fl. Ins. Mar. Pac. 183. 1890.
Trevesia pleiosperma B. & H. f. ex Jackson, Ind. Kew. **2**: 1100. 1895.

A large tree, glabrous throughout; leaves imparipinnate (or perhaps sometimes even-pinnate by loss of the terminal leaflet), large, up to 90 cm. long, the petiole and rachis subterete, the petiole of mature leaves 20–40 cm. long, swollen to a clasping base and angled in the proximal 1.5–3 cm. (if alate, the wings soon lost), the leaflets 10–15, the petiolules slender, 5–20 mm. long, the blades papyraceous or subcoriaceous, lanceolate, 8–17 cm. long, 3–6 cm. broad, unequally rounded to broadly obtuse at base, gradually acuminate at apex (acumen 7–15 mm. long, slender, obtuse, marginally recurved), undulate-denticulate at margin (teeth, if present, inconspicuous, about 1 mm. long, callose-recurved), the costa raised above, prominent beneath, the secondary nerves 10–15 per side, spreading, prominulous on both surfaces, the veinlet-reticulation intricate, plane on both surfaces; inflorescences paniculate, up to 35 cm. long, not umbelliferous, the peduncle and rachis subterete, stout (3–5 mm. in diameter), the peduncle 13–17 cm. long, the secondary branches 12–17, alternate or irregularly whorled (with 4–6 borne apically), 4–13 cm. long, bearing flowers irregularly or 2–5 loosely whorled at 2 or 3 nodes and apically, the primary bracts (subtending secondary branches) oblong-lanceolate, 2–5 mm. long, caducous, the flower-subtending bracteoles about 1 mm. long, evanescent, the pedicels 5–10 mm. long (to 15 mm. in fruit); calyx cupuliform, 4–5 mm. long and in diameter, with a flaring undulate or irregularly lobed rim about 1 mm. long; petals (?8–) 10 or 11, narrowly oblong-lanceolate, at anthesis 6–7 mm. long and 1–2 mm. broad, unguiculate at apex, at length strongly reflexed and introrsely costate; stamens (?8–) 10 or 11, the filaments carnose, at length 4–5 mm. long, the anthers oblong, about 3 mm. long, versatile; stylopodium laterally flattened, about 1 mm. high, with (?16–) 20 or 22 congested radiating stigmas; fruits compressed-subglobose, sulcate, about 5 mm.

long and 6 mm. broad, surmounted by the calycular rim and the truncate-conical stylar column 1–1.5 mm. high bearing linear stigmas radiating on its slightly concave apex, the pyrenes (?16–) 20–22.

TYPE LOCALITY: Savaii, Samoa; the type is the U.S. Exploring Expedition collection cited below. Christophersen (in Bishop Mus. Bull. **128**: 161. 1935) has pointed out that Gray's original material came from two species, which were kept apart in the description but combined in the original plate; he has designated the fruiting specimen as the type, a choice here followed.

DISTRIBUTION. Samoa, and thus far known with certainty only from Savaii, where Christophersen indicates it to be a common tree of considerable size in forests at 700–1,700 meters altitude. It attains a height of more than 10 meters and its trunk has a diameter of 70–200 centimeters.

LOCAL NAME AND USES. *Vi vao* is the name recorded by Christophersen, who states that the fleshy fruits make it a favorite tree for pigeons and consequently well known to natives.

Samoa. SAVAII: Le To, above Salailua, *Christophersen 2935* (BISH); above Letui, *Christophersen 772* (A, BISH); Olo, above Safotu, *Christophersen & Hume 2319* (BISH, US); Mt. Maugaloa, *Vaupel 463* (BISH, US); Savaii, without further locality, *U.S. Expl. Exped.* (US 62432 type, GH fragm.). SAMOA, without other locality: *Whitmee 97* (K, photos at BISH, US).

Reynoldsia pleiosperma remained the only Samoan species of the genus recognized until 1925, when Hochreutiner described *R. lanutoensis* from Upolu, redescribed and discussed below. In 1935 Christophersen clarified the situation caused by the mixed materials in the original Exploring Expedition collection, indicating the non-type portion as a new species, *R. grayana*. We agree that this separation is warranted, and below we provide a first description for Christophersen's species and indicate points of difference between it and *R. pleiosperma*.

2. **Reynoldsia lanutoensis** Hochreutiner in Candollea 2: 482. 1925; Christophersen in Bishop Mus. Bull. **128**: 160. 1935.

A tree, glabrous throughout; leaves imparipinnate or sometimes even-pinnate, large, up to 55 cm. long, the petiole and rachis slender, subterete, the petiole of mature leaves 16–22 cm. long, swollen to a clasping base and narrowly alate in the proximal 1–2 cm. (wings free in the distal 1–2 mm.), the leaflets 10–13, the petiolules slender, of lateral leaflets 3–13 mm. and of terminal leaflet to 23 mm. long, the blades papyraceous, ovate- or oblong-lanceolate, (4.5–) 6–12 cm. long, (2–) 2.5–5.5 cm. broad, rounded to broadly obtuse at base, acuminate at apex (acumen 5–10 mm. long, obtuse, marginally recurved), conspicuously dentate at margin (teeth widely spaced, 3–5 per side, callose-obtuse and marginally recurved), the costa plane or canaliculate above, prominent beneath, the secondary nerves 10–15 per side, spreading, with the intricate veinlet-reticulation usually plane above, prominulous beneath; inflorescences paniculate-umbellate, up to 20 cm. long, the primary axis 7–14 cm. long, the secondary branches few, to 12 cm. long, bearing umbels whorled at several nodes (or umbels sometimes solitary), the umbel-subtending bracts lanceolate, 2–4 mm. long, entire or with a few marginal teeth, the ultimate peduncles 1.5–3 cm. long; flowers 5–10 per umbel, subtended by ovate-deltoid bracteoles about 1 mm. long, the pedicels slender, 7–9 mm. long, not articulated; calyx about 3 mm. long and 4 mm. broad, with a subtruncate or undulate rim; petals (?10–) 12, 4.5–5 mm. long; stamens (?10–) 12, the filaments short, the anthers oblong, about 2 mm. long, versatile; stylopodium laterally flattened, 1–1.5 mm. high, with 20–24 congested radiating stigmas; fruits compressed-globose, sulcate, 4–5 mm. long, 5–7 mm. broad, surmounted by the truncate-conical, bilobed, flattened stylar column bearing linear stigmas, the pyrenes 20–24.

TYPE LOCALITY: Lake Lanuto, Upolu, Samoa; the type is *Hochreutiner 3270* (deposited at Geneva), collected March 22, 1905, in forest at an altitude of about 670 meters. We have not seen this collection, but the original description leaves no doubt of its identity.

DISTRIBUTION. Samoa, and thus far known only from Upolu, where it occurs in forest or open grassland at altitudes of 650–750 meters. It has been noted as a tree 6–10 meters high, with green fruit.

LOCAL NAME. *Vi vao* has been recorded by Christophersen.

Samoa. UPOLU: Near Malololelei, *Christophersen 951* (A, BISH, US); above Malololelei, ridge to Mt. Vaitou, *Christophersen 262* (BISH, US); summit of Mt. Fao, *Christophersen 551* (BISH).

From the other three species now known from Samoa, *R. lanutoensis* differs in having its leaflet-blades conspicuously dentate with widely spaced teeth. Although the actual teeth are small, callose-obtuse, and marginally recurved (and not very different from those of *R. pleiosperma* and the other Samoan species), they surmount undulations some 2–5 mm. deep, the blades thus appearing more coarsely dentate than in the related species. While the flowers of *R. lanutoensis* are clearly umbellate, a second whorl of flowers is sometimes borne on the peduncle just below the apical umbel, suggesting that the mode of flower-bearing in this species and in *R. pleiosperma* is not basically very diverse. Nevertheless the two species are readily separable, at least on the basis of the collections currently available.

3. **Reynoldsia grayana** Christophersen in Bishop Mus. Bull. 128: 161. 1935.

Reynoldsia pleiosperma A. Gray, Bot. U.S. Expl. Exped. 1: 725, p.p. 1854, Atlas *pl. 93,* pro parte alabastro et foliacea. 1857.

A tree, glabrous throughout: leaves imparipinnate, large, probably more than 40 cm. long, the petiole and rachis subterete, the leaflets at least 7, the petiolules slender, of lateral leaflets 8–15 and of terminal leaflet to 20 mm. long, the blades broadly ovate, (6–) 12–14.5 cm. long, (3–) 6–8 cm. broad, rounded or truncate-obtuse at base, acute to gradually acuminate at apex, undulate or obscurely denticulate at margin (teeth, if present, 2 or 3 per margin, callose-obtuse, scarcely 1 mm. long), the costa raised above, prominent beneath, the secondary nerves 8–15 per side, spreading, prominulous on both surfaces, the veinlet-reticulation intricate, immersed or impressed on both surfaces; inflorescences racemose-umbellate, up to 22 cm. long, the peduncle at least 10 cm. long, the secondary branches few (about 5), about 7 cm. long, simply umbelliferous at apex; flowers 5 or 6 per umbel, the pedicels comparatively stout (1–2 mm. in diameter), 15–20 mm. long, gradually swollen distally, not articulated; calyx obconical, 3–4 mm. long and in diameter, with an erect undulate rim; petals 8–10, narrowly oblong-lanceolate, about 1.5 mm. broad, 4–5 mm. long and calyptrate in bud but doubtless free at anthesis, unguiculate at apex; stamens 8–10, the filaments carnose, about 2 mm. long in bud, the anthers oblong, 2–2.5 mm. long in bud, versatile; stylopodium truncate-conical, laterally flattened, about 2 mm. in diameter at the slightly concave apex, the stigmas about 18, linear, radiating.

TYPE LOCALITY: Savaii, Samoa; the type is the U.S. Exploring Expedition collection cited below.

DISTRIBUTION. Samoa, known only from the type material. It is indicated by Pickering (Geogr. Distr. Animals and Plants 2: 294. 1876) that the Exploring Expedition Samoan material included only one collection referable to *Reynoldsia*. For that reason one may assume that both parts of the mixture treated by Gray and illustrated in the Atlas were indeed "brought by the forest-king from Interior Savaii," to use Pickering's words.

Samoa. Savaii, without further locality: *U.S. Expl. Exped.* (US 73913 type, GH fragm.).

As discussed under *R. pleiosperma,* we follow Christophersen in his choice of the fruiting material available to Gray as the type of that species, the balance serving as the type of *P. grayana.* The latter species has not previously been described, but Christophersen referred to a portion of Gray's earlier comments and to part of an illustration, thus seeming to have met the letter of the International Code. The Exploring Expedition specimen deposited as *R. pleiosperma* in the U.S. National Herbarium includes poorly preserved material which quite clearly came from two different plants. We have now separated this material as two herbarium sheets, one of which may serve as the holotype of Gray's species and the other as the holotype of Christophersen's.

Reynoldsia grayana differs from *R. pleiosperma* in having its inflorescences clearly umbelliferous, the umbels being long-pedunculate and the pedicels much longer. The leaflet-blades of *R. grayana* are broadly ovate and about twice as long as broad, those of *R. pleiosperma* being lanceolate and about three times as long as broad. From *R. lanutoensis,* the present species differs very obviously in the shape and margins of its leaf-blades, in its simpler inflorescences, long umbel-peduncles, and long pedicels. On the basis of material now available, *R. grayana* seems to have fewer petals and stamens than either *R. pleiosperma* or *R. lanutoensis*, but we consider this variation of minor significance.

4. **Reynoldsia tauensis** A. C. Smith & B. C. Stone, sp. nov.

Reynoldsia sp. Christophersen in Bishop Mus. Bull. **128**: 161. 1935; Yuncker in Bishop Mus. Bull. **184**: 55. 1945.

Arbor ubique glabra; foliis ad 60 cm. longis videtur paripinnatis, petiolo et rhachidi subteretibus, petiolo 22–25 cm. longo ad basim amplectentem incrassato et 1–2 cm. anguste alato, rhachidi petiolulorum basi contracta, foliolis 10–12, petiolulis gracilibus 5–15 mm. longis, laminis papyraceis ovato-lanceolatis, 7–12 cm. longis, 3–5 cm. latis, basi subaequaliter rotundatis, apice in acuminem obtusum margine recurvatum breviter cuspidatis, margine anguste recurvatis cartilagineis inconspicue undulatis et dentibus callosis haud 1 mm. longis raro et remote denticulatis, costa supra paullo elevata subtus prominente, nervis secundariis utrinsecus 10–15 supra planis subtus prominulis, rete venularum intricato supra immerso subtus conspicuo plano; inflorescentiis apices ramulorum versus infra folia congestis, juvenilibus ad 15 cm. longis racemoso-verticillatis, pedunculo gracili ad 9 cm. longo, umbellulis 5–8 in nodis 2 vel 3 laxe verticillatis, bracteis umbelliferis papyraceis anguste lanceolatis 5–15 mm. longis (superioribus interdum 2–3 mm. longis) margine minute serrulatis, umbellularum pedunculis gracilibus 1.5–3 cm. longis interdum verticillum secundarium gerentibus; floribus 8–12 per umbellulam pedicellatis, pedicellis in alabastro 2–3 mm. longis non articulatis, bracteolis floriferis oblongo-deltoideis 1–2 mm. longis acutis; calyce turbinato circiter 2.5 mm. longo et lato, limbo erecto ad 1 mm. longo undulato et irregulariter 3–5-denticulato; petalis 8–10 in alabastro oblongo-deltoideis valvatis apice unguiculatis; staminibus 8–10; stylopodio in alabastro vadose concavo, stigmatibus 16–18 sessilibus radiatis.

Type locality: Tau, Manua Islands, Samoa; the type is *Garber 752*.

Distribution. Known only from the type collection and probably endemic to the Manua Islands; at least Paul L. Guest indicated to Yuncker (*loc. cit.* 1945) that the species is abundant on all the (Manua) islands. The only documented collection was taken from a tree about 3 meters high at an altitude of 685 meters.

Local name. No name was indicated on the original label, but Yuncker (*loc. cit.* 1945) has listed *vi vao*, which apparently is applied to the genus in Samoa.

Samoa. Tau, Manua Islands: Top of peak back of Tau, January 28, 1922, *Garber 752* (bish type).

Both Christophersen and Yuncker implied that the cited Tau specimen represents an undescribed species; even though it lacks mature flowers and fruits we venture to describe it. In having the inflorescence compound and the flowers umbellate it clearly resembles *R. lanutoensis*, differing in its essentially entire rather than conspicuously dentate leaflet-blades and in its comparatively large umbel-subtending bracts. From *R. grayana* the new species differs in its more complex inflorescence, its short umbel-peduncles, its presumably shorter pedicels, and its ovate-lanceolate, proportionately narrower leaflet-blades.

5. **Plerandra** A. Gray, Bot. U.S. Expl. Exped. **1**: 729. 1854, in Ann. Sci. Nat. IV. Bot. **4**: 178. 1855, in Proc. Am. Acad. Arts Sci. **3**: 129. 1857; Seem. in Jour. Bot. **2**: 241. 1864, Fl. Vit. 117. 1865; Harms in E. & P. Nat. Pflanzenfam. 3(8): 28. 1894; A. C. Sm. in Bishop Mus. Bull. **141**: 116. 1936, in Jour. Arnold Arb. **36**: 286. 1955; Hutchinson, Gen. Fl. Pl. **2**: 61. 1967.

Bakeria Seem. in Jour. Bot. **2**: 248. 1864, Fl. Vit. 117. 1865, *op. cit.* 429. 1873.
Nesopanax Seem. in Jour. Bot. **2**: 249. 1864, Fl. Vit. 116. 1865.

Plerandra, typified by the Fijian *P. pickeringii*, is believed to include about 14 species occurring in New Guinea, the Solomons, and Fiji; it has not yet been discovered in the New Hebrides. Seven endemic species terminate its range in Fiji.

The Fijian species of *Plerandra* have been puzzling, but the reasonably adequate herbarium material now available indicates that they are well differentiated. They are probably all polygamo-dioecious, or perhaps sometimes polygamo-monoecious, and consequently there have been misinterpretations of floral dimensions and of the shape of the stylopodium, since these differ in staminate and perfect flowers. There is remarkable variation in the number of stamens from 15 in *P. bakeriana* to as many as 500 in *P. pickeringii*, and in the number of styles, stigmas, and ovary-locules from 5 to 17. While such numbers do not always permit rigid specific delimitation, they are usable within limits. Seemann's genus *Bakeria*, based on the species now known as *P. bakeriana*, does not consistently have 15 stamens and 5 ovary-locules as originally supposed by him; the stamens are actually 15–20 and the ovary-locules and stigmas are 5–8, indicating that even this distinct species cannot be separated from *Plerandra*. As a matter of fact, in 1873 Seemann himself emended *Bakeria* to note that its stamens could be as many as 23, but we have not observed more than 20. Seemann's genus *Nesopanax*, based on the species currently known as *P. vitiensis*, was said to differ from *Plerandra* in having its petals free rather than calyptrate, and by having 5–7 ovary-locules and free styles. In fact, however, in *P. vitiensis* the ovary-locules vary from 5 to 11; all the *Plerandrae* have eventually separating petals, whether or not they are connate in bud; and the styles of *P. vitiensis* become proximally connate in the stylopodium of the fruit.

The most distinct species is perhaps *P. insolita*, with short-pedicellate flowers congested on the distal portion of short rays and scarcely umbellate. Also very distinct is *P. pickeringii*, with the largest number of stamens (200–500) and with a very conspicuously elongated stylopodium of firmly connate styles. *Plerandra bakeriana* is readily distinguished by its reduced number of stamens, but otherwise it is not strikingly different from several other of our species. *Plerandra grayi* is likely to be confused with *P. vitiensis* but is actually reasonably distinct on the basis of its numerous stamens (as many as 250), its large flowers, and its broad leaflets with obviously rounded apices. The remaining three species form a related group, but characters referring to stamen-number, fruit shape, stylopodium, and number and size of leaflets are useful in recognizing them.

Key to the Species

Inflorescences composed of umbels, the flowers borne at the apices of elongate rays rarely less than 5 cm. long and usually much longer.

  Stylopodium inconspicuous, in fruit 1–2.5 mm. long, the styles sometimes completely or partially separate, sometimes connate with marginally projecting stigmas.

    Styles and ovary-locules 5–11; stamens not more than 150; flowers comparatively small, the petals 4–7 mm. long; leaflet-blades rarely more than 10 cm. broad.

      Stamens usually 1-seriate, 15–20; styles and ovary-locules usually 5 or 6 (rarely 7 or 8); flowers small, the petals about 4 mm. long; fruits 10–12 × 8–10 mm., the stigmas projecting marginally from the truncate-concave apex of the stylopodium; leaflets 5–8 (–10). .... 1. *P. bakeriana.*

      Stamens at least 2-seriate, 25 or more; flowers with the petals 5–7 mm. long.

        Leaflets 3–6 (–7); fruits oblong-ellipsoid, about 20 × 10 mm., the stigmas obviously separate on the truncate-concave apex of the inconspicuous stylopodium; ovary-locules 5–8; stamens 50–75. .. .. 2. *P. grandiflora.*

        Leaflets 5–10 (rarely 4–12); fruits ellipsoid, not much longer than broad, 8–14 × 7–11 mm.

          Stamens 2-seriate, 25–35; ovary-locules 5–8; stylopodium in fruit composed of connate styles and minutely concave at apex; leaflets usually 5–7, the blades 8–15 × 3.5–7 cm. .. 3. *P. victoriae.*

          Stamens 3–5-seriate, 75–155; ovary-locules usually 7–10 (sometimes 5–11); stylopodium in fruit composed of styles connate proximally but free at the spreading or erecto-patent apices; leaflets usually 7–10, the blades usually 13–23 × 4–9 cm. .... 4. *P. vitiensis.*

    Styles and ovary-locules usually 12–15 (rarely 11); stamens 3–5-seriate, 120–250; flowers comparatively large, the petals 8–12 mm. long; fruits 11–20 × 10–15 mm., the stylopodium composed of short, stout styles connate into a centrally concave ring; leaflet-blades usually 14–30 × 6–14.5 cm., broadly rounded at apex. .... 5. *P. grayi.*

  Stylopodium obvious, in fruit 5–10 mm. long, conical-cylindric, composed of 9–17 firmly connate styles with stigmas marginal on the truncate apex; stamens numerous, 200–500; flowers large, the petals 9–16 mm. long; fruits large, 20–40 × 17–25 mm. .... 6. *P. pickeringii.*

Inflorescences lacking true umbels, the flowers congested distally on short rays (4–8 cm. long) in a strobilus-like pseudo-umbel 1–5 cm. long; stamens 50–75; flowers comparatively large, the petals 7–8 mm. long; fruits large, 25–

36 × 18–30 mm., with a persistent calycular rim and a short (1–2 mm. long) stylopodium, the 9–12 styles firmly connate. . . . . 7. *P. insolita.*

1. **Plerandra bakeriana** A. C. Sm. in Bishop Mus. Bull. **141:** 118. 1936; J. W. Parham, Pl. Fiji Isl. 84. *fig. 34.* 1964.
PL. VII, FIGS. 3, 4.

Bakeria vitiensis Seem. in Jour. Bot. **2:** 249. *fig.* (p. 248). 1864, Fl. Vit. 117. *pl. 21.* 1865; Anon. in Gartenfl. **36:** 71. 1887, in Kew Bull. **1888:** 95. 1888.
Plerandra vitiensis B. & H. f. ex Drake, Ill. Fl. Ins. Mar. Pac. 183. 1890; Harms in E. & P. Nat. Pflanzenfam. 3(8): 29. 1894; non Baill. (1880).

A small tree, glabrous throughout; leaves clustered near ends of branchlets, digitately compound, the petioles subterete, up to 25 cm. long, expanded at base into a coriaceous sheath 10–15 mm. broad, the ligule broadly ovate, as much as 7 mm. long, thinner at margin, the leaflets 5–8 (–10), the petiolules 1–4 (–6) cm. long, the blades subcoriaceous, elliptic-obovate, usually 8–17 cm. long and 4–7 cm. broad, acute to attenuate at base, subacute to broadly obtuse at apex, the costa prominent beneath, the secondary nerves usually 7–12 per side, inconspicuously raised on both surfaces, the veinlet-reticulation immersed; inflorescences umbellate, composed of 8–15 umbels radiating from a stout peduncle 1–2.5 cm. long, the rays 4.5–23 cm. long, the subtending bracts soon caducous, the flowers often 15–40 (but sometimes as few as 10) per umbel, on pedicels 1.5–3 cm. long; staminate flowers with a short calyx 2.5–3 mm. long, flaring and sinuate at margin; calyx slightly larger in perfect flowers; petals 5, thick, deltoid-ovate, acute, unguiculate, about 4 mm. long; stamens usually 1-seriate and often 15, sometimes as many as 20, about 2 mm. long, the anthers oblong, obtuse, about 1.5 mm. long; disk concave; stigmas minute, like the locules usually 5 or 6, sometimes 7, rarely 8; fruits ellipsoid to subglobose, inconspicuously costate when dried, usually 10–12 × 8–10 mm., the stylopodium 1–2 mm. long, the stigmas projecting as obtuse, inconspicuous, marginal protuberances on the truncate-concave apex, the pyrenes lunulate.

TYPE LOCALITY: Namosi Province, Viti Levu, Fiji; the type is *Seemann 209*, cited below.

DISTRIBUTION. Known only from the island of Viti Levu, Fiji, and there infrequently collected. Insofar as data are available, the species occurs in ridge and crest thickets at 900–1,100 meters, but the Seemann and MacGillivray & Milne specimens may come from lower elevations. Field notes are inadequate, but the plant is recorded as a small tree about 5 meters high, the fruit being black at maturity.

LOCAL NAME. *Sole* has been noted by Parham, but this is essentially a generic name in Fiji.

Fiji. VITI LEVU: MBA: Mt. Evans Range, *Greenwood 382* (K, photos at BISH, US). NAMOSI: Mt. Naitarandamu, *Gillespie 3153* (BISH, GH, NY, UC); Korombasambasanga Range, *Fiji Dept. Agr. 2197* (A, SUVA); Mt. Voma, *Gillespie 2712* (BISH), *Fiji Dept. Agr. 1723* (A, BISH, SUVA); probably near Namosi Village, *See-*

mann 209 (K type, photos at BISH, US; GH isotype); Viti Levu without locality, *MacGillivray & Milne 99* (K, photos at BISH, US).

This species, with a comparatively small number of stamens and carpels, is readily distinguished from other Fijian *Plerandrae* on that basis, but its floral parts are not as consistent in number as believed by Seemann. It is the sole species of the genus *Bakeria* Seem., which subsequent authors have merged with *Plerandra*.

2. **Plerandra grandiflora** A. C. Sm. in Bishop Mus. Bull. **141**: 117. *fig. 61*. 1936; J. W. Parham, Pl. Fiji Isl. 85. 1964.

Shrub or slender tree, glabrous throughout, the leaves and inflorescences aggregated toward ends of branchlets, the branchlets terete, sparsely lenticellate; leaves digitately compound, the petioles subterete, 6–20 cm. long, expanded at base into a sheath 15–20 mm. broad, the ligule coriaceous, subentire, 5–9 mm. long, the leaflets 3–6, rarely 7, the petiolules subterete, 1–5 cm. long, the blades subcoriaceous, elliptic, 7–18 cm. long, 3.5–8 cm. broad, attenuate at base, obtuse or rounded at apex, narrowly revolute at margins, the costa prominent on both surfaces, the secondary nerves 7–16 per side, slightly raised on both surfaces or subimmersed, the veinlet-reticulation immersed; inflorescences umbellate, with several or numerous umbels radiating from a very short peduncle, the rays usually 11–17 cm. long, the subtending bracts caducous, the flowers (11–) 20–25 per umbel, on stout pedicels 1–2 cm. long; calyx smooth, coriaceous, cylindric-ellipsoid, at anthesis 6–8 mm. long and about 5 mm. in diameter, truncate at margin; petals 5, carnose, deltoid-ovate, 5–6 mm. long, 3–4 mm. broad, thickened and slightly unguiculate at apex; stamens 2- or 3-seriate, 50–75, the filaments filiform, usually about 4 mm. long, the anthers oblong, about 1.5 mm. long, obtuse; styles 5–8, separate, short and obscure, forming a small ring of papillae on the flattened or rounded summit of the gynoecium, the locules 5–8, with thick walls; fruits oblong-ellipsoid, carnose when fresh and smooth or inconspicuously ridged when dry, about 2 × 1 cm. at apparent maturity, the stylopodium projecting about 1 mm., the stigmas obviously separate on the truncate-concave apex, the pyrenes lunulate, about 15 × 4 mm., with straight inner margins.

TYPE LOCALITY: Mt. Kasi, Yanawai River region, Thakaundrove Province, Vanua Levu, Fiji; the type is *Smith 1777*, cited below.

DISTRIBUTION. Known only from two collections made on the island of Vanua Levu, Fiji, where it occurs at elevations of 300–1,030 meters in dense crest thickets. Field notes indicate the plant as a shrub or slender tree about 3 meters high; the petals and stamens are pale yellow and the fruit black. The available specimens were collected in May and November, each bearing flowers and the type fruits as well.

LOCAL NAME. *Ndanindani* was recorded for no. *1777*, although this name otherwise seems to refer to the genus *Polyscias* in Fiji.

Fiji. VANUA LEVU: THAKAUNDROVE: Mt. Kasi, Yanawai River region, *Smith*

1777 (BISH type, GH, K, NY, UC, US); summit of Mt. Mbatini, *Smith 680* (BISH, GH, K, NY, UC, US).

In stamen number *P. grandiflora* is intermediate between *P. bakeriana* and *P. victoriae* on the one hand and *P. vitiensis* on the other. On the basis of the type collection the reduced number of leaflets (to three) is noteworthy. The second collection cited above was in 1936 (in Bishop Mus. Bull. **141**: 117) referred to *P. victoriae* by the first author, but on reconsideration we prefer to place it in *P. grandiflora*. The number of leaflets seems of secondary importance in comparison with such characters as the comparatively elongate fruit and the intermediate number of stamens.

3. **Plerandra victoriae** Gibbs in Jour. Linn. Soc. Bot. **39**: 150. 1909; A. C. Sm. in Bishop Mus. Bull. **141**: 117, *quoad typum*. 1936; J. W. Parham, Pl. Fiji Isl. 86. 1964. PL. VII, FIG. 5.

Plerandra sp. A. C. Sm. in Bishop Mus. Bull. **141**: 118. 1936.

A glabrous shrub or small tree; leaves digitately compound, the petioles up to 23 cm. long, expanded at base into a coriaceous sheath 2–3 cm. broad, the ligule deltoid-lanceolate, as much as 2 cm. long, acute, thinner at margin, the leaflets usually 5–7 (rarely 4 or 8), the petiolules (1–) 2–4 cm. long, the blades subcoriaceous, elliptic, usually 8–15 cm. long and 3.5–7 cm. broad, obtuse to attenuate at base, rounded or broadly obtuse at apex, narrowly revolute at margin, the costa prominent on both surfaces, the secondary nerves usually 10–14 per side, prominulous on both surfaces, the veinlet-reticulation immersed; inflorescences umbellate, composed of 5–12 umbels borne near the apex of a variable peduncle 2–12 cm. long, the rays 4–9 cm. long, the subtending bracts soon caducous, the flowers usually 12–16 per umbel, on pedicels 5–12 mm. long; calyx about 6 mm. long in perfect flowers but shorter in staminate flowers, sinuate-truncate at margin; petals 5, deltoid-ovate, usually 6–7 × 3–4 mm., unguiculate; stamens usually biseriate and 25–35, the filaments slender, about 2.5 mm. long, the anthers 2–3 mm. long, obtuse; stigmas small, on subconnate short styles, like the locules 5–7, rarely 8; fruits ellipsoid, smooth or inconspicuously costate, 8–12 × 7–9 mm., the stylopodium 1–2.5 mm. long, truncate-conical, composed of the short connate styles and minutely concave at apex.

TYPE LOCALITY: Mt. Tomanivi (Mt. Victoria), Mba Province, Viti Levu, Fiji; the type is *Gibbs 784*, cited below.

DISTRIBUTION. Endemic to Fiji and known only from the two largest islands at elevations of 1,000–1,323 meters (on Viti Levu) and 700 meters (on Vanua Levu). The species occurs infrequently in the dense mossy forest and thickets of ridges and summits, as a compact or slender tree or shrub 2–3 meters high; the petals are blackish without and white within, the stamens are yellow, and the fruits are deep purple, doubtless becoming black at maturity.

LOCAL NAME. *Sole*, as for other Fijian *Plerandrae*.

Fiji. VITI LEVU: MBA: Summit ridge of Mt. Tomanivi, *Gibbs 784* (BM type, photo at US), *Gillespie 4112* (BISH), *Smith 5145* (A, BISH, US). VANUA LEVU: THAKAUNDROVE: Mt. Ndikeva, eastern buttress, *Smith 1890* (BISH, NY, US).

In 1936 the first author took his no. *680*, from Vanua Levu, to represent *P. victoriae*, but in our reconsideration we believe this specimen better placed in *P. grandiflora*, as noted above. *Smith 1890*, in 1936 suggested as a possibly undescribed relative of *P. bakeriana*, is now seen to have no basic characters separating it from *P. victoriae*, otherwise not recorded from Vanua Levu.

The closest relative of *P. victoriae* is probably *P. vitiensis*, but its stamens are notably fewer, its ovary-locules are usually (but not invariably) fewer, its styles are firmly connate in the stylopodium of the fruit rather than distally free, and its usually fewer leaflet-blades are quite consistently smaller. Both of these species differ from *P. grandiflora* most obviously in fruit shape, but also in stamen number and in (usually) more numerous leaflets. The three species form a series in various characters but seem readily distinguishable.

4. **Plerandra vitiensis** (Seem.) Baill. Hist. Pl. 7: 169. *fig. 221.* 1879; A. C. Sm. in Bishop Mus. Bull. **141**: 116. 1936; J. W. Parham, Pl. Fiji Isl. 86. 1964. PL. VII, FIGS. 1, 2.

Nesopanax vitiensis Seem. in Jour. Bot. 2: 249. *fig.* 1864, Fl. Vit. 117, *pl. 20.* 1865; Anon. in Gartenfl. **36**: 71. 1887, in Kew Bull. **1888**: 110. 1888.
Plerandra seemanni B. & H. f. ex Drake, Ill. Fl. Ins. Mar. Pac. 183. 1890.
Plerandra nesopanax Harms in E. & P. Nat. Pflanzenfam. 3(8): 29. 1894.

A tree usually 5–20 m. high, glabrous throughout; leaves digitately compound, the petiole often stout, up to 60 cm. long, expanded at base into a coriaceous sheath often 3 cm. broad, the ligule broadly ovate-deltoid, to 1 cm. long, the leaflets 6–12 (usually 7–10), the petiolules usually 2–5 (sometimes 1–7) cm. long, the blades thin-coriaceous, oblong-obovate to oblanceolate or elliptic, as much as 27 × 10.5 cm. but usually 13–23 cm. long and 4–9 cm. broad, acute to attenuate at base, rounded to obtuse at apex, narrowly recurved at margin, the costa raised above, prominent beneath, the secondary nerves usually 10–17 per side and prominulous on both surfaces, the veinlet-reticulation immersed; inflorescences umbellate, composed of 9–35 umbels radiating from a stout peduncle usually 2–3 cm. long, the rays diverse in length, 6–26 cm. long, the subtending bracts deltoid-lanceolate, to 1.5 cm. long, caducous, the flowers (3–) 10–40 per umbel, on pedicels usually 2–4 cm. long; calyx conical, 5–6 mm. long (staminate somewhat smaller), truncate-sinuate at margin; petals 5, deltoid, 5–6 mm. long; stamens usually 3–5-seriate and 100–120 (sometimes 75–155), the filaments slender, 2–2.5 mm. long, the anthers narrowly oblong, obtuse, 1.5–2 mm. long; disk flat or slightly convex; styles usually 7–10 (sometimes 6 or 11, possibly rarely 5), short, separate, with terminal stigmas, the locules rarely as many as 12; fruits ellipsoid, inconspicuously costate when dried, at maturity 8–14 × 9–11 mm., the stylopodium 1–2.5 mm.

long, the styles connate proximally, with spreading or erecto-patent apices and often pale terminal stigmas.

TYPE LOCALITY: Southern Ovalau, Fiji; the type is *Seemann 207*, cited below. Seemann indicated his specimen as from "Port Kinnaird," a name used at the time of his 1860 visit for the waters between Ovalau and Moturiki sheltered by the Yanutha Islands. In his book *Viti* (pp. 67–68. 1862), Seemann discusses the possibility of Port Kinnaird being developed into the capital of Fiji, an unrealized hope of a few settlers.

DISTRIBUTION. Endemic to Fiji, and thus far known from the islands of Viti Levu, Ovalau, and Vanua Levu, occurring with some frequency in dense or open forest at elevations of 100–1,150 meters. It is reported as a tree 5–20 meters high, often slender; the petals at anthesis are rich purple without and pale green within, the anthers are pale yellow, the stylopodium and styles are white, and the fruits are dark purple to black at maturity.

LOCAL NAMES. *Sole* is generally referred to this species, for which the first author has also recorded on Vanua Levu the names *kaikai* and *ndanindani*; both of these are doubtful, and the last generally denotes the genus *Polyscias*.

Fiji. VITI LEVU: MBA: Slopes of Mt. Nairosa, Mt. Evans Range, *Smith 4060* (A, BISH, K, NY, US); vicinity of Nandarivatu, *Parks 20749* (BISH, UC, US), *Degener 14380* (A, BISH, K, NY, UC, US); Mt. Nanggaranambuluta, near Nandarivatu, *Smith 4756* (A, BISH, K, NY, US), *Greenwood 870* (A); east of Nandala Creek, south of Nandarivatu, *Smith 5943* (A, BISH, K, NY, US); Mt. Tomanivi, *Smith 5124* (A, BISH, K, NY, US). NANDRONGA & NAVOSA: Northern portion of Rairaimatuku Plateau, between Nandrau and Rewasau, *Smith 5422* (A, BISH, K, NY, US); between Nandrau and Nanga, *Smith 5492* (A, BISH, K, NY, US). SERUA: North of Komave, *St. John 18965* (BISH, US). NAMOSI: Mt. Vakarongasiu *Gillespie 3270* (US). OVALAU: West of Lovoni Valley, on ridge south of Mt. Korolevu, *Smith 7515* (BISH, US); east of Lovoni Valley, *Smith 7275* (BISH, US); vicinity of Levuka, *Gillespie 4533* (BISH, GH, UC); southern Ovalau, *Seemann 207* (GH, K type, photos at BISH, US). VANUA LEVU: MBUA: Southern slope of Mt. Seatura, *Smith 1621* (BISH, GH, K, NY, UC, US). MATHUATA: Southern base of Mathuata Range, north of Natua, *Smith 6773* (A, BISH, K, US). THAKAUNDROVE: Mt. Mariko, *Smith 412* (BISH, GH, K, NY, UC, US). FIJI, without other locality: *Tothill 224* (K, photos at BISH, US).

This fairly variable species is distinguished from the first three species in this treatment most readily by the greater number of stamens, which are usually 100–120. Its fruit is also characteristic, the styles being obviously free in the apical part of the stylopodium. In comparison with our first three species *P. vitiensis* usually has more numerous and larger leaflets, although foliage characters in *Plerandra* are by no means dependable. The following species, *P. grayi*, will superficially often be mistaken for *P. vitiensis*.

5. **Plerandra grayi** Seem. Viti 437, *nomen*. 1862, in Jour. Bot. **2**: 242. *fig*. (p. 241). 1864, Fl. Vit. 117, *pl. 22*. 1865; Drake, Ill. Fl. Ins. Mar.

Pac. 183. 1890; A. C. Sm. in Bishop Mus. Bull. **141**: 116. 1936; J. W. Parham, Pl. Fiji Isl. 85. *fig. 35*. 1964. PL. VII, FIGS. 6–9.

Plerandra sp. A. Gray in Proc. Am. Acad. Arts Sci. **5**: 318. 1862, in Bonplandia **10**: 36. 1862.

Plerandra graeffei Anon. in Gartenfl. **36**: 71. 1887, in Kew Bull. **1888**: 117. 1888.

A small tree, glabrous throughout; leaves digitately compound, the petiole subterete, stout, up to 60 cm. long, expanded at base into a coriaceous sheath 2–3 cm. broad, the ligule broadly ovate, 1–2 cm. long, the leaflets 4–10 (usually 6–9), the petiolules 2.5–7 cm. long, the blades subcoriaceous, usually broadly obovate, less frequently oblanceolate or lanceolate, (11–) 14–30 cm. long, (5–) 6–14.5 cm. broad, acute and decurrent at base, usually broadly rounded at apex, recurved or nearly plane at margin, the costa flattened above, prominent beneath, the secondary nerves usually 9–16 per side, prominulous on both sides or plane above, the veinlet-reticulation immersed; inflorescences umbellate, composed of 7–30 umbels radiating from a variable peduncle up to 10 cm. long, the rays (5–) 12–30 cm. long, the subtending bracts oblong-deltoid, subcoriaceous, 1–2 cm. long, caducous, the flowers 15–40 per umbel, on pedicels 1.5–3 cm. long; calyx of perfect flowers broadly cupuliform, 6–8 mm. long and 5–7 mm. broad, truncate-sinuate at margin; petals 5, carnose, deltoid, 8–12 mm. long, 5–7 mm. broad, unguiculate; stamens usually 3–5-seriate, (120–) 175–250, the filaments slender, diverse but usually 2–3 mm. long, the anthers oblong, obtuse, 2–2.5 mm. long; disk slightly concave at center, flat marginally; stigmas minute, essentially sessile, like the locules 11–15; fruits ellipsoid or nearly subglobose, usually obviously costate, at apparent maturity 11–20 × 10–15 mm., subtruncate at apex, the stylopodium scarcely exceeding the broad scar of staminal attachment, the short, stout styles connate into a centrally concave ring and terminated by minutely grooved stigmas, the pyrenes lunulate.

TYPE LOCALITY: Viti Levu, Fiji; the type is *Seemann 208*, cited below. Although Seemann indicated no detailed locality, the holotype bears the note "July 1860." In the early part of that month Seemann was in southern Viti Levu between the Navua River and the present town of Ngaloa (*Viti*, pp. 95–117. 1862); during the rest of July he seems to have been in Ovalau, Mbau, and Tailevu not primarily engaged in botanical work. Therefore we may assume his no. *208* to have been collected along the Serua coast.

DISTRIBUTION. Endemic to Fiji and thus far known only from Viti Levu, where it occurs apparently infrequently at elevations up to 400 meters in forested areas. It is indicated as a usually slender tree 5–10 meters high; the petals are greenish with copious rich purple markings without, or at least obviously purple-tinged, and greenish white within; the stamens are cream white to greenish white; and the fruits are black at maturity.

LOCAL NAME. The generic name *sole* is commonly used for *P. grayi*.

Fiji. VITI LEVU: SERUA: Vatutavathe, vicinity of Ngaloa, *Degener 15201* (A, BISH, K, NY, UC, US). NAMOSI: Hills bordering Wainavindrau Creek, vicinity of Wainimakutu, *Smith 8523* (BISH, US), *8568* (US); east of Wainikoroiluva River, near Namuamua, *Smith 8902* (BISH, US), *9046* (BISH, US). NAITASIRI: Tamavua, *Gillespie 2464* (BISH, UC); Prince's Road, *Meebold 16558* (K, photos at BISH, US), *Fiji Dept. Agr. 196* (SUVA). TAILEVU: East of Wainimbuka River, vicinity of Ndakuivuna, *Smith 7140* (BISH, US). REWA: Mt. Korombamba, *Parks 20118* (BISH, UC); "vicinity of Suva," *Meebold 16555* (BISH). VITI LEVU without other locality (probably Serua Province): *Seemann 208* (K type, photos at BISH, US; isotypes at BM, GH, erroneously labelled *209*, photo at US).

Although *P. grayi* and *P. vitiensis* are superficially similar, the broader and more obviously rounded leaflet-blades of the former are characteristic, but this is not completely dependable. The petals and fruits of *P. grayi* are larger than those of *P. vitiensis,* and the stamens are also more numerous. The ovary-locules of *P. grayi* are 11–15, those of *P. vitiensis* being 5–11. The very short stylopodium of the fruit of *P. grayi* bears very short styles connate into a centrally concave ring, whereas the stylopodium of the fruit of *P. vitiensis* is comparatively obvious, the styles being definitely free distally.

6. **Plerandra pickeringii** A. Gray, Bot. U.S. Expl. Exped. **1**: 729. 1854, Atlas *pl. 95.* 1857, in Ann. Sci. Nat. IV. Bot. **4**: 178. 1855, in Proc. Am. Acad. Arts Sci. **3**: 129. 1857; Seem. in Jour. Bot. **2**: 242. 1864, Fl. Vit. 117. 1865; Drake, Ill. Fl. Ins. Mar. Pac. 183. 1890; A. C. Sm. in Bishop Mus. Bull. **141**: 116. 1936, in Jour. Arnold Arb. **33**: 103. 1952; J. W. Parham, Pl. Fiji Isl. 86. 1964.

PL. VIII, FIGS. 1, 2.

A tree to 15 m. high or shrub, glabrous throughout; leaves digitately compound, the petiole stout (to 1.5 cm. in diameter), subterete, up to 100 cm. long, sometimes verrucose-lenticellate, expanded at base into a coriaceous sheath 2–4 cm. broad, the ligule oblong-deltoid, 1–2 cm. long, the leaflets 6–12 (usually 7–11, rarely as many as 16), the petiolules stout, (1.5–) 3–13 cm. long, the blades subcoriaceous, obovate or oblong-obovate or oblanceolate, usually 16–40 cm. long and 6–22 cm. broad, occasionally up to 47 × 24 cm., acute to attenuate at base, rounded to obtuse or broadly acute at apex, usually plane at margin, the costa often prominent on both surfaces, the secondary nerves usually 10–20 per side, raised on both surfaces or plane above, the veinlet-reticulation prominulous to immersed; inflorescences umbellate, composed of 7–15 umbels radiating from a stout, short peduncle usually 2–3 cm. long, the rays 10–50 cm. long, subtended by lanceolate-deltoid bracts 1.5–2 cm. long, these soon caducous, the flowers 20–60 per umbel, on pedicels 3–5.5 cm. long; flowers borne terminally or closely aggregated on the clavate ultimate 3 cm. of the ray, subtended by coriaceous oblong bracts 1–1.5 cm. long, these soon caducous; perfect flowers with an obconical-cupuliform calyx 8–12 mm. long and 7–10 mm. broad at the sinuate-undulate margin, the calyx of staminate flowers usually 5–7 mm. long and broad; petals usually 5, rarely 4–6, appearing calyptrate in bud but eventually free, carnose, oblong-deltoid, 9–16 mm. long, 6–10 mm. broad, subacute, inconspicuously unguiculate; stamens usually 5–7-seriate, numerous, usually 400–500 in staminate flowers and 200–350 in pistillate flowers, the filaments slender, very variable (2–10 mm.) in length, the anthers narrowly oblong, obtuse, similarly variable (2–5 mm.) in length; disk flattened or slightly convex, the stylopodium at anthesis bluntly conical, about 1 mm. long, composed of firmly connate styles and minute terminal stigmas; styles usually 11–16 (rarely 9–17), the locules similar in number; fruits ellipsoid or subglobose, at maturity strongly costate, 20–25 (–40) mm. long (excl. stylopodium), 17–20 (–25) mm. broad, the stylopodium conspicuous, broadly conical at base, cyclindric above, 5–10 mm. long, ridged, with extrorse stigmas marginal on the truncate apex, the pyrenes lunulate.

TYPE LOCALITY: Ovalau, Fiji; the type is a U.S. Exploring Expedition specimen, cited below.

DISTRIBUTION. Endemic to Fiji and doubtless to be expected on most of the high islands from near sea-level to 1,050 meters. It occurs in many types of forest as a slender tree 3–15 meters high (rarely noted as a shrub), with the leaves and the large terminal inflorescences clustered at apices of branchlets. The calyx and petals are white to green or yellowish, usually purple-tinged; the filaments and anthers are white to pale yellow; the stylopodium in flower is yellowish white with pale green stigmas; and the fruits are black at maturity.

LOCAL NAMES AND USES. This species is most commonly known as *sole* or *sole ndina* (i.e., the true *sole*). In interior Viti Levu the name *sole ngua* has been reported, and also the use of trunks as posts for fish weirs. The local name *vola* has been reported from Vanua Levu, and also *ndanindani*, both of these being of questionable application to *Plerandra*.

Fiji. VITI LEVU: MBA: Mt. Nairosa, Mt. Evans Range, *Smith 4021* (A, BISH, K, NY, US); vicinity of Nandarivatu, *Gillespie 3707* (BISH); between Nggaliwana and Nandala Creeks, south of Nauwanga, *Smith 5803* (A, BISH, US). SERUA: Between Navua River and Wainiyavu Creek, near Namuamua, *Smith 8978* (BISH, US). RA: Mataimeravula, near Vaileka, *Degener 15440* (A, BISH, K, NY, UC, US). NAITASIRI: Matawailevu, Wainamo Creek, *St. John 18223* (BISH, US); Tamavua, *Gillespie 2156* (BISH, GH, NY); Nasinu, *Gillespie 3432* (BISH, GH); Kalambo, *Tothill 222* (A, BISH, K), *Fiji Dept. Agr. 11242* (SUVA). REWA: Namboro, *Fiji Dept. Agr. 5916 p. p.* (BISH, SUVA). KANDAVU: Mt. Mbuke Levu, *Smith 205* (BISH, GH, K, NY, UC, US); without locality, *Fiji Dept. Agr. 11943* (SUVA). OVALAU: *U.S. Expl. Exped.* (US 62359 type; fragmentary isotype at GH). KORO: Eastern slope of main ridge, *Smith 936* (BISH, GH, K, NY, UC, US). NGAU: East of Herald Bay, inland from Sawaieke, *Smith 7751* (BISH, US). VANUA LEVU: MBUA: Southern portion of Seatovo Range, *Smith 1524* (BISH, GH, K, NY, UC, US). MATHUATA: Seanggangga Plateau, vicinity of Natua, *Smith 6896* (A, BISH, K, NY, US). THAKAUNDROVE: Maravu, near Salt Lake, *Degener & Ordonez 14274* (A, BISH, K, NY, UC, US). TAVEUNI: Western slope near Waiyevo and Wairiki, *Gillespie 4678* (BISH, NY, UC). MOALA: Near Naroi, *Smith 1309* (BISH, GH, K, NY, UC, US).

The type species of *Plerandra*, *P. pickeringii*, is remarkably robust in its foliage and inflorescence dimensions, but its distinctness among our species rests on its characteristic fruits, which have the stylopodium conspicuous (5–10 mm. long) and composed of completely connate styles. The fruit is also comparatively large; when smaller than about 20 × 17 mm. one may suspect it to be immature. Nevertheless certain specimens, such as *Smith 6896* (the subject of our PLATE VIII, FIG. 1), have comparatively small and globose fruits that are not entirely characteristic. The functionally staminate flowers have the extraordinary number of 400–500 stamens, while the perfect flowers seem to have 200–350 stamens, remarkably high for the genus.

7. **Plerandra insolita** A. C. Sm. in Jour. Arnold Arb. 33: 103. 1952; J. W. Parham, Pl. Fiji Isl. 86. 1964. PL. VIII, FIGS. 3–7.

A slender tree to 9 m. high, glabrous throughout; leaves digitately compound, the petiole stout, subterete, 40–70 cm. long, often verrucose-lenticellate, expanded at base into a coriaceous sheath 2–4 cm. broad, the ligule oblong, 1.5–3 cm. long, the leaflets 5–12 (usually 8–11), the petiolules stout, 2–7 (–10) cm. long, the blades subcoriaceous, oblong- or obovate-elliptic or oblanceolate, 20–41 cm. long, 5–22 cm. broad, acute to attenuate at base, obtuse to rounded at apex, narrowly recurved at margin, the costa prominent on both surfaces, the secondary nerves 12–25 on each side, raised on both surfaces, the veinlet-reticulation prominulous beneath or immersed; inflorescences compound-pseudo-umbellate, arising from branchlets below leaves, composed of 5–7 rays borne at or near the apex of a short, stout peduncle 1–5 cm. long, the rays 4–8 cm. long, conspicuously swollen in the distal 1–5 cm. and copiously cicatricose, the flowers 15–35 or perhaps more per ray, congested in a strobilus-like pseudo-umbel, the pedicels very short at anthesis, elongating to 6–18 mm. in fruit, subtended by subcoriaceous oblong bracts about 1.5 cm. long, these persistent through anthesis; calyx of perfect flowers obconical-cupuliform, 7–9 mm. long and 5–7 mm. broad, irregularly lobed on the margin of the short spreading limb; calyx of staminate (and usually distal) flowers 3–5 mm. long; petals 5 or 6, rarely 4, carnose, subconnate into a conical calyptra, deltoid, 7–8 × 4–6 mm., inconspicuously unguiculate; stamens 2- or 3-seriate, 50–75, the filaments slender, 1–3.5 mm. long, the anthers oblong, obtuse, 2–3 mm. long; disk flattened, the stylopodium short-conical or umbonate, sulcate, composed of firmly connate styles with minute stigmas; styles and locules 9–12; fruits ellipsoid or subglobose, carnose and smooth when fresh, when dried coriaceous and strongly costate, 25–36 mm. long, 18–30 mm. broad, the calycular rim apically persistent, the stylopodium stout, 1–2 mm. long and 3–5 mm. in diameter, with grooved stigmas conspicuously projecting marginally on the truncate apex, the pyrenes falcate-obovoid.

TYPE LOCALITY: Southern slopes of Mt. Ndelainathovu, on the escarpment west of Nandarivatu, Mba, Viti Levu, Fiji; the type is *Smith 4922*, cited below.

Distribution. Endemic to Fiji and thus far known only from Viti Levu, where it occurs infrequently at elevations from near sea-level to 1,160 meters. It has been found in dense or open forest as a slender tree, unbranched or sparingly branched, with a sticky colorless latex. The petals are purple without and pale green or white within; the filaments are white or greenish and the anthers yellow; the disk is pale green at anthesis; and the fruits are black at maturity.

Local names. While *sole* is the general name for this species, it has also been recorded as *sole lailai* and *sole ngua* in interior Viti Levu.

Fiji. Viti Levu: Mba: Mt. Ndelainathovu, west of Nandarivatu, *Smith 4922* (a type, bish, k, us); vicinity of Nandarivatu, *Parks 20753* (bish, uc), *Gillespie 4319* (bish, uc). Serua: Mbuyombuyo, near Namboutini, *Tabualewa 15584* (a, bish, k, ny, uc, us); Vatuvilakia, vicinity of Ngaloa, *Degener 15172* (a, bish, k, ny, uc, us); north of Ngaloa, in drainage of Wainninggere Creek, *Smith 9166* (bish, us); Nakavu, Navua River, *Parks 20384* (bish, uc, us). Namosi: East of Wainikoroiluva River, near Namuamua, *Smith 8912* (bish, us); hills near Navua River, *Greenwood 1048* (a, bish, ny). Naitasiri: Wainisavulevu-Numbulolo divide, *St. John 18325* (bish, us); Viria, *Meebold 16557* (bish); Central Road, *MacDaniels 1149* (bish); Suva Ditch trail, *Bryan 376* (bish); near Nanduna Village, *Fiji Dept. Agr. 12593* (bish, suva); Tamavua, *Gillespie 2465* (bish, gh, us). Rewa: Namboro, *Fiji Dept. Agr. 5916 p. p.* (suva). Viti Levu without further data: *Seemann 206* (bm, gh, k, photos at bish, us) (July 1860; probably from the Serua coast; cf. comment on type locality of *P. grayi*, above).

A redescription of this striking species seems desirable in view of the number of available collections not at hand in 1952; these collections permit a few emendations but only serve to strengthen the status of the species. *Plerandra insolita* suggests *P. pickeringii* in the robustness of its foliage parts, but it is the most distinct of our species because of its contracted inflorescence, of which the flowers are not borne in umbels but rather in congested spirals on the clavate or cylindric distal portion of each ray. A further differentiating character is the comparatively large and persistent calycular rim. The fruits are as large as those of *P. pickeringii* but very different in characters of the stylopodium; and of course the stamens are not comparable in number to those of *P. pickeringii*. While a rigid concept of *Plerandra* might incline students of the family to segregate *P. insolita* generically, we feel that the circumscription of the genus is not greatly disturbed by the inclusion of this remarkably distinct species. In Hutchinson's 1967 system *P. insolita* would fall into the tribe Cussonieae, far removed from *Plerandra*, and the concept would probably require a new genus.

6. **Schefflera** J. R. & G. Forst. Char. Gen. Pl. 45, *nomen conservandum*. 1776; Seem. in Jour. Bot. **3**: 175. 1865, Fl. Vit. 116. 1865; Harms in E. & P. Nat. Pflanzenfam. 3(8): 35. 1894, in Bot. Jahrb. **56**: 385. 1920; Hutchinson, Gen. Fl. Pl. **2**: 69. 1967.

Schefflera, typified by the New Zealand *S. digitata* J. R. & G. Forst., is a widespread tropical and subtropical genus, but its limits are still open to interpretation. In his 1894 review of the family, Harms used *Schefflera* in a broad sense, including *Heptapleurum* Gaertn. and *Agalma* Miq. On the other hand, Hutchinson in 1967 reinstated *Agalma* (at least in the sense of Miquel's type species and some 22 others) and also combined *Cephaloschefflera* Merr. (*Schefflera* sect. *Cephaloschefflera* Harms) with a greatly expanded *Brassaia* Endl.

As the family is under further consideration by specialists, we cannot suggest reasonable limits for *Schefflera* on the basis of our restricted review. It is evident that our first five species, with paniculate-racemose inflorescences and free styles, belong in *Schefflera* in even the limited sense. The remaining four species, with compound-umbellate inflorescences, would fall into Harms' concept of his subsection *Agalma* (but this concept may not be strictly identical with Miquel's genus in a narrow sense). Of our species, *S. actinostigma* has free styles, whereas both this and *S. tannae* show transitional stages between paniculate-racemose and compound-umbellate inflorescences. It would seem that even among our few species inflorescence-characters of a satisfactory generic nature are evasive.

For present purposes we adopt *Schefflera* in the more inclusive sense, retaining in it species with strictly compound-umbellate inflorescences as well as with connate styles, but we refrain from suggesting its synonymy.

KEY TO THE SPECIES

Inflorescences paniculate-racemose, with numerous lateral branches bearing flowering umbels racemosely arranged; fruits comparatively small, usually less than 6 × 6 mm. at maturity, with 5–10 locules; leaflet-blades with 7–18 secondary nerves per side.

  Indument (on young parts, some foliage parts, and inflorescence-axes) composed of conspicuous, coarse, scale-like, many-celled hairs 2–10 mm. long; primary inflorescence-bracts conspicuous, 25–40 mm. long, the umbel-subtending bracts 5–10 mm. long. .... 1. *S. euthytricha.*

  Indument lacking or composed of minute, inconspicuous hairs (in nos. 2 and 3 the hairs sometimes scale-like and 0.5–3.5 mm. long, but sparse and usually evanescent); primary inflorescence-bracts comparatively small, 3–15 mm. long, the umbel-subtending bracts 1–6 mm. long.

    Leaflet-blades of normal adult leaves copiously denticulate-serrate at margin (teeth spinulose, 1–7 per centimeter); styles and ovary-locules often more than 5.

      Styles and ovary-locules (6–) 7–10, the styles in fruit conspicuous, 1–1.2 mm. long; flowers comparatively small, with petals 1.3–1.5 mm. long; leaflets with petiolules 5–15 mm. long and blade-margins finely denticulate, the teeth irregular, 2–7 per centimeter. .... 2. *S. samoensis.*

      Styles and ovary-locules 5 or 6, the styles in fruit 0.5–0.7 mm. long; flowers with petals about 2 mm. long; leaflets with conspicuous petiolules 20–40 mm. long and blade-margins coarsely denticulate, the teeth 1–3 per centimeter. .... 3. *S. neo-ebudica.*

Leaflet-blades of normal adult leaves entire or crenulate at margin (teeth not spinulose or evanescently so, rarely as many as 2 per centimeter); flowers apparently consistently 5-merous, with 5 styles and ovary-locules.

Inflorescences comparatively compact, the lateral branches 3–5 cm. long; leaflets 9–13, the blades rounded to broadly obtuse at apex. .... 4. *S. tannae.*

Inflorescences comparatively ample, the lateral branches usually 15–40 cm. long; leaflets (5–) 7–9, the blades acute to acuminate at apex. .... 5. *S. vitiensis.*

Inflorescences compound-umbellate, with comparatively few branches, 1–3 times divided, the flowering umbels aggregated at apices of rays; fruits comparatively large, usually more than 6 × 6 mm. (sometimes to 13 × 11 mm.) at maturity, with 5–12 locules; leaflet-blades with 20–30 secondary nerves per side, these often interspersed with others nearly as obvious.

Fruits truncate at apex, surmounted by the subpersistent calycular rim, the stylopodium flattened, the styles 5–7, divergent, 1–1.5 mm. long; inflorescences racemose-umbellate (tertiary branches whorled at a median node and also aggregated at ray-apex); leaves with the petiole 36–50 cm. long, the petiolules 3–5 cm. long, the blades 11–22 × 6–9 cm., rounded or broadly retuse at apex. .... 6. *S. actinostigma.*

Fruits with an obvious stylopodium projecting beyond the inconspicuous calycular rim or scar, the styles connate into an obvious column 1.5–2 mm. long; inflorescences strictly compound-umbellate; leaves with the petiole less than 22 cm. long, the petiolules 1–3.5 cm. long.

Leaves with a conspicuous petiolar ligule free in the distal 3–4 cm., the leaflet-blades conspicuously acuminate at apex; fruits with 8–12 costae and locules, the stylar column stout, conical, about 1.5 mm. long and 1–1.5 mm. in apical diameter. .... 7. *S. costata.*

Leaves (not known for no. 9) with a petiolar ligule free for less than 1 cm., the leaflet-blades rounded or obtusely short-acuminate at apex; fruits with 5–9 costae and locules, the stylar column slender, about 2 mm. long.

Infructescences comparatively compact, the peduncles of rays 2–9 cm. long; fruits 11–13 × 9–11 mm., 5–7-costate, the stylopodium conical, projecting (at base of stylar column) about 2 mm. above the calycular rim. .... 8. *S. seemanniana.*

Infructescences ample, the peduncles of rays 4–12 cm. long; fruits 7–9 × 8–10 mm., 6–9-costate, the stylopodium rounded, projecting (at base of stylar column) 2–3 mm. above the calycular rim. . . 9. *S. sp.*

1. **Schefflera euthytricha** A. C. Sm. in Contr. U.S. Natl. Herb. 37: 86. 1967. PL. VI.

As no additional specimens have been located since the recent original description, it is not necessary to supplement that, other than by the illustration.

TYPE LOCALITY: Namosi Province, Viti Levu, Fiji; the type is *Smith 8908*, cited below.

DISTRIBUTION. Endemic to Fiji, and thus far known from only two localities in the vicinity of the junction of the Wainikoroiluva and Navua

Rivers, south-central Viti Levu, where it occurs in dense forest at an elevation of 50–200 meters. The available specimens are from slender trees 5–6 meters high, with a conspicuous, dull brown inflorescence-tomentum; the calyx, petals, and filaments are greenish white, and the anthers white. Both known specimens, in flowering condition, were obtained in October 1953.

LOCAL NAME. The type collection was indicated as *sole tangane*.

Fiji. VITI LEVU: SERUA: Hills between Navua River and Wainiyavu Creek, near Namuamua, *Smith 8983* (BISH, US). NAMOSI: Hills east of Wainikoroiluva River, near Namuamua, *Smith 8908* (BISH, US 2192113 type).

As indicated in connection with the original description, *S. euthytricha* agrees with its only close ally in Fiji, *S. vitiensis*, in basic inflorescence-characters, differing obviously in its striking indument and large inflorescence-bracts. In respect to its indument, *S. euthytricha* is approached by *S. samoensis* and *S. neo-ebudica*, endemic to Samoa and the New Hebrides respectively, but the three species are sharply distinct in the several characters utilized in our key.

2. **Schefflera samoensis** (A. Gray) Harms in E. & P. Nat. Pflanzenfam. 3(8): 39. 1894; Reinecke in Bot. Jahrb. **25**: 663. 1898; Rechinger in Denkschr. Akad. Wiss. Wien **85**: 325. 1910; Christophersen in Bishop Mus. Bull. **128**: 164. 1935. PL. IV, FIGS. 3–5.

Paratropia samoensis A. Gray, Bot. U.S. Expl. Exped. **1**: 722. 1854.
Cheirodendron samoense Seem. in Jour. Bot. **5**: 237. 1867.
Heptapleurum samoense B. & H. f. ex Drake, Ill. Fl. Ins. Mar. Pac. 183. 1890.

A small tree or shrub, the young branches, petioles, petiolules, and sometimes leaflet-costae beneath densely or sparsely hirsute with pale linear-lanceolate many-celled hair-like scales 1–3.5 mm. long, soon glabrate; leaves digitately compound, the petiole slender, 10–25 cm. long, expanded to an inconspicuously clasping sheath, the ligule free in the distal 3–5 mm., obscurely bifid at apex, the leaflets (5–) 6–9, the petiolules slender, 5–15 mm. long, the blades papyraceous, oblanceolate to narrowly obovate, (4–) 8–20 cm. long, (1.5–) 2.5–7.5 cm. broad, gradually attenuate at base, usually conspicuously acuminate at apex, strongly denticulate-serrulate at margins (teeth spinulose, irregular, 2–7 per centimeter), the costa elevated on both surfaces, the secondary nerves 7–13 per side, arcuate-ascending, with the veinlet-reticulation usually plane above and prominulous beneath; inflorescences paniculate-racemose, the axes irregularly pilose but sometimes sparsely hirsute like vegetative parts, soon glabrate, the main rachis stout, up to 30 cm. long, the primary branches subopposite or irregularly disposed, 13–25, up to 25 cm. long, the umbels borne on slender peduncles (1–) 5–18 mm. long at anthesis and up to 30 mm. long in fruit, the flowers usually 3–10 per umbel, the pedicels 1–5 mm. long (to 7 mm. in fruit), the primary inflorescence-bracts oblong-deltoid, 3–6 mm. long, the umbel-subtending bracts 1–3 mm. long; flowers 1.5–2 mm. long at anthesis, the calyx broadly cupuliform, 0.5–1 mm. long, with a slightly flaring rim of 4–6 minute deltoid lobes; petals 4–6, oblong-deltoid, 1.3–1.5 mm. long, 0.7–1.2 mm. broad, unguiculate-thickened at apex; stamens 4–6, the filaments slender, 1–1.5 mm. long, the anthers oblong, rounded, versatile, 0.5–0.6 mm. long; ovary-apex rounded, the stigmas more numerous than petals, (6–) 7–10 (like ovary-locules), the styles minute, about 0.2 mm. long at anthesis, appressed in a small umbonate projection; fruits broadly subglobose, 2–3 mm. long and 3–3.5 mm. broad, conspicuously (6–) 7–10-costate, broadly conical at apex, the styles 1–1.2 mm. long, radiating or reflexed, clavate at apex and with oblique stigmas.

TYPE LOCALITY: Upolu, Samoa; the type is the U.S. Exploring Expedition specimen cited below.

DISTRIBUTION. Endemic to Samoa, and definitely known only from the islands of Savaii and Upolu, where it occurs with some frequency in forests and ridge thickets at elevations of 700–1,500 meters (according to Christophersen's notes). It is indicated as a tree or shrub 3–5 meters high, with green or yellowish petals, and with dark brown or perhaps black fruits.

LOCAL NAME. The only name we find recorded is *maialeale* (*Christophersen 234*).

Samoa. SAVAII: Above Matavanu Crater, *Christophersen 634* (BISH); inner slopes of Matavanu Crater, *Christophersen & Hume 2225* (A, BISH, US); near Olo, above Safotu, *Christophersen & Hume 2270* (A, BISH, US); "Mataana," *Vaupel 351* (BISH, NY, US). UPOLU: Above Malololelei, *Christophersen 234* (BISH, NY); without definite locality: *U.S. Expl. Exped.* (US 47926 type). SAMOA, without definite locality: *Whitmee 56* (K, photos at BISH, US), *s. n.* (BM, GH). We have not seen the following numbers cited by Rechinger: *Rechinger 1610* and *1753* from Savaii, *1847* and *1919* from Upolu.

Schefflera samoensis is sharply characterized by its finely denticulate leaflet-margins and by its small flowers and fruits. Whereas the other species of this relationship have the ovary-locules and styles similar in number to the other flower-parts, *S. samoensis* has usually 7–10 locules and styles, although the petals and stamens are 4–6 in number. The conspicuous and radiating styles in fruit further distinguish this very distinct Samoan endemic.

3. **Schefflera neo-ebudica** Guillaumin in Bull. Mus. Hist. Nat. II. **9**: 289. 1937, in Jour. Linn. Soc. Bot. **51**: 554. 1938. PL. IV, FIG. 6.

Schefflera sp. Guillaumin in Jour. Arnold Arb. **12**: 263. 1931.

A small tree, glabrous throughout or with a few coarse many-celled hair-like scales 0.5–1 mm. long at base of petioles and on leaf-sheaths (and rarely with a few obscure, minute, stellate hairs on inflorescence-branches); leaves digitately compound, the petiole stout, 15–27 cm. long, expanded at base into a coriaceous clasping sheath, the ligule rounded, free in the distal 1 cm., the leaflets 7–10, the petiolules 2–4 cm. long, the blades papyraceous, narrowly elliptic to oblanceolate, 12–25 cm. long, 4–7 cm. broad, attenuate at base, caudate-acuminate (but easily broken) at apex with an obtuse tip 1.5–2 cm. long, coarsely dentate at margin (teeth spinulose, 1–3 per centimeter), the costa slightly raised above and prominent beneath, the secondary nerves usually 8–12 per side, erecto-patent, with the veinlet-reticulation plane above and prominulous beneath; inflorescences paniculate-racemose, up to 40 cm. in length, pedunculate, the main rachis up to 28 cm. long, the primary branches 10 or more in number, usually 12–17 cm. long, the umbels borne on slender peduncles 4–8 mm. long, the flowers usually 5–7 per umbel, the pedicels 2–5 mm. long, the primary inflorescence-bracts oblong-deltoid, 4–6 mm. long, the umbel-subtending bracts 2–3 mm. long; flowers with a small cupuliform calyx with 5 or 6 minute deltoid lobes; petals 5 (or 6?), deltoid, about 2 mm. long; stamens 5 (or 6?), the filaments about as long as the anthers; styles (and ovary-locules) 5 or 6, the styles minute in flower; fruits broadly subglobose, 3–3.5 mm. long, 3.5–4 mm. broad, and strongly 5- or 6-costate when dried (up to 6 × 5 mm. when fresh, ex Kajewski), the stylopodium extending about 1 mm. above the calycular scar and sharply angled, the styles 0.5–0.7 mm. long, free and spreading or recurved from a shortly connate basal portion, the stigmas minute.

TYPE LOCALITY: New Hebrides; Guillaumin does not indicate a type but cites three specimens: *de la Rüe* from Ambrym, *de la Rüe* from Pentecost, and *Kajewski 114* from Lenakel, Tanna. We have seen duplicates of the latter two, and the last is an excellent fruiting specimen with duplicates in several herbaria. Therefore, we herewith designate *Kajewski 114* (holotype at Paris) as the lectotype. This was one of the two Kajewski specimens cited without an epithet by Guillaumin in 1931.

DISTRIBUTION. Endemic to the New Hebrides, and thus far known from the islands of Espiritu Santo, Pentecost, Ambrym, Tanna, and Aneityum, at elevations of 200–1,000 meters in forested areas. It is recorded as a tree 5–7 meters high; the only color notes (on *Kajewski 845*) indicate the fruit as cream-colored.

LOCAL NAMES. The name *narku* is recorded from Espiritu Santo, and *kassaskelimbueret* from Pentecost.

New Hebrides. ESPIRITU SANTO: Between Ladhogh and Turworsoksok, *I. & Z. Baker 138* (BM). PENTECOST: Between Kumre and Lasup, *de la Rüe* (A). AMBRYM: Mt. Toüo, *de la Rüe* (not seen in this study). TANNA: Lenakel, March 6, 1928, *Kajewski 114* (isotypes at A, K, NY, photos at BISH, US). ANEITYUM: Anelgauhat Bay, *Kajewski 845* (A, BISH, K, NY, photos at BISH, US).

In 1931 Guillaumin cited *Kajewski 114* and *845* as presumably representing two separate species, but they seem without doubt to be conspecific. Among the species of our area, *S. neo-ebudica* suggests only *S. samoensis*, clearly differing in its leaves with conspicuous petiolules and more coarsely denticulate blade-margins, the larger flowers, and the normal number (5 or 6) of ovary-locules and styles, the latter being comparatively short, although also free, in fruit.

4. **Schefflera tannae** A. C. Smith & B. C. Stone, sp. nov. PL. V.

Schefflera sp. Guillaumin in Jour. Arnold Arb. **12:** 263. 1931.

Arbor ad 15 m. alta ubique mox glabra, partibus novellis forsan parce puberulis; foliis digitatis, petiolis subteretibus 15–30 cm. longis, basi in vaginam coriaceam parce lenticellatam incrassatis, ligula late rotundata 4–6 mm. longa; foliolis 9–13, petiolulis gracilibus 1–3 cm. longis, superne anguste alatis, laminis papyraceis oblanceolatis vel obovatis, 8–22 cm. longis, 3.5–8 cm. latis (lateralibus saepe minoribus), basi attenuatis et in petiolulum longe decurrentibus, apice rotundatis vel late obtusis, margine anguste revolutis et subintegris vel obscure crenatis (dentibus haud 1 per centimetrum), costa supra elevata subtus prominente, nervis secundariis utrinsecus 8–12 adscendentibus subtus prominulis, rete venularum plano vel utrinque prominulo; inflorescentiis (immaturis solis visis) paniculato-racemosis ad 22 cm. longis, rhachide crassa et pedunculo ad 4 cm. longis, ramulis secundariis erecto-patentibus circiter 5 bracteis papyraceis ad 15 mm. longis mox caducis subtentis, ramulis tertiariis brevibus (3–5 cm. longis) oppositis vel aggregatis, bracteis mox caducis; umbellularum pedunculis gracilibus 3–6 mm. longis, floribus 6–12 per umbellulam, pedicellis in alabastro circiter 1 mm. longis bracteolis deltoideo-rotundatis haud 0.5 mm. longis subtentis; calyce cupuliformi haud 0.5 mm. longo, lobis 5 deltoideis minutis; petalis 5 oblongo-deltoideis in alabastro circiter 1 mm. longis apice cucullatis; disco subplano, staminibus 5, stylis in alabastro minutis erectis contiguis; fructibus non visis.

TYPE LOCALITY: Lenakel, Tanna, New Hebrides; the type is *Kajewski 131*.

DISTRIBUTION. Known only from the type collection and presumably endemic to the New Hebrides. The species is indicated by the collector to be common in rain-forest at an elevation of 200 meters; the available material is from a tree about 15 meters high, with a trunk 50 centimeters in diameter.

New Hebrides. TANNA: Lenakel, March 7, 1928, *Kajewski 131* (A type, BISH, K, NY).

Although the single collection here described does not bear fully mature inflorescences, we venture to describe it because the foliage- and inflorescence-characters are strikingly distinct from those of *S. neo-ebudica*, which is known from the same locality. From the earlier species our novelty differs sharply in its essentially entire leaflet-blades with rounded or obtuse apices. It is also characterized by more compact inflorescences with fewer and shorter lateral branches, which appear to be aggregated at two or three nodes along the rachis, suggesting a transition toward a compound-umbellate condition that is further emphasized in *S. actinostigma*, discussed below.

5. **Schefflera vitiensis** (A. Gray) Seem. in Jour. Bot. 3: 176. 1865, Fl. Vit. 116. 1865; Drake, Ill. Fl. Ins. Mar. Pac. 182. 1890; Harms in

E. & P. Nat. Pflanzenfam. 3(8): 39. 1894; Gibbs in Jour. Linn. Soc. Bot. **39**: 148. 1909; J. W. Parham, Pl. Fiji Isl. 86. 1964.
PL. IV, FIGS. 1, 2.

Aralia vitiensis A. Gray, Bot. U.S. Expl. Exped. 1: 715. 1854, Atlas *pl. 89.* 1857.

A tree, glabrous throughout at maturity, or with a close, scaly, minute indument subpersistent on lower surfaces of leaflets, inflorescence-axes, etc.; leaves digitately compound, the petiole 12–42 cm. long, expanded to a coriaceous sheathing base, the ligule ovate-oblong, subacute and sometimes bifid at apex, free in the distal 1–3 cm., the leaflets (5–) 7–9, the petiolules (0.5–) 2–10 cm. long, the blades papyraceous, oblanceolate or narrowly obovate or elliptic, (5–) 10–34 cm. long, (2.5–) 4–12 cm. broad, attenuate to acute at base, acute to acuminate at apex, usually entire or crenulate at margin on mature leaves but sometimes sparsely denticulate (teeth 1 or 2 per centimeter, evanescently spinulose), the costa slightly raised above, prominent beneath, the secondary nerves 8–18 per side, erecto-patent, often prominulous above and sharply raised beneath, the veinlet-reticulation immersed or prominulous beneath; inflorescences lateral on branchlets below terminal clusters of leaves, paniculate-racemose, glabrous to scurfy-pilose on axes, up to 100 cm. in length, short-pedunculate, the main rachis often stout and subflexuose, the primary branches usually 15–25 in number, alternate or subopposite, usually 15–40 cm. long, the primary bracts papyraceous to subcoriaceous, oblong, subacute, 3–8 mm. long (or longer on peduncular portion); umbels borne on slender peduncles 4–7 mm. long at anthesis and up to 15 mm. long in fruit, the flowers usually 5–10 per umbel, the pedicels 2–4 mm. long, subtended by minute bracteoles, the umbel-subtending bracteoles up to 5 mm. long; flowers 2–3.5 mm. long at anthesis, the calyx cupuliform, 1–2 mm. long, with 5 minute deltoid lobes; petals 5, oblong-deltoid, 1.2–1.7 mm. long, unguiculate at the acute apex; stamens 5, the filaments slender, at length about 1 mm. long, the anthers oblong, obtuse, 0.5–0.8 mm. long; ovary-apex flattened or rounded, the stigmas 5, sessile in flower, papilliform, soon elongating; fruits depressed-subglobose, at maturity 4–6 mm. long and broad, conspicuously 5-costate when dried, broadly conical at apex, the styles free except at base, sharply reflexed, 0.4–0.6 mm. long.

TYPE LOCALITY: Ovalau Fiji; the type is the U.S. Exploring Expedition specimen cited below.

DISTRIBUTION. Endemic to Fiji and probably occurring on most of the high islands, being common at elevations of about 50–1,130 meters in various types of forest, crest-thickets, etc. It is usually noted as a slender, freely branched, or gnarled tree 3–18 meters high, with a trunk up to 20 centimeters in diameter, and with characteristically congested leaves at the apices of branchlets and profuse inflorescences lateral just below the leaves. The inflorescence-axes and calyces are purple or purple-tinged; the petals and filaments are pale green to pale yellow, with nearly white anthers; the disk is green in flower; and the mature fruit is dull purple to black.

Local names and uses. Frequently recorded names on Viti Levu are *sole*, *sole lewa*, *sole ngga*, and *sangole*. On Vanua Levu the names *ndanindani*, *kaikai*, and *kai-i-voli* have been noted, and on Ovalau *ndaindainga*. In Serua Province a decoction of the leaves has been recorded as having been drunk for lung trouble, and in upland Naitasiri Province the plant is indicated as an antidote for poison.

Fiji (because of abundance only island and province are cited): Viti Levu: Mba: *Gibbs 580* (BM), *Tothill 221* (BISH, K), *225* (BISH), K), *Greenwood 337* (K), 865 (A), *Parks 20536* (BISH, UC), *Gillespie 3714* (BISH, GH, UC), *4348* (BISH, GH, NY, UC), *Degener 14627* (A, BISH, K, NY, UC, US), *Smith 4082* (A, BISH, K, US), *4095* (A, BISH, K, US), *4875* (A, US), *4952* (A), *5894* (A, BISH, K, NY, US), *6177* (A, BISH, K, NY, US), *Fiji Dept. Agr. 2325* (K), *2327* (K, SUVA), *7136* (SUVA). Nandronga & Navosa: *Degener 14901* (A, NY), *Smith 5508* (A, BISH, K, NY, US). Serua: *St. John 18966* (BISH, US), *Degener 15147* (A, BISH, K, NY, US), *Smith 9190* (US). Namosi: *Gillespie 2869* (BISH), *3137* (BISH, GH, UC), *Smith 8508* (BISH, US), *8627* (BISH, US), *Fiji Dept. Agr. 11660* (SUVA). Ra: *Degener 15354* (A, BISH, K, NY, US), *15439* (A, BISH, K, NY, US), *15510* (A, BISH, K, NY, UC, US). Naitasiri: *Jeoward 87* (K), *Bryan 369* (A, BISH, UC, US), *Tothill 223* (K), *Parks 20075* (BISH, UC), *Gillespie 3449* (BISH, GH, UC), *St. John 18286* (BISH, US), *18333* (BISH, US), *Smith 6132* (A, BISH, K, NY, US), *Fiji Dept. Agr. 119* (SUVA), *12786* (SUVA). Tailevu: *Smith 7106* (BISH, US). Rewa: *Meebold 16554* (K), *Fiji Dept. Agr. 1179* (SUVA). Kandavu: *Smith 264* (BISH, GH, K, NY, UC, US). Ovalau: *U.S. Expl. Exped.* (US 47685 type), *Gillespie 4435* (BISH), *Smith 7372* (BISH, US), *7513* (BISH, US). Ngau: *Smith 7791* (BISH, US). Vanua Levu: Mbua: *Smith 1562* (BISH, GH, K, NY, UC, US). Thakaundrove: *Smith 371* (BISH, GH, K, NY, UC, US), *513* (BISH, GH, K, NY, UC, US). Taveuni: *Seemann 203* (GH, K), *Gillespie 4650* (BISH, UC), *Smith 748* (BISH, GH, K, NY, UC, US), *8237* (BISH, US). Fiji, without other locality: *Harvey* (K), *Horne 68* (GH, K), *136* (K), *Jeoward 36* (K).

The cited material of this locally abundant species is reasonably uniform, but variations in the degree of indument are noteworthy. Most of the specimens, as to the lower surfaces of leaflets and the inflorescences, are glabrous, or evanescently puberulent with pale, minute trichomes. However, at the other extreme several specimens have the inflorescence-branches (and umbel-peduncles, calyces, and often the lower leaflet-surface on or near the costa and secondaries) more or less persistently scurfy with ferruginous, irregular, subfimbriate scales 0.1–0.15 mm. in diameter; or sometimes such indument is composed of simple, several-celled trichomes up to 0.2 mm. long. As all intermediate degrees of occurrence and persistence of indument are noted, we believe this feature lacks nomenclatural significance. The following specimens, cited above, have obvious indument: *Gillespie 3137, St. John 18966, Smith 371, 513, 748, 4952, 5894, 8508.*

Another feature not included in our description deals with the margin of leaflet-blades. Juvenile plants (like those of many species with compound leaves) have deeply pinnatifid leaflets, of which the lobes may be rounded, 5–8 per side, and copiously and irregularly spinulose-denticulate.

Lobes and teeth are normally lacking from mature leaflets, but rarely the denticulations persist on younger leaves.

Schefflera vitiensis seems to have the floral parts uniformly five, agreeing in that respect with *S. euthytricha* and *S. tannae.* From the former it shows obvious differences in indument and inflorescence-bracts; from the latter it differs in its ample, spreading inflorescences, and in its leaves with fewer leaflets, these being obviously acute to acuminate at apex.

6. **Schefflera actinostigma** A. C. Smith & B. C. Stone, sp. nov.

PL. IV, FIG. 7.

Schefflera sp. Guillaumin in Jour. Arnold Arb. **12:** 263. 1931.

Arbor ad 10 m. alta ubique glabra; foliis digitatis, petiolis crassis 36–50 cm. longis basi incrassatis (vagina et ligula non visis); foliolis 7–10, petiolulis comparative gracilibus 3–5 cm. longis, laminis subcoriaceis obovatis vel ellipticis, 11–22 cm. longis, 6–9 cm. latis, basi attenuatis et in petiolum decurrentibus, apice rotundatis vel late retusis, margine undulato-integris et anguste recurvatis, costa supra elevata subtus prominente, nervis secundariis numerosis utrinsecus 25–30 cum aliis interspersis utrinque prominulis, rete venularum subimmerso; inflorescentiis sub fructu racemoso-umbellatis 35 cm. vel ultra longis, pedunculo crasso integro non viso, radiis primariis paucis divaricatis ad 30 cm. longis pedunculo subcomplanato ad 13 cm. longo incluso, ramulis tertiariis circiter 10 e verticillo mediano paucis orientibus et apice radii aliis aggregatis graciliter pedunculatis (5–10 cm. longis) et medium versus inconspicue geniculatis; fructibus (forsan immaturis) plerumque 3–6 per umbellulam pedicellis 7–9 mm. longis enatis, subgloboso-urceolatis, 6–8 mm. longis latisque, obtuse et valde 5–7-costatis, 5–7-locularibus, apice truncatis et marginem calycinum undulatum subpersistentem circiter 1 mm. altum gerentibus; stylis gracilibus basi divergentibus rotatis 1–1.5 mm. longis.

TYPE LOCALITY: Anelgauhat Bay, Aneityum, New Hebrides; the type is *Kajewski 758.*

DISTRIBUTION. Known only from the type collection and presumably endemic to the New Hebrides. The available specimens were taken from a small tree about 10 meters high, said to be common in rain-forest at an elevation of about 60 meters; the fruit was stated to be black when mature but only about half grown when collected.

New Hebrides. ANEITYUM: Anelgauhat Bay, February 13, 1929, *Kajewski 758* (A type, K, NY, photos at BISH, US).

Although to be placed among the *Scheffleræ* of our area with compound-umbellate inflorescences, this new species is noteworthy as being transitional in character. Its primary inflorescence-rays, instead of radiating exclusively from the apex of the peduncle, are additionally clustered at a mid-point of the rachis; they are also jointed near the middle, thus suggesting further an intermediate stage between the paniculate-racemose and strictly umbellate inflorescences of *Schefflera.* The new species further differs from its Fijian allies, *S. costata* and *S. seemanniana*, in having its styles free in fruit, radiating on the flattened stylopodium that is surmounted by an obvious calycular rim.

7. **Schefflera costata** A. C. Sm. in Bishop Mus. Bull. **141**: 119. *fig. 62.* 1936; J. W. Parham, Pl. Fiji Isl. 86. 1964. PL. IV, FIG. 8.

As this species is still known only from the type collection, the original description requires supplementation only by our illustration and the following few notes:

Petioles expanded at base into a clasping sheath, the ligule prominent, oblong, free in the distal 3–4 cm., suberose at the obtuse apex, at length caducous and leaving a conspicuous scar; leaflets usually 4–9 (sometimes only 2), the blade up to 12 × 7 cm.; infructescence twice-divided, the peduncles of primary rays 3–4 cm. long, of secondary rays 1.5–2 cm. long; costae and locules of fruit 8–12, the stylopodium broadly conical into a stout stylar column about 1.5 mm. long and 1–1.5 mm. in apical diameter, the stigmas conspicuous, about 0.5 mm. long and laterally decurrent on the column.

TYPE LOCALITY: Taveuni, Fiji; the type is *Smith 886*, cited below.

DISTRIBUTION. Apparently endemic to Fiji and known only from the type collection; noted as a tree 5 meters high in forest at an elevation of 600–900 meters.

Fiji. TAVEUNI: Western slope between Somosomo and Wairiki, *Smith 886* (BISH type, GH, K, NY, UC, US).

It is surprising that this very distinct species has been collected only once, as its Taveuni locale has been visited by several collectors. From its only close relative, *S. seemanniana*, it differs in its conspicuous foliar ligule, its long-acuminate leaflet-apices, its increased number of ovary-locules, and its conical, rather than slenderly cylindric, column of connate styles.

8. **Schefflera seemanniana** A. C. Sm. in Bishop Mus. Bull. **141**: 118. 1936; J. W. Parham, Pl. Fiji Isl. 86. 1964. PL. IV, FIGS. 9, 10.

Agalma vitiensis Seem. Fl. Vit. 116. 1865; Anon. in Kew Bull. **1888**: 91. 1888. Non *Schefflera vitiensis* Seem. (1865).

Agalina vitiensis Anon. in Gartenfl. **36**: 71. 1887.

Heptapleurum vitiense Seem. ex Drake, Ill. Fl. Ins. Mar. Pac. 183. 1890; B. & H. f. ex Drake, *op. cit.* 409. 1892; Gillespie in Bishop Mus. Bull. **91**: 24. *fig. 27.* 1932.

A tree, glabrous throughout; leaves digitately compound, the petiole slender, (5–) 10–22 cm. long, expanded to a coriaceous clasping sheath, the ligule rounded, often erose toward apex, free in the distal 3–10 mm., the leaflets 4–8 (rarely fewer), the petiolules 1–3.5 cm. long, narrowly alate distally, the blades papyraceous to subcoriaceous, elliptic to obovate, (3.5–) 6–17 cm. long, (2–) 3.5–8 cm. broad, acute to attenuate at base and decurrent on the petiolule, rounded to obtusely short-acuminate at apex, entire and narrowly recurved at margin, the costa slightly raised above and prominent beneath, the secondary nerves numerous, 20–30 per side and interspersed with others nearly as obvious, spreading, prominulous on both sides or plane above, the veinlet-reticulation usually immersed above and prominulous beneath; inflorescence compound-umbellate, usually 2 (sometimes 1 or 3) times divided, the peduncle usually stout, 1–6 cm. long, bearing at apex 3–7 primary rays, these with comparatively slender peduncles 3–9 cm. long, the secondary rays (if present) with peduncles 2–6 cm. long; ultimate umbels with 5–12 flowers (primary rays sometimes terminated by an umbel of perfect flowers and also bearing secondary rays); flowers perfect or staminate, sometimes mixed in the same umbel, the pedicels usually 5–12 mm. long at anthesis (to 20 mm. in fruit), the ray- and flower-subtending bracts subcoriaceous, orbicular-ovate, inconspicuous, 1–2 mm. long, laterally contiguous, the pedicels also subtended by lanceolate evanescent bracteoles about 1 mm. long; perfect flowers about 1 cm. long at anthesis, the calyx narrowly urceolate, 4–7 mm. long and 4–5 mm. in diameter at the short, flaring, obscurely sinuate rim; petals 5 (or 6), subpersistently calyptrate, oblong-deltoid, 4–5 × 3–4 mm., apically thickened and unguiculate; stamens 5 (or 6), the filaments slightly flattened, about 2 mm. long, the anthers versatile, oblong, obtuse, 1.5–2.5 mm. long; ovary-apex conical, produced into a conspicuous stylopodium of firmly connate styles about 1 mm. long at anthesis; staminate flowers similar but the calyx much smaller, subrotate, the inferior portion of the ovary obviously sterile; fruits ovoid-subglobose, at apparent maturity (but dried) 11–13 mm. long (excluding stylar column) and 9–11 mm. broad, sharply 5–7-costate, the calycular rim obvious about 2 mm. below base of stylar column, the stylopodium conical, terminated by a slender stylar column about 2 mm. long.

TYPE LOCALITY: Viti Levu, Fiji; the type is *Graeffe 38*, deposited in the National Herbarium of Victoria at Melbourne. We have not seen the type, but an isotype is cited below.

DISTRIBUTION. Endemic to Fiji and perhaps to be expected on most of the high islands, but at present noted infrequently at elevations of 150–900 meters in dense forest or in crest-thickets. Specimens have been obtained from trees 6–25 meters high, with a trunk up to 70 centimeters in diameter; the calyx is greenish or bright green; the petals and filaments greenish yellow or pale green; the anthers pale yellow; and the fruit black at maturity.

LOCAL NAME. *Sole* has been noted for a single specimen from Ovalau.

Fiji. VITI LEVU: (without further locality) *Graeffe 38* (BM isotype, US photo). MBA: Mt. Nandende Levu, *Fiji Dept. Agr. 14058* (BISH, SUVA). NAMOSI: North of Wainavindrau Creek, between Korombasambasanga Range and Mt. Naitarandamu, *Smith 8480* (BISH, US); hills bordering Wainavindrau Creek, vicinity of Wainimakutu, *Smith 8543* (BISH, US); Mt. Voma, *Fiji Dept. Agr. 1717* (A, SUVA), *Gillespie 2668* (BISH). NAITASIRI: Central Road, *Tothill 220* (K, photos at BISH, US). REWA: Near summit of Mt. Korombamba, *Gillespie 2357* (BISH, GH). KANDAVU: Mt. Mbuke Levu, *Smith 242* (BISH, GH, K, NY, UC, US). OVALAU:

U.S. Expl. Exped. (US 73841); summit of Mt. Tana Lailai and adjacent ridge, *Smith 7703* (BISH, US). NGAU: Hills east of Herald Bay, inland from Sawaieke, *Smith 7852* (BISH, US).

Schefflera seemanniana is variable in its inflorescences, although basically these are strictly compound-umbellate. The primary rays usually bear flowering umbels at their apices, but sometimes they are directly floriferous, and sometimes they also are compound-umbellate (i.e. the inflorescence may be once, twice, or three times compound). Additionally, a flowering umbel may sometimes bear complete umbels lateral to its own flowers. It is probable that the central flowers of each umbel tend to be perfect and the peripheral flowers staminate, but this condition is not uniform. Leaf- and fruit-characters amply distinguish this species from the allied *S. costata*.

9. **Schefflera** sp. PL. IV, FIG. 11.

A tree known only from the infructescence, this compound-umbellate, 3-times divided, the peduncle 5–10 cm. long, bearing at apex 5 or 6 primary rays, these with slender peduncles 6–12 cm. long, the secondary rays (6–8 in number) with peduncles 4–9 cm. long; umbels with 4–11 fruits (on pedicels 11–18 mm. long), these depressed-subglobose, 7–9 mm. long (excluding stylar column), 8–10 mm. broad, sharply 6–9-costate, the minute calycular rim evident 1–3 mm. below the rounded apex, the styles firmly connate in a column about 2 mm. long.

Fiji. MBA: Nauwanga, vicinity of Nandarivatu, alt. 750–900 m., *Degener 14540a* (A, BISH, US) (as to infructescence only, excl. leaves; *sole*).

The infructescence here described apparently represents an undescribed species, but it was collected from the forest floor together with fallen leaves of a *Plerandra*, and the material is not a suitable basis for a new species. From the allied *S. seemanniana*, this inadequately known taxon differs in its more ample and spreading infructescence and smaller fruits, which have more numerous costae and pyrenes, and of which the stylopodium is rounded rather than conical below the stylar column.

7. **Brassaia** Endl. Nov. Stirp. Dec. 89. 1839; Hutchinson, Gen. Fl. Pl. 2: 73, 622. 1967.

As greatly expanded by Hutchinson in 1967, *Brassaia* has about 45 species and is said to have a range from India and western China through Malaysia to the Philippines, New Guinea, and northeastern Australia (the reference to Hawaii being only to a cultivated plant). However, it must be noted that the long list of new combinations presented by Hutchinson in his 1967 work includes eleven from South America, which is not indicated as part of the range. It seems very unlikely that students of the family will accept this disposition of species previously referred to *Schefflera* (including *Sciadophyllum, Heptapleurum, Cephaloschefflera*, etc.). We believe it more likely that *Brassaia* will eventually be submerged in

Schefflera, as indeed suggested by Harms (under his section *Cephaloschefflera*) and Airy Shaw (in Willis, Dict. Fl. Pl. & Ferns ed. 7. 155. 1966). No indigenous species of this complex occur in our area, but as a matter of convenience we retain *Brassaia* for its widely cultivated type species.

1. **Brassaia actinophylla** Endl. Nov. Stirp. Dec. 89. 1839; J. W. Parham, Pl. Fiji Isl. 83. 1964.

Schefflera actinophylla Harms in E. & P. Nat. Pflanzenfam. 3(8): 36. 1894.

TYPE LOCALITY: Queensland, Australia.

DISTRIBUTION. Widely cultivated in tropical areas, and doubtless often naturalized. It commonly attains a height of 15 meters or more.

LOCAL NAMES. *Queensland umbrella tree, umbrella tree,* and *octopus tree* are used for this striking plant as cultivated.

Fiji. VITI LEVU: NAITASIRI: Nasinu, *Fiji Dept. Agr. 11241* (BISH, SUVA).

The species is certainly more widely grown in our area than the above record would indicate. In Fiji, as in Hawaii, it is a frequent street tree or garden tree and it is also becoming naturalized. The cited specimen is from a naturalized plant, and the species is now commonly seen in second growth areas in southeastern Viti Levu.

8. **Dizygotheca** N. E. Br. in Kew Bull. **1892:** 197. 1892; Harms in E. & P. Nat. Pflanzenfam. **3**(8): 31. 1894; Hutchinson, Gen. Fl. Pl. **2:** 70. 1967.

Both Harms and Hutchinson maintain *Dizygotheca* as a genus of the general affinity of *Schefflera*; it is typified by *D. vieillardii* (Baill.) Viguier (*D. nilssonii* N. E. Br.) and includes 12 to 17 species, usually indicated as New Caledonian. However, Guillaumin has noted the apparently indigenous occurrence of *D. elegantissima* in the New Hebrides, and this species has also been noted as cultivated in Fiji.

Dizygotheca is characterized by having digitately compound leaves, pedicellate flowers, 5 petals and stamens, and a 10–locular ovary with free styles. All of these characters also occur in *Schefflera*, where 10 or more ovary-locules are sometimes found. Perhaps the only consistent character is the 4–locular anther of *Dizygotheca* (cf. Harms in *op. cit.* 9. *fig. 2, A-C*), contrasting with the the 2-locular anther of *Schefflera*.

1. **Dizygotheca elegantissima** (Hort.) Viguier & Guillaumin in Not. Syst. **2:** 258. 1912; Guillaumin in Bull. Mus. Hist. Nat. II. **9:** 289, as *Dyzygotheca e.* 1937; J. W. Parham, Pl. Fiji Isl. 83. 1964.

Aralia elegantissima Hort. in Gard. Chron. **1873:** 782. 1873.

We have seen no material of this species from our area, but include the record on the basis of the mention by Guillaumin and Parham.

TYPE LOCALITY: The type collection was a cultivated plant often assumed to have been introduced from New Caledonia, but quite possibly it is indigenous to the New Hebrides.

DISTRIBUTION. Widely cultivated in tropical areas and in temperate greenhouses; the original distribution is conjectural.

LOCAL NAMES. Certain horticultural plants known as *aralia* are referable to this and perhaps other species of *Dizygotheca*. Neal (Gard. Hawaii 654. 1965) lists the plant cultivated in Hawaii as *D. elegantissima* as *false aralia*.

New Hebrides. AMBRYM: (Not seen, but a specimen collected by de La Rüe, at an altitude of 650–800 m., apparently indigenous, is referred here by Guillaumin).

Fiji. (Not seen, but noted by Parham as introduced and commonly cultivated).

The species of *Dizygotheca* will doubtless remain confused, both in circumscription and in origin, until a detailed study of the cultivated variants is made in connection with a new search for wild relatives in at least New Caledonia and the New Hebrides. A second species sometimes indicated as having come from the latter archipelago is *D. reginae* (Hort.) Hemsl. L. H. Bailey (Stand. Cycl. Hort. 1062, 2746. 1925 and later editions) has presented an informative discussion of this group of horticultural "aralias." A second *Dizygotheca* from Ambrym, New Hebrides, is listed as a young form by Guillaumin in his 1937 paper on de La Rüe's collections.

9. **Boerlagiodendron** Harms in E. & P. Nat. Pflanzenfam. 3(8): 31. 1894, in Bot. Jahrb. **56**: 377. 1920; Hutchinson, Gen. Fl. Pl. **2**: 72. 1967.

Eschweileria Zipp. ex Boerl. in Ann. Jard. Bot. Buitenzorg. **6**: 112. 1887. Non *Eschweilera* Mart. (1828).

Boerlagiodendron, typified by *B. palmatum* (Zipp.) Harms, is a genus of about 40 species extending from Formosa, the Philippines, the Marianas and Palau Islands, and Malaysia through New Guinea and the Solomons to the New Hebrides, where its range is terminated by a single species. It is well represented in New Guinea, from which at least 17 species have been described.

1. **Boerlagiodendron orientale** Guillaumin in Jour. Linn. Soc. Bot. **51**: 554. 1938.

Having seen no other material of this species than the type, we refrain from adding to the original description.

TYPE LOCALITY: Espiritu Santo, New Hebrides; the type is *I. & Z. Baker 258*, cited below.

DISTRIBUTION. Known only from the type collection. Recorded as occurring in rain-forest and as having large, long-petioled leaves and a compound-umbellate inflorescence 30 centimeters in diameter.

LOCAL NAME. *Varakü* was recorded by the collectors.

New Hebrides. ESPIRITU SANTO: Hog harbour, January 25, 1934, *I. & Z. Baker 258* (BM type).

The species is noted by Guillaumin as a relative of *B. novo-guineense* (Scheff.) Harms, with which it agrees in having pinnatifid leaves and pedicellate flowers; it differs in having only 5 ovary-locules.

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MALAYSIA

EXPLANATION OF PLATES

PLATE I

FIGS. 1–5. *Polyscias joskei*: 1–4 from *Smith 4975*, 5 from *Smith 6161*. 1, leaflet, × ½; 2, ultimate axis of inflorescence, × 1; 3 and 4, flowers, × 5; 5, fruit, × 5. FIGS. 6–8. *Polyscias neo-ebudarum*: all from *Kajewski 291*. 6, leaflet, × ½; 7, flower, × 5; 8, fruit, × 5. FIGS. 9–12. *Polyscias culminicola*: all from *Smith 4514*. 9, leaflet, × ½; 10, umbel with one attached flower, × 5; 11, details of flowers, × 5; 12, immature fruit with persistent petals, × 5. FIGS. 13, 14. *Polyscias scutellaria*: from *Anderson* (lectotype of *P. pinnata*). 13, details of flowers, × 5; 14, detailed view of two of the four styles of one flower, greatly enlarged. FIGS. 15–17. *Polyscias samoensis*: all from *Setchell 374*. 15, bud just before anthesis, × 5; 16, flower with some parts removed, × 5; 17, fruit, × 5.

PLATE II

FIGS. 1–9. *Polyscias multijuga*: 1, 2, and 7–9 from *Smith 122*, 3–6 from *Seemann 205*, after Fl. Vit. 1, leaflet, × ½; 2, ultimate axis of inflorescence, × 1; 3 and 4, staminate flower, × 5; 5 and 6, perfect flower, × 5; 7 and 8, young fruit in side and top views, × 5; 9, mature fruit, × 5. FIGS. 10–14. *Polyscias corticata*: all from *Smith 5804*. 10, leaflet, × ½; 11, part of inflorescence, × ¼; 12, ultimate branch of inflorescence with terminal and lateral umbels, × 1; 13, perfect flower, × 5; 14, fruit, × 5.

PLATE III

FIGS. 1–6. *Polyscias reineckei*: all from *Christophersen & Hume 2616*. 1, flower, × 5; 2, stamens, × 5; 3, upper part of calyx and stylopodium, × 5; 4, enlarged top view of stigmas; 5, top view of fruit, × 5; 6, fruit, × 5. FIGS. 7–9. *Polyscias fruticosa*: 7 from *Smith 7496*, 8 and 9 from *Judd s. n.* (Hawaii). 7, details of flowers, × 5; 8, top view of trilocular fruit, × 5; 9, bilocular fruit, × 5. FIGS. 10–13. *Delarbrea collina*: 10 from *Kajewski 269*, 11–13 from *Kajewski 412*. 10, details of flowers, × 5; 11, cross-section of fruit, × 5; 12, top view of fruit, × 5; 13, fruit, × 5.

PLATE IV

FIGS. 1 and 2. *Schefflera vitiensis*: 1 from *Smith 8627*, 2 from *Parks 20075*. 1, details of flowers, left figures × 2½, right figure × 5; 2, fruit, × 2½. FIGS. 3–5. *Schefflera samoensis*: 3 and 4 from *Vaupel 351*, 5 from *Christophersen 234*. 3, details of flowers, upper left figures × 2½, others × 5; 4, primary inflorescence-bract, × 2½; 5, fruit, × 2½. FIG. 6. *Schefflera neo-ebudica*: fruit in profile and top view, from *Kajewski 114*, × 2½. FIG. 7. *Schefflera actinostigma*: fruit in profile and top view from *Kajewski 758*, × 2½ FIG. 8. *Schefflera costata*: fruit, from *Smith 886*, × 2½. FIGS. 9 and 10. *Schefflera seemanniana*: 9 from *Smith 7852* (♀ ♂) and *7703* (♂), 10 from *Smith 242*. 9, details of flowers,

× 2½; 10, fruit, × 2½. Fig. 11. *Schefflera sp.*: fruit, from *Degener 14540a*, × 2½.

PLATE V

Schefflera tannae: from *Kajewski 131*. Habit and inflorescence, × ¼; portion of inflorescence, × 2½.

PLATE VI

Schefflera euthytricha: from *Smith 8908*. Tip of branchlet and leaf, and detached inflorescence, the latter partly diagrammatic, × ¼.

PLATE VII

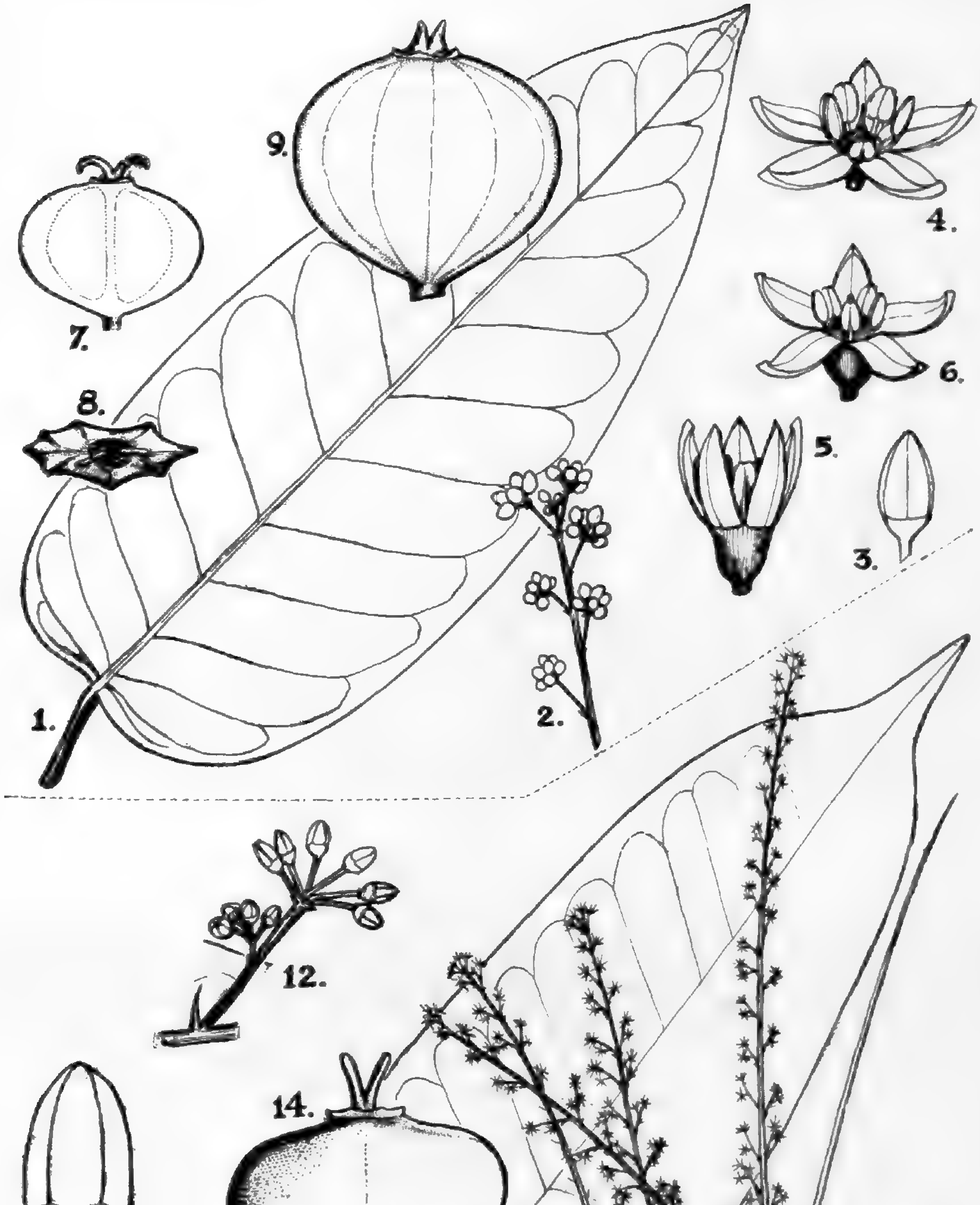
Figs. 1 and 2. *Plerandra vitiensis*. 1, fruit, from *Seemann 207* (type); 2, fruit, from *Greenwood 870*; both × 2½. Figs. 3 and 4. *Plerandra bakeriana*. 3, fruit, from *Greenwood 382*; 4, flower, from *Seemann 209* (type); both × 2½. Fig. 5. *Plerandra victoriae*, fruit, from *Gillespie 4122*, × 2½. Figs. 6–9. *Plerandra grayi*: all from *Smith 8523*. 6, fruit, × 2½; 7, apex of fruit, × 2½; 8, stamen-scars, enlarged; 9, pistillate flower, × 2½.

PLATE VIII

Figs. 1 and 2. *Plerandra pickeringii*: both from *Smith 6896*. 1, immature fruit, × 2½; 2, part of umbel, × 1. Figs. 3–7. *Plerandra insolita*: 3–5 from *Smith 9166*, 6 and 7 from *Smith 8912*. 3, fruit, × 2½; 4, ray of inflorescence, × 1; 5, pistillate flower, × 2½; 6, staminate flower, × 2½; 7, staminate flower with petals and most stamens detached, × 2½.

PLATE I

SMITH & STONE, ARALIACEAE



SMITH & STONE, ARALIACEAE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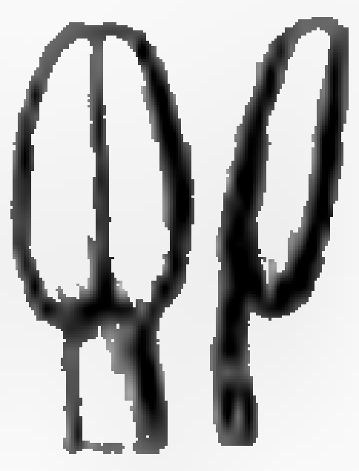
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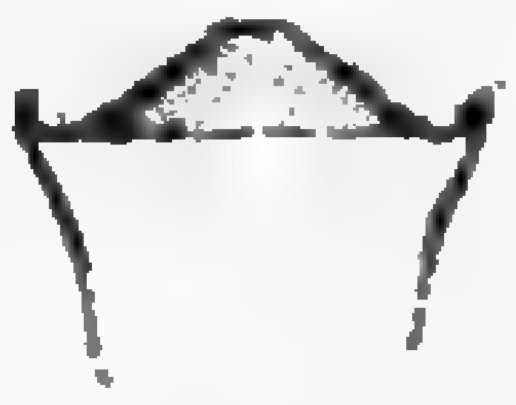
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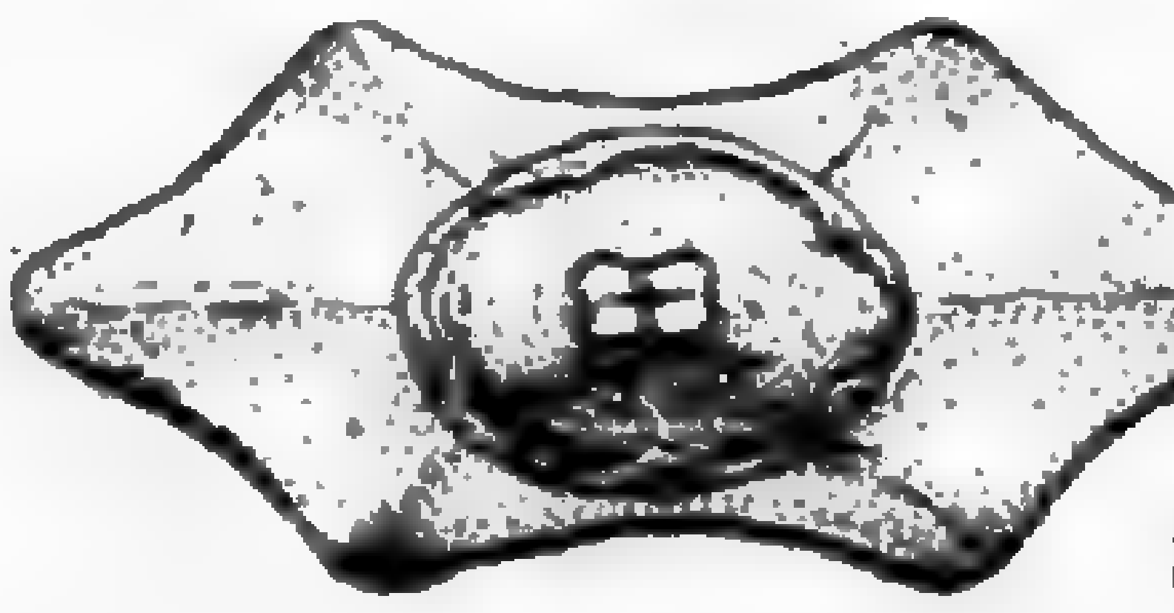
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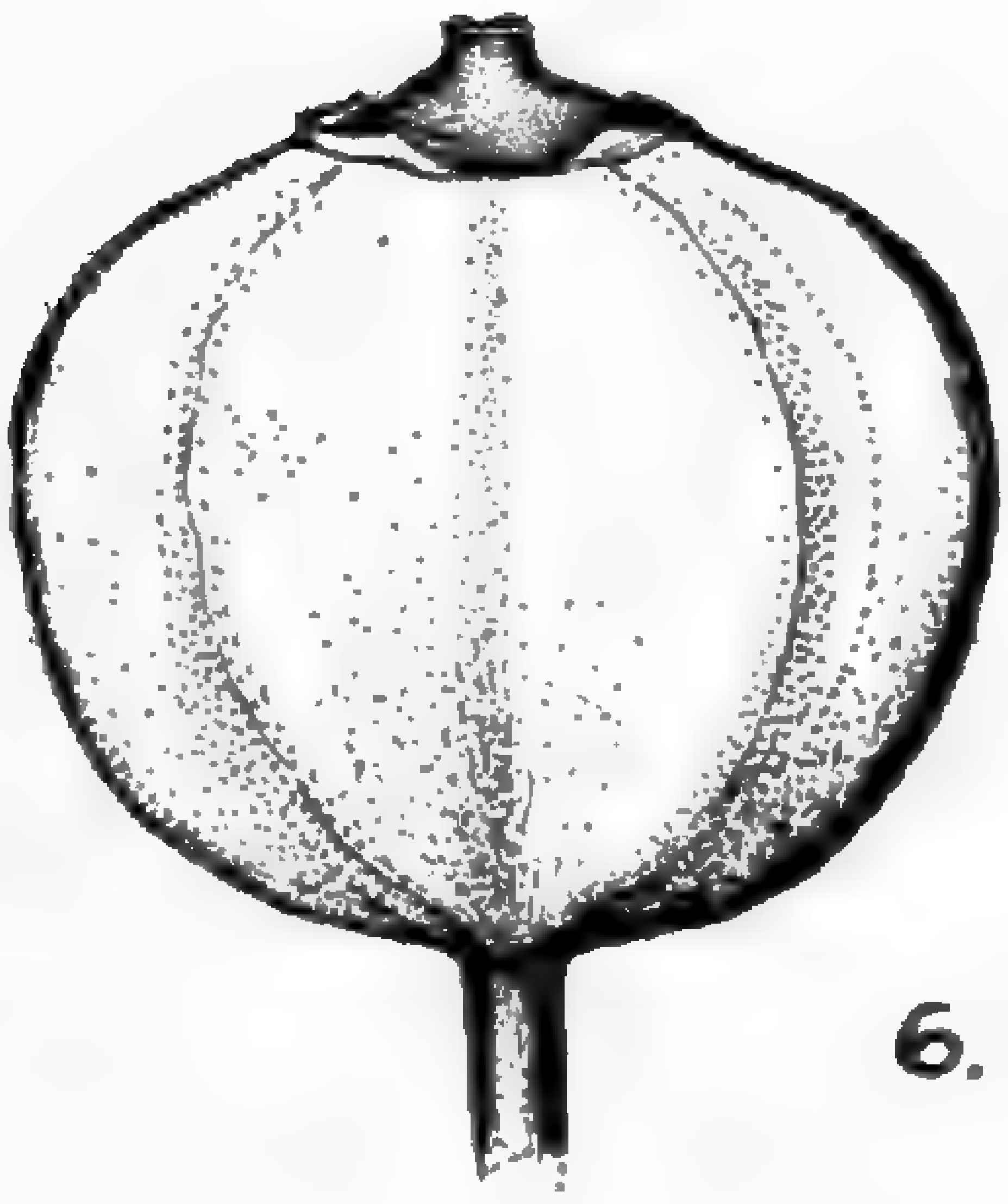
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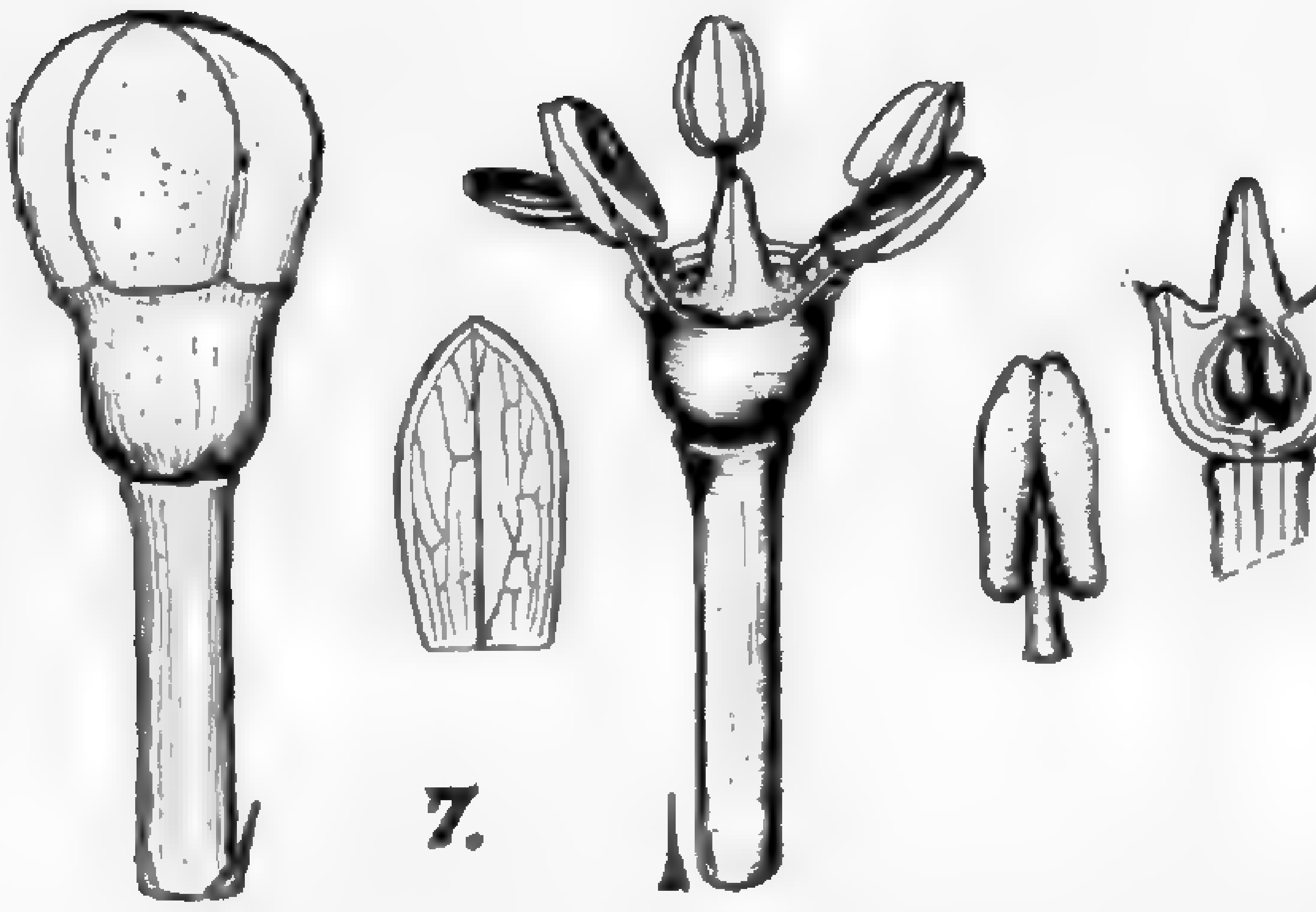
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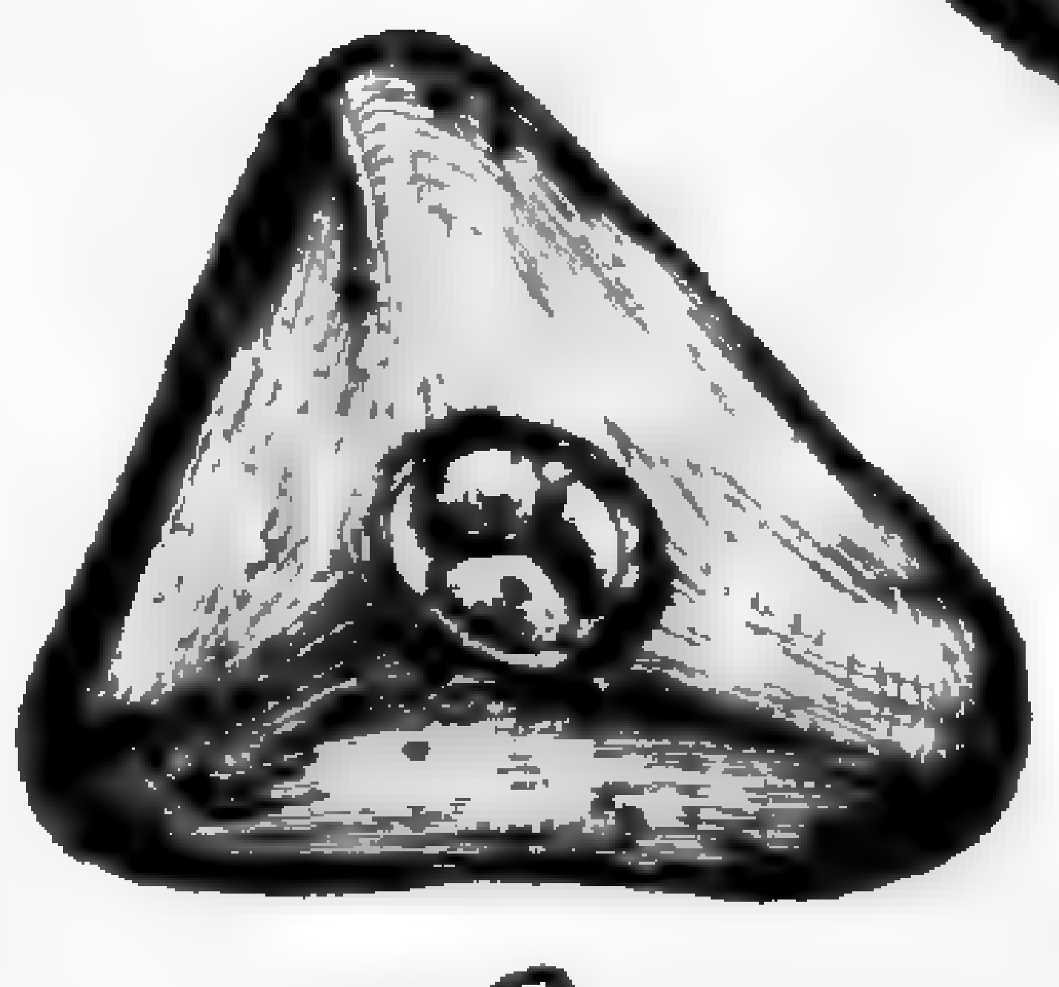
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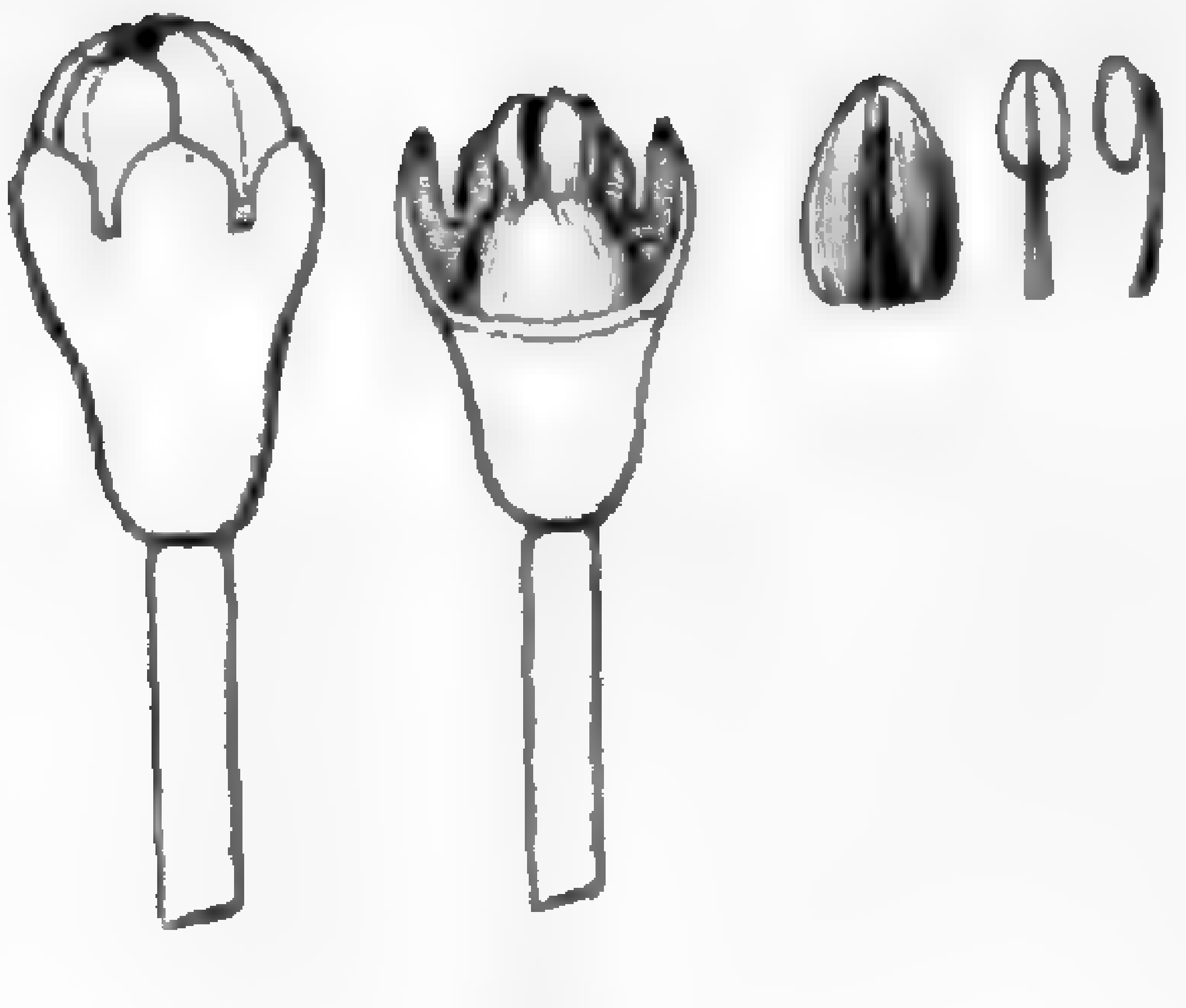
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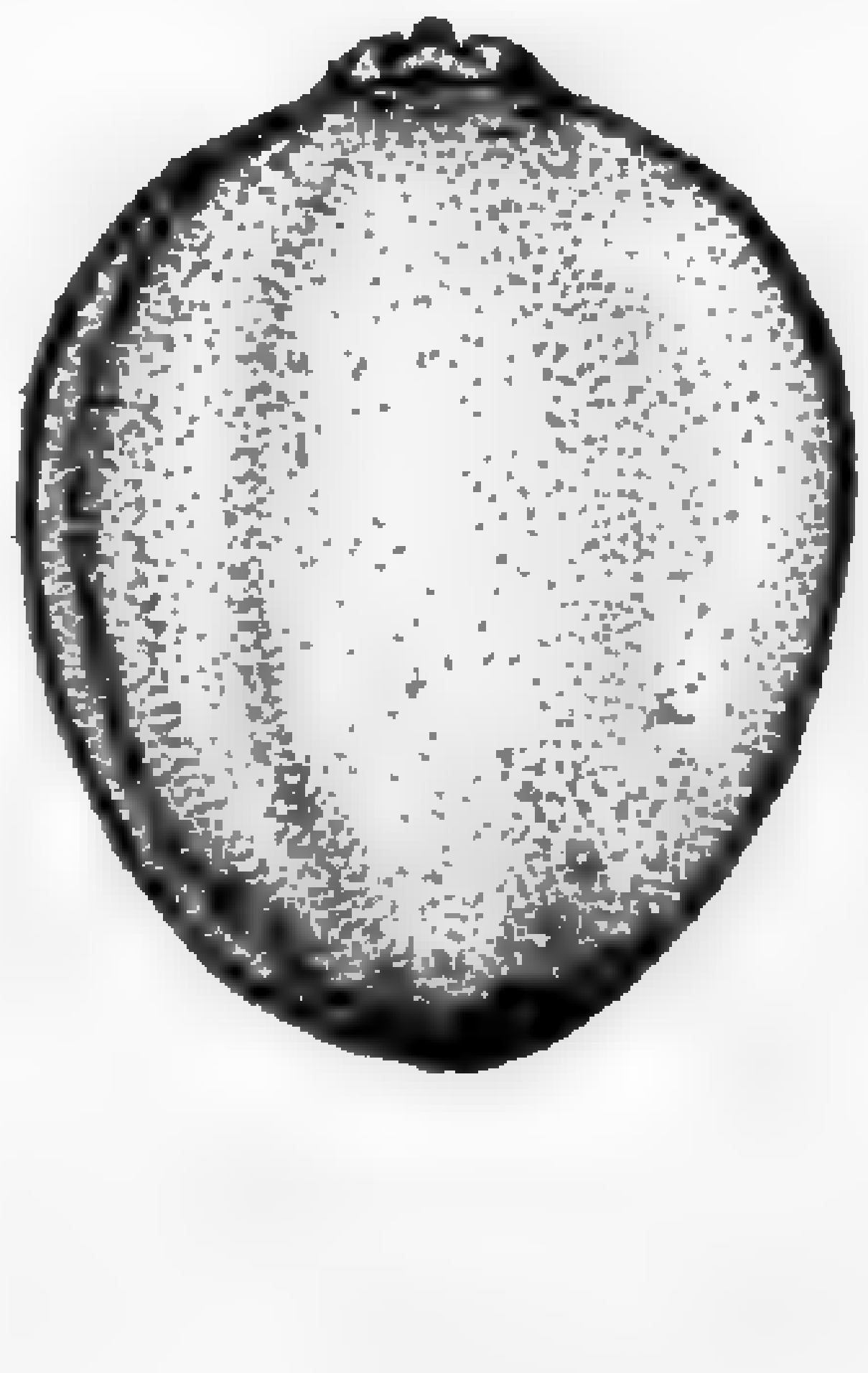
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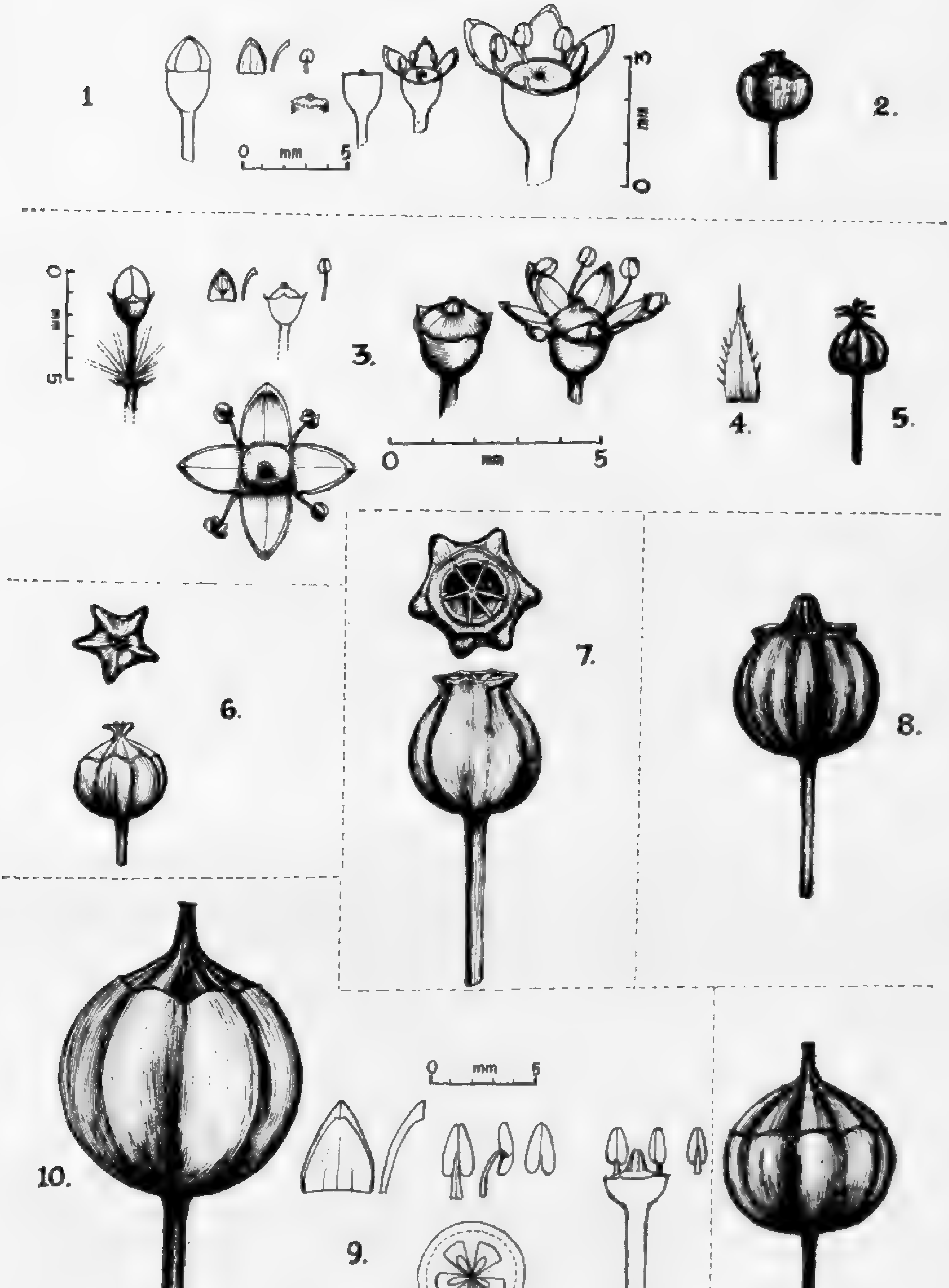
SMITH & STONE, ARALIACEAE

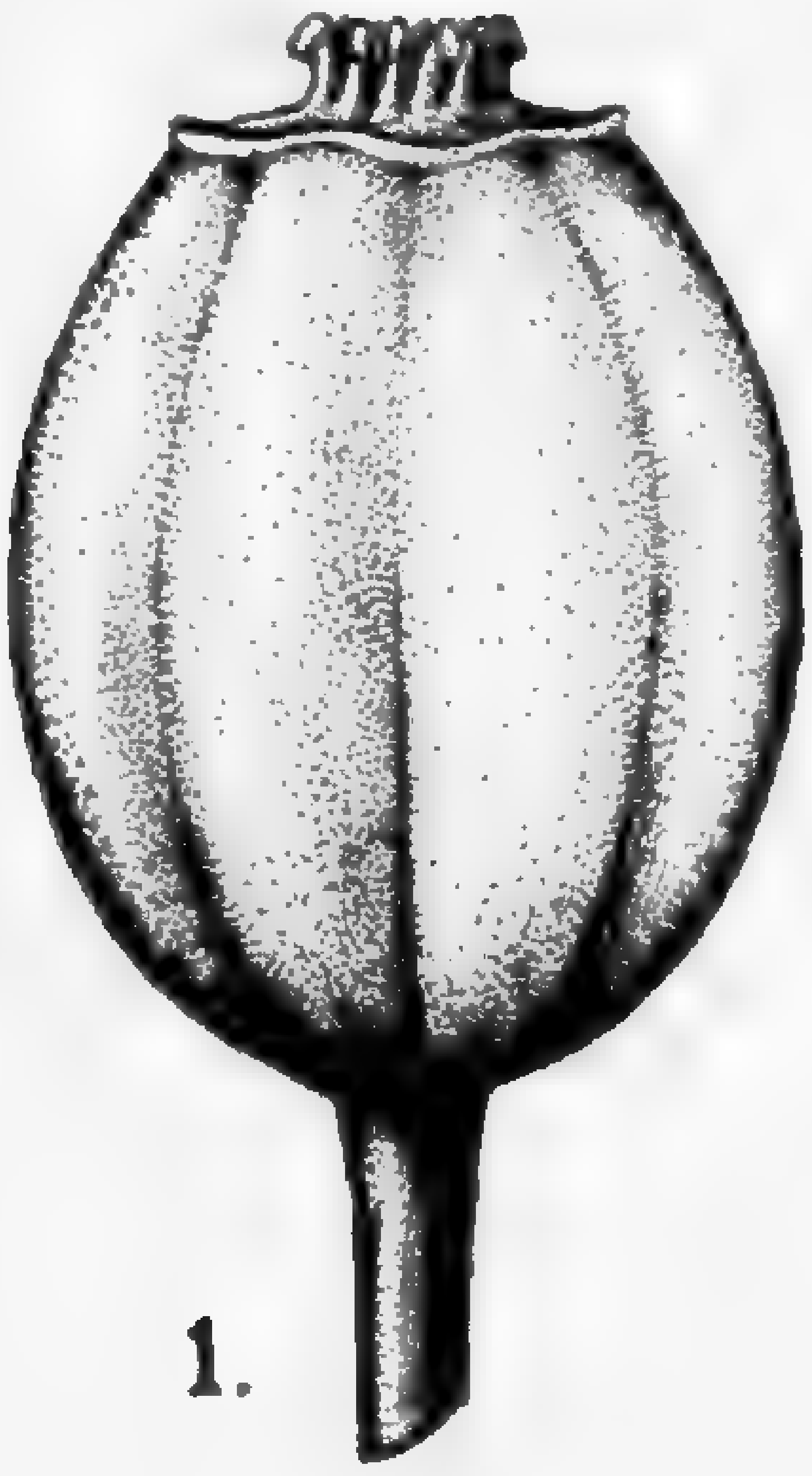


SMITH & STONE, ARALIACEAE

SMITH & STONE, ARALIACEAE

Plate VI

Smith & Stone, Araliaceae



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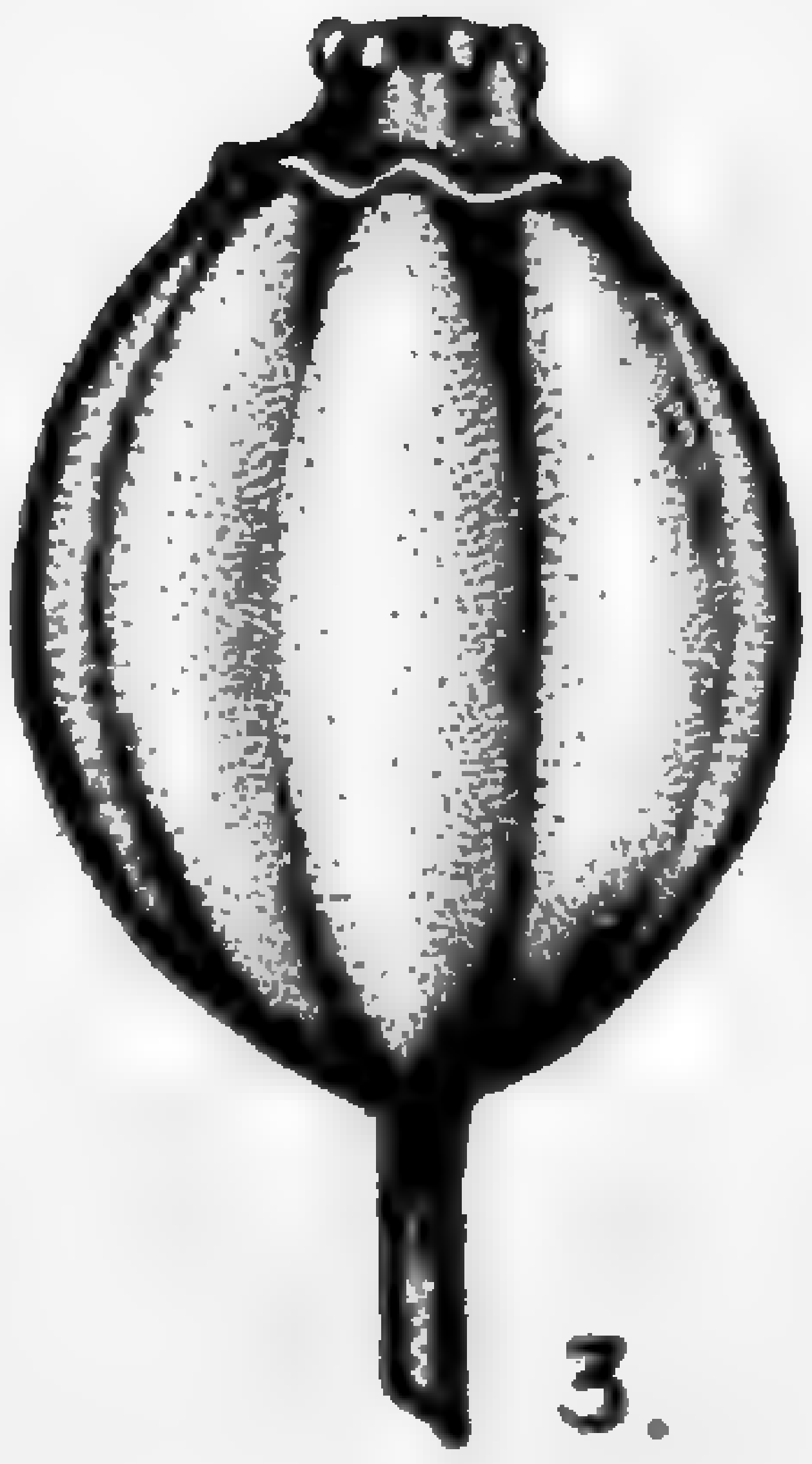

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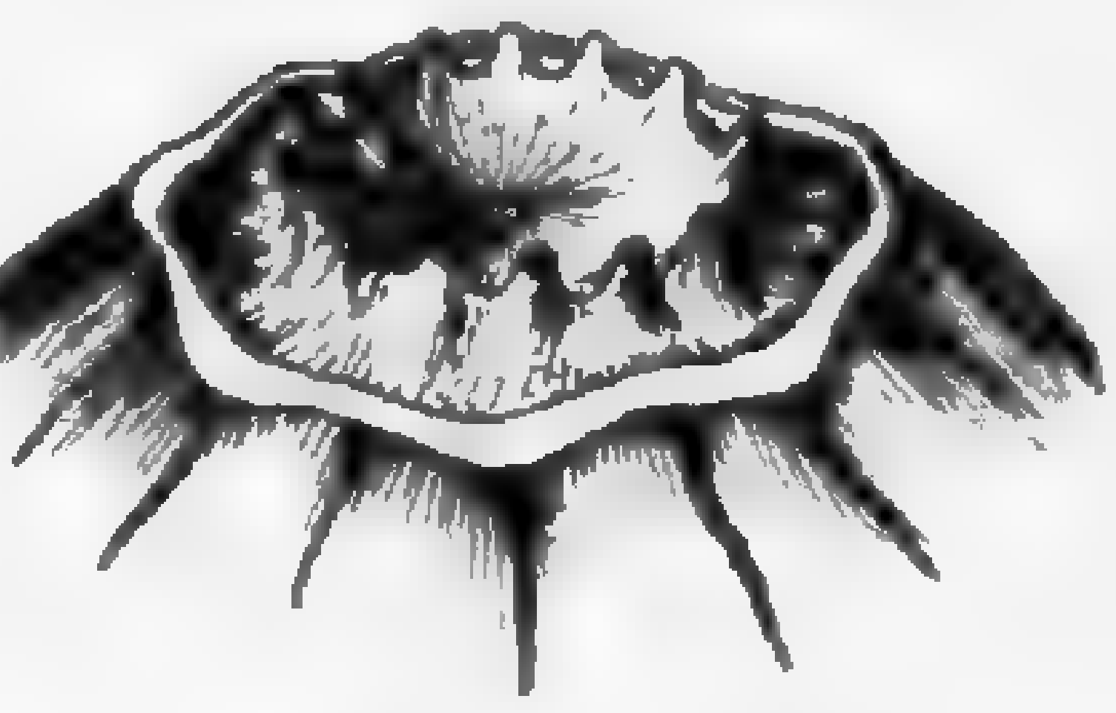

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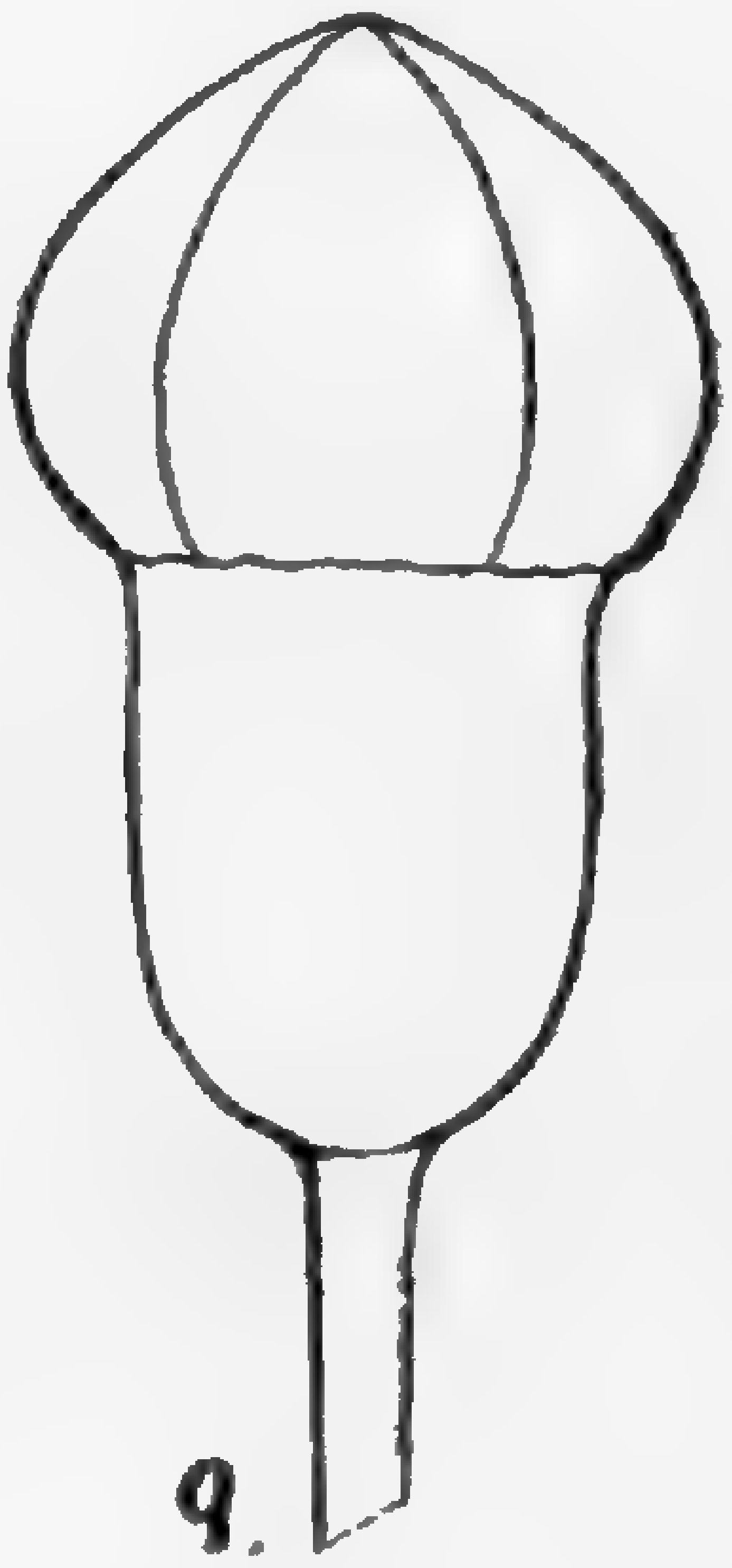

9.

Smith & Stone, Araliaceae

SMITH & STONE, ARALIACEAE

SORBUS AND THE PROBLEM OF GENERIC TYPIFICATION

† GEORGE K. BRIZICKY

HAVING BY CHANCE opened volume two of the Ray Society's facsimile (1959) of Linnaeus's *Species Plantarum* at page xi of W. T. Stearn's excellent preface I read: "The printing of an index to the *Species Plantarum* has thus provided a convenient opportunity for summarizing opinions on the typification of most Linnaean genera. The need for this is emphasized by Article 22 of the *International Code of Botanical Nomenclature 1956* which rules that 'the subgenus or section including the type species of the correct name of the genus to which it is assigned repeats that name unaltered as its epithet' . . . Its effect may be exemplified by the nomenclature of the sections of the genus *Sorbus*. Thus, if *Sorbus domestica* L. is accepted as the lectotype of *Sorbus*, as, following Hitchcock and Green, it should be, then section *Cormus* (Spach) C. K. Schneider to which it belongs must be renamed section *Sorbus* and section *Sorbus* Pers. (1806) becomes section *Sorbaria* Schauer. In genera, such as *Sorbus*, for which more than one lectotype has been proposed, it is undesirable to disturb established nomenclature until general agreement has been reached on a suitable lectotype."

Although I value most highly Stearn's "summarizing opinions on the typification of most Linnaean genera," I can not agree with his concluding sentence in the quotation above for a number of reasons: 1) following Stearn's suggestion not to disturb established nomenclature until general agreement has been reached on a suitable lectotype in genera for which more than one lectotype has been proposed means to admit and tolerate two or three different type species and, eventually, two or three different typical subgenera and/or sections in about 113 Linnaean genera; 2) of two or three lectotypes proposed for a generic name only one is correct, i.e., chosen in conformity with the *International Code of Botanical Nomenclature*; 3) when a correctly chosen lectotype is found, this choice must be followed, and no general agreement is necessary for its adoption; and 4) with regard to the importance of typification of genera, verifying the lectotype choices and/or typifications of the genera should be encouraged, not discouraged. For convenience in illustrating these points I shall use the same example as that given by Stearn, i.e., the typification of *Sorbus* L.

In his *Species Plantarum* (1: 477. 1753), Linnaeus established the genus *Sorbus* with two species, *S. aucuparia* and *S. domestica*. In 1908, Britton (N. Am. Trees 427) designated *Sorbus domestica* L. as type of the generic

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† Dr. Brizicky had completed the manuscript for this paper some time before his death on June 15, 1968.

name. This choice of lectotype, made without explanation, was adopted by Britton and Brown in 1913 (Illus. Fl. No. U.S. 2: 287). In 1929, Hitchcock & Green (Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. p. 158) independently proposed *S. domestica* L. as the lectotype species of *Sorbus* L., with the following argumentation: "The choice of standard-species lies between *S. Aucuparia* and *S. domestica*. *Sorbus* was restricted to *S. domestica* in 1789 by Medicus, Phil. Bot. 138, who treated *S. Aucuparia* as the type of an independent genus *Aucuparia* Rivin. The type of Tournefort's *Sorbus* was evidently *S. domestica* judging from the vernacular name "Sorbier" and from citations given by him. Therefore, *S. domestica* is chosen as the standard-species."

Britton's choice of *S. domestica* as the lectotype of *Sorbus*, supported by Hitchcock & Green's argumentation, has generally been adopted, except by Rehder, who designated *S. aucuparia* L. as the lectotype species of *Sorbus*, but without explanation of this choice (Bibliogr. Cult. Trees Shrubs 252. 1949). The general adoption of Britton's choice of *S. domestica* does not necessarily mean that his selection of lectotype was correct from the standpoint of the International Code, and, since it was challenged by that of Rehder, the typification of *Sorbus* must be reviewed.

The genus *Sorbus* of Linnaeus, originally founded by him in 1737 (Gen. Pl. 144), was described from a living plant as having flowers with three styles and twenty stamens inserted on the calyx. In the same year Linnaeus (Hort. Cliffort. 188) also established the single species "Sorbus foliis pinnatis" (with the synonyms: "Sorbus sylvestris. *Dalech. hist. 332.* Sorbus sylvestris alpina. *Lob. hist. 544.* Sorbus sylvestris, foliis domesticae similis. *Bauh. pin. 415.* Sorbus aucuparia. *Bauh. hist. 1. p. 62. Boerh. lugdb. 2. p. 248.* Aucuparia rivini. *Rupp. jen. 112.*"). There was appended [var.] *α*. "Sorbus sativa. *Bauh. pin. 415.*" (with the synonyms: "Sorbus domestica. *Lob. hist. 544.* Sorbus legitima. *Clus. hist. 1. p. 10.* Sorbus. *Bauh. hist. 1. p. 59. Dalech. hist. 330. Dod. pempt. 803.*"). Although a detailed description of the species was lacking, the references to the synonyms characterized the species proper and its variety *α* quite well. In addition, the ranges were given separately for the species proper and the [var.] *α*: "*Crescit in* Lapponia, Norvegia, Finlandia, Suecia, Dania, Germania, Helvetia, Anglia, Gallia & *locis umbrosis & spongiosis*, at (*α*) *in* Italia, Germania, Helvetia." In *Species Plantarum* (1: 477. 1753) the "Sorbus foliis pinnatis" of *Hortus Cliffortianus* received the name *Sorbus aucuparia*, and its [var.] *α* was raised to the rank of species with the name *Sorbus domestica*.

The occurrence of three styles ("Styli tres . . ."), i.e., of three carpels, in *Sorbus* was considered by Linnaeus to be a generic character, on the basis of which *Sorbus* was placed by him in the special order *Trigynia* of the Class *Icosandria* (Gen. Pl. ed. 5. p. xxiii). In 1777, in his *Illustratio systematis sexualis Linnaei*, Iohn [John] Miller gave a rather detailed description of *Sorbus* (based on *S. aucuparia*) as the representative of *Icosandria-Trigynia*, and this was accompanied by an excellent detailed drawing of *S. aucuparia*. The pistil was described and illustrated as having three styles and the cross section of fruit showed three locules.

In 1793, Medicus (Geschichte der Botanik, 86, 87) divided *Sorbus* L. into two distinct genera, *Aucuparia*, a new genus, based on *S. aucuparia* L. (*Aucuparia silvestris* Medic.) and *Sorbus*, based on *S. domestica* L. The two genera differed in the following characters: *Aucuparia*, "Zahl der Griffel drei bis fünf . . . Drei bis fünf Pericarpien . . . In jedem Gefache zwei Saamen"; *Sorbus*, "Fünf Griffel, selten weniger. Innerhalb dem Fleische sitzt ein fünffächerichtes Pericarpium . . . In jedem Gefache ein Saame."

In 1834, Spach (Hist. Nat. Vég. **2**: 91–98) also divided the original *Sorbus* L. into two genera: *Sorbus* L., including *S. aucuparia, S. hybrida* L., *S. lanuginosa* Kit., *S. foliosa* Wall., and *S. americana* Pursh; and *Cormus* Spach, a new genus, based on *Sorbus domestica* L. The distinguishing characters were: *Sorbus*, "Ovaire adhérent, à 3 (quelquefois à 2 ou 4) loges biovulées. Styles en même nombre que les loges de l'ovaire . . . Pyridion globuleux ou subturbiné, ombiliqué aux deux bouts, à 2–4 loges 1-spermes; endocarpe mince, crustacé"; *Cormus*, "Ovaire adhérent, à 5 loges biovulées. Styles 5, filiformes . . . Pyridion pyriforme ou subglobuleux, subquinquéloculaire; endocarpe membraneux."

Neither Medicus's nor Spach's segregation has generally been adopted, and *Sorbus*, including both original species, has usually been treated either as a subgenus of *Pyrus* L. or as a distinct genus (subdivided into two to four subgenera and/or sections). Although some authors have placed both of the original Linnaean species in the same subgenus (e.g., Persoon, Synop. Pl. **2**: 38. 1806; Koch, Hort. Dendrol. 177. 1853) or in the same section (e.g., Dumortier, Florula Belg. 93. 1827; Neilreich, Fl. Nieder-Oesterr. 886. 1858), others have separated the two and placed each of them in a different subgenus (e.g., Duchartre in D'Orbigny, Dict. Univ. Hist. Nat. **11**: 685. 1848) or in a different section (e.g., Boissier, Fl. Orient. **2**: 657. 1872). Only Decaisne (Nouv. Arch. Mus. Hist. Nat. Paris **10**: 156, 157. 1874) and Koehne (Gartenflora **40**: 35, 39. 1891 and Deutsch. Dendrol. 246, 254. 1893) followed Spach in recognizing *Sorbus* L. and *Cormus* Spach as distinct genera (which Koehne even placed in different subdivisions of the family, Sorboideae and Maloideae, respectively).

After this brief review of the establishment of the genus and some facts important for its typification, it is pertinent to return to Hitchcock and Green's argument in support of the choice of *Sorbus domestica* as the lectotype species of the genus. Their main points were these: 1) "*Sorbus* was restricted to *S. domestica* in 1789 by Medicus, Phil. Bot. 138, who treated *S. Aucuparia* as the type of an independent genus *Aucuparia* Rivin." and 2) "The type of Tournefort's *Sorbus* was evidently *S. domestica*." The second point may be dismissed here as irrelevant, because one must consider the typification of *Sorbus* of Linnaeus, 1753, and not of that of Tournefort. The first point, however, deserves a detailed discussion.

"One of the first things to do in selecting a type is to exclude from consideration those species that definitely disagree with the generic description," wrote Hitchcock (Am. Jour. Bot. 10: 511. 1923) a few years before his and Green's proposal of *S. domestica* as the standard-species of *Sorbus.* Later, in the preface to their "Standard-species of Linnaean genera of Phanerogamae (1753–54)" (Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 112. 1929) Hitchcock and Green mentioned this and another criterion for the typification of genera accepted in the Type-basis Code, "[Art.] (6c) species which definitely disagree with the generic description (provided others agree) are to be excluded from consideration; (7a 1) the type-species is often indicated by closer agreement with the generic description." Regrettably, these very sound criteria were not utilized by Hitchcock and Green in their choice of the lectotype species of *Sorbus,* for they unquestioningly accepted Medicus's segregation of *Aucuparia* as "typification by elimination." The most recent *International Code of Botanical Nomenclature* (1966) is, however, very explicit in regard to the typification of taxa, providing a "Guide for determination of types" (pp. 71, 72), and *Sorbus* must be typified as outlined below.

There can be hardly a doubt that *Sorbus* L., of 1737 (Gen. Pl. 144), was based on and its generic description drawn from the "Sorbus foliis pinnatis" proper (Hort. Cliffort. 188) and not from its variety α. Since the generic description of *Sorbus* in the fifth edition of Linnaeus's *Genera Plantarum* (1754, p. 213) was identical with that of the first, we may assume that the typical species must have remained the same, i.e., "Sorbus foliis pinnatis" of *Hortus Cliffortianus,* 1737 = *Sorbus aucuparia* L. of *Species Plantarum,* 1753.

Moreover, after describing *Sorbus* as having three styles, Linnaeus placed it in the order *Trigynia* of *Icosandria.* Miller (Illus. Syst. Sexual. Linnaei 1777) exemplified this order by *Sorbus aucuparia,* the pistil of which was described and illustrated as having three styles. Medicus (Gesch. Bot. 1793; see above) mentioned three to five styles and three to five pericarpia in *S. aucuparia,* and five, rarely fewer, styles and a five-locular pericarpium in *S. domestica.* His observations, except the occurrence of five styles and five pericarpia in *S. aucuparia,* have been confirmed by numerous taxonomists. Thus, Spach (Hist. Nat. Vég. 2: 91–98. 1834) mentioned the three-, sometimes two- or four-locular ovary in *Sorbus,* as represented by *S. aucuparia,* and the five-locular ovary in *Cormus,* based on *S. domestica.* Düll (Die *Sorbus*-Arten und ihre Bastarde in Bayern und Thüringen. Ber. Bayer. Bot. Ges. 34: 11–65. 1961) speaks of "mostly 5 carpels and styles" in *S. domestica* and of "ovary with 3, rarely 4 carpels" in *S. aucuparia* [translation supplied]. Kovanda (Flower and fruit morphology of *Sorbus* in correlation to the taxonomy of the genus. Preslia 33: 1–16. 1961) reports, "Most often 3 carpels, rarely 4, in singular cases 2" in *S. aucuparia,* while in *S. domestica* "There are always 5 carpels. Their number is absolutely constant and is not subject to any fluctuations."

These old and recent data regarding the gynoecium in the two original species of *Sorbus* clearly demonstrate that *S. aucuparia* definitely agrees and *S. domestica* disagrees with the generic description of *Sorbus* L. (1754) in the characters of the gynoecium. Consequently, *S. domestica* can not be the type of *Sorbus*, and Medicus's *Aucuparia*, based on the same type as *Sorbus* L. (i.e., on *S. aucuparia*), is illegitimate and must be reduced to synonymy with the latter. *Sorbus* Medic. then becomes a later homonym of *Sorbus* L. In fact, Miller (1777) had already indicated the typification of this genus by *S. aucuparia*. Spach (1834), too, correctly based *Sorbus* on *S. aucuparia* in segregating *S. domestica* as a distinct genus, *Cormus*. Also Duchartre (in D'Orbigny, Dict. Univ. Hist. Nat. **11**: 685. 1848), Beck von Mannagetta (in Reichenbach, Ic. Fl. Germ. Helvet. **25**(1): 35, 36. 1910?), and Boissier (Fl. Orient. **2**: 657. 1872) correctly based the typical subdivision of *Sorbus* on *S. aucuparia* with "ovarium triloculare (raro 2–4-loculare)" (Boissier), while *S. domestica* was placed in the subgenus (Duchartre, Beck) or section (Boissier) *Cormus* with "ovarium quinqueloculare, styli 5" (Boissier). Bentham & Hooker (Gen. Pl. **1**: 626. 1865) regarded three styles as a distinctive character of *Sorbus*, and Beck von Mannagetta (Fl. Nieder-Österr. 708, footnote. 1892) stated that "Linnés Gattung *Sorbus* begreift nach der Beschreibung (Styli 3, bacca globosa) wohl nur *S. aucuparia*."

Thus, the situation regarding the typification of *Sorbus* was clear and unquestionable until 1908, when Britton, contrary to both the then current usage and Linnaeus's protologue, completely reversed it and created the basis for confusion by his choice of *Sorbus domestica* as the lectotype of *Sorbus*. According to the *International Code* (1966, Guide for the determination of types, p. 72, point 4f), "The first choice of a lectotype must be followed by subsequent workers (Art. 8) unless the original material is rediscovered, or unless it can be shown that the choice was based upon a misinterpretation of the protologue." It is clear that the first formal choice of the lectotype species of *Sorbus*, made by Britton, can not be followed because it was based upon "a misinterpretation of the protologue," i.e., upon disregard of an important part of the original generic description. Thus, as already shown, *Sorbus domestica* disagrees with the statement of the generic description "Styli 3" and with the position of the genus in *Icosandria-Trigynia*. Rehder's choice (Bibliogr. Cult. Trees Shrubs 252. 1949) of *Sorbus aucuparia* as the lectotype of *Sorbus*, although tardy and unexplained by him, turns out to be correct since *S. aucuparia*, with its usually three-carpellate gynoecium with three styles, entirely fits the generic description and the position of the genus in *Icosandria-Trigynia*. The circumstance that Medicus segregated *S. aucuparia* as a distinct genus can not affect the typification, since "If it can be shown that the element best fitting the protologue has been removed, it should be restored and treated as the lectotype" (Int. Code Bot. Nomencl. 72, point 4e).

It is rather unfortunate that the authors of such important reference works as Hutchinson's *Genera of Flowering Plants* (vol. 1, 1964) and Schultze-Motel's *Verzeichnis forstlich kultivierter Pflanzenarten* (Kulturpflanze Beih. 4. 1966), and some recent monographers of the genus, such as Kovanda (Preslia **33**: 1–16. 1961) and Düll (Ber. Bayer. Bot. Ges. **34**: 11–65. 1961), have adopted Britton's (and Hitchcock and Green's) choice of *Sorbus domestica* as the lectotype of *Sorbus* without verification. (For the typification of *Melochia* L., another genus for which two lectotypes have been proposed, see Brizicky, Jour. Arnold Arb. **47**: 70, 71, footnote 4. 1966.)

I hope that from this rather detailed account of the typification of *Sorbus* it will be evident why I disagree with the opinions expressed by my esteemed colleague, Dr. Stearn, and why I think that it is essential, in the interests of nomenclatural stability, to verify immediately and to establish clearly the typification of *all* generic names, *especially* those for which more than one lectotype species has been chosen.

INTRAGENERIC CLASSIFICATION OF SORBUS

There has been much discrepancy in the citation of the names of the original authors of the subgeneric and sectional names in *Sorbus*, and, consequently, many unnecessary new combinations in these categories have been made. It seems expedient, therefore, to present as an addendum the intrageneric classification of *Sorbus* with the correct authorship of the subgeneric and sectional names. Only the most important synonyms are included.

Sorbus Linnaeus, Sp. Pl. **1**: 477. 1753; Gen. Pl. ed. 5. 213. 1754. LECTOTYPE SPECIES: *S. aucuparia* L.; see A. Rehder, Bibliogr. Cult. Trees Shrubs 252. 1949.

SUBGENERA

Subg. **Sorbus** [*Sorbus* subg. *Sorbus* Pers. Synop. Pl. **2**: 38. 1806, emend. Duchartre in D'Orbigny, Dict. Univ. Hist. Nat. **11**: 685. 1848.] (*Aucuparia* Medic. Gesch. Bot. 86. 1793, *nom. illegit. Sorbus* subg. *Aucuparia* Kovanda, Preslia **33**: 14. 1961; Düll, Ber. Bayer. Bot. Ges. **34**: 23. 1961.)

Subg. **Cormus** (Spach) Duchartre in D'Orbigny, Dict. Univ. Hist. Nat. **11**: 685. 1849. (*Cormus* Spach, Hist. Nat. Vég. **2**: 96. 1834. *Sorbus* Medic. Gesch. Bot. 87. 1793, non L. Gen. Pl. ed. 5. 213. 1754. *Sorbus* subg. *Sorbus* Kovanda, Preslia **33**: 14. 1961; Düll, Ber. Bayer. Bot. Ges. **34**: 15. 1961.) TYPE SPECIES: *S. domestica* L.

Subg. **Aria** Persoon, Synop. Pl. **2**: 38. 1806. TYPE SPECIES: *S. aria* (L.) Crantz; cf. Int. Code Bot. Nomencl. Art. 22. 1966.

Subg. **Torminaria** (Reichenb.) Koch, Hort. Dendrol. 178. 1853. (*Pyrus* L. subg. *Torminaria* (DC.) Reichenb. Consp. Reg. Veg. **1**: 168. 1828.) TYPE SPECIES: *S. torminalis* (L.) Crantz.

Subg. **Chamaemespilus** (Reichenb.) Koch, Hort. Dendrol. 176. 1853. (*Pyrus* L. subg. *Chamaemespilus* (Lindley) Reichenb. Consp. Reg. Veg. **1**: 168. 1828.) TYPE SPECIES: *S. chamaemespilus* (L.) Crantz.

SECTIONS

Sect. **Sorbus** [Sect. *Eusorbus* Boiss. Fl. Orient. **2**: 657. 1872.]

Sect. **Cormus** (Spach) Boiss. Fl. Orient. **2:** 657. 1872. (*Cormus* Spach, Hist. Nat. Vég. **2:** 96. 1834.) TYPE SPECIES: *S. domestica* L.

Sect. **Aria** (DC.) Dumortier, Florula Belg. 93. 1827. (*Pyrus* L. sect. *Aria* DC. Prodr. **2:** 635. 1825.) TYPE SPECIES: *S. aria* (L.) Crantz; cf. Int. Code Bot. Nomencl. Art. 22. 1966.

Sect. **Torminaria** (DC.) Dumortier, Florula Belg. 93. 1827. (*Pyrus* L. sect. *Torminaria* DC. Prodr. **2:** 636. 1825.) TYPE SPECIES: *S. torminalis* (L.) Crantz.

Sect. **Chamaemespilus** (Lindley) Schauer, Uebers. Arbeit. Veränder. Schles. Ges. Vaterl. Kult. **1847:** 295. 1848. (*Pyrus* L. sect. *Chamaemespilus* Lindley, Trans. Linn. Soc. London **13:** 98. 1822.) TYPE SPECIES: *S. chamaemespilus* (L.) Crantz.

EMBRYOLOGY OF DRIMYS WINTERI

N. N. Bhandari and Revathi Venkataraman

Drimys is one of six genera of the vesselless family, Winteraceae. The genus includes nearly 40 species of which 36 occur in the Old World and the rest are found in the Americas. The family is of interest because of the presence of numerous primitive characters such as the undifferentiated stamens in some members; a complete series from an open conduplicate to a closed carpel which may be sessile or stipitate; stigmatic crest; laminar placentation, and primitive xylem without vessels.

Bailey (1944), Bailey and Nast (1943a, b; 1944a, b; 1945), and Nast (1944) have dealt extensively with the morphology and vegetative anatomy of various members of the Winteraceae. However, literature on its embryology is rather meager. Maheshwari (1950), while discussing the relationships of angiosperms with other groups, has remarked "Regarding the relationship of the angiosperms with other groups, we are at present entirely in the dark. It is possible that a study of morphology and embryology of Degeneriaceae, Winteraceae, Trochodendraceae etc., may throw some light on the problem." So a study of the embryology of the Winteraceae was taken up (see Bhandari, 1963) and the present investigation is a continuation of that project.

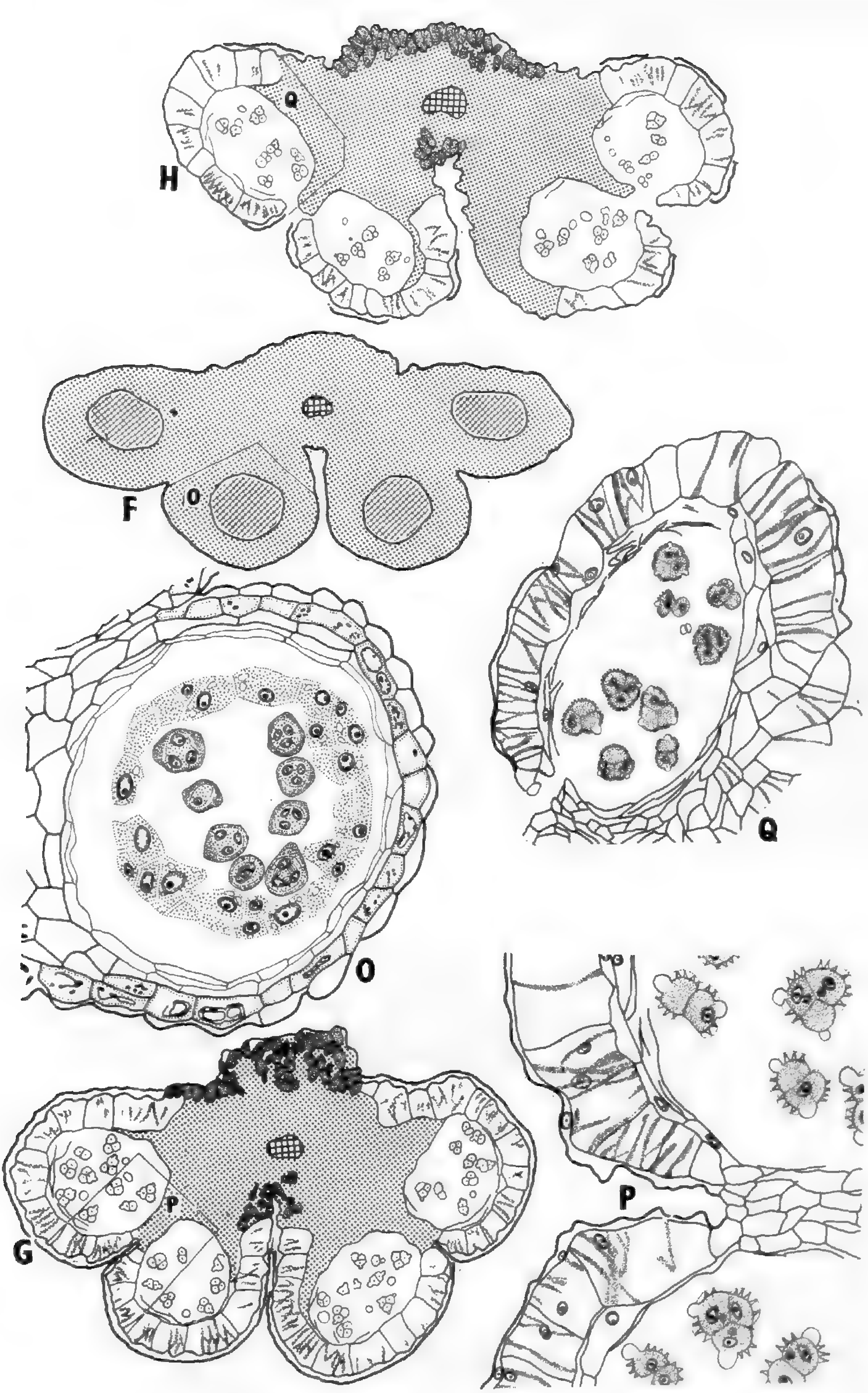
PREVIOUS WORK

Strasburger (1905) made some preliminary observations on the ovule and embryo sac of *Drimys winteri* var. *winteri* and reported normal embryo sac and nuclear endosperm. Bhagawathi Kutti Amma (1938) studied the details of microsporogenesis in *Drimys* and recorded amoeboid anther tapetum. On the other hand, Swamy (1952) observed secretory tapetum, normal embryo sac, and cellular endosperm in *Zygogynum baillonii*. In *Pseudowintera colorata* (Bhandari, 1963) the tapetum is amoeboid but in *P. axillaris* (Sampson, 1963) it is secretory. In both species the embryo sac is of the Polygonum type, and endosperm is cellular. Post-fertilization stages in the ovules and pericarp have been followed only in *P. colorata* (Bhandari, 1963).

MATERIAL AND METHODS

The buds, flowers, and fruits of *Drimys winteri* were obtained by the late Professor P. Maheshwari through the courtesy of Dr. V. Garcia of Argentina. The collections were fixed on the spot in FAA and later stored in 70 percent ethanol. The material was passed through alcohol-

FIG. 1. *Drimys winteri*, microsporangium. A, I, transection of anther showing archesporium; B, J, transection of anther (J is an enlargement of a portion of B showing some archesporial cells in division, sporogenous tissues, and a parietal layer); C, K, cross section of anther at the stage of organization of wall layers (wall comprises an epidermis, two parietal layers, and central



sporogenous tissue; C is diagrammatic); D, a diagrammatic sketch for L; L, representation of a locule enlarged to show a dividing cell of inner parietal layer which contributes to the tapetum and middle layer II; E, M, transection of anther, one locule showing the epidermis, endothecium, 2 middle layers, tapetum, and the sporogenous tissue; N, *the same*, note that the tapetum is well developed; F, O, cross sections of anther, O is a portion enlarged to show numerous microspore mother cells, surrounding them during meiosis is the detached tapetum; G, P, *the same*, showing pollen grains, the septum is intact in P; H, Q, transection of dehisced anther, the portion marked Q in H is enlarged, note that at time of dehiscence mainly the endothecial layer persists while the others degenerate. A–E, all × 165; F–H, all × 80; I–K, all × 640; L, × 540; M, × 540; N, × 300; O, × 300; P, × 220; Q, × 125.

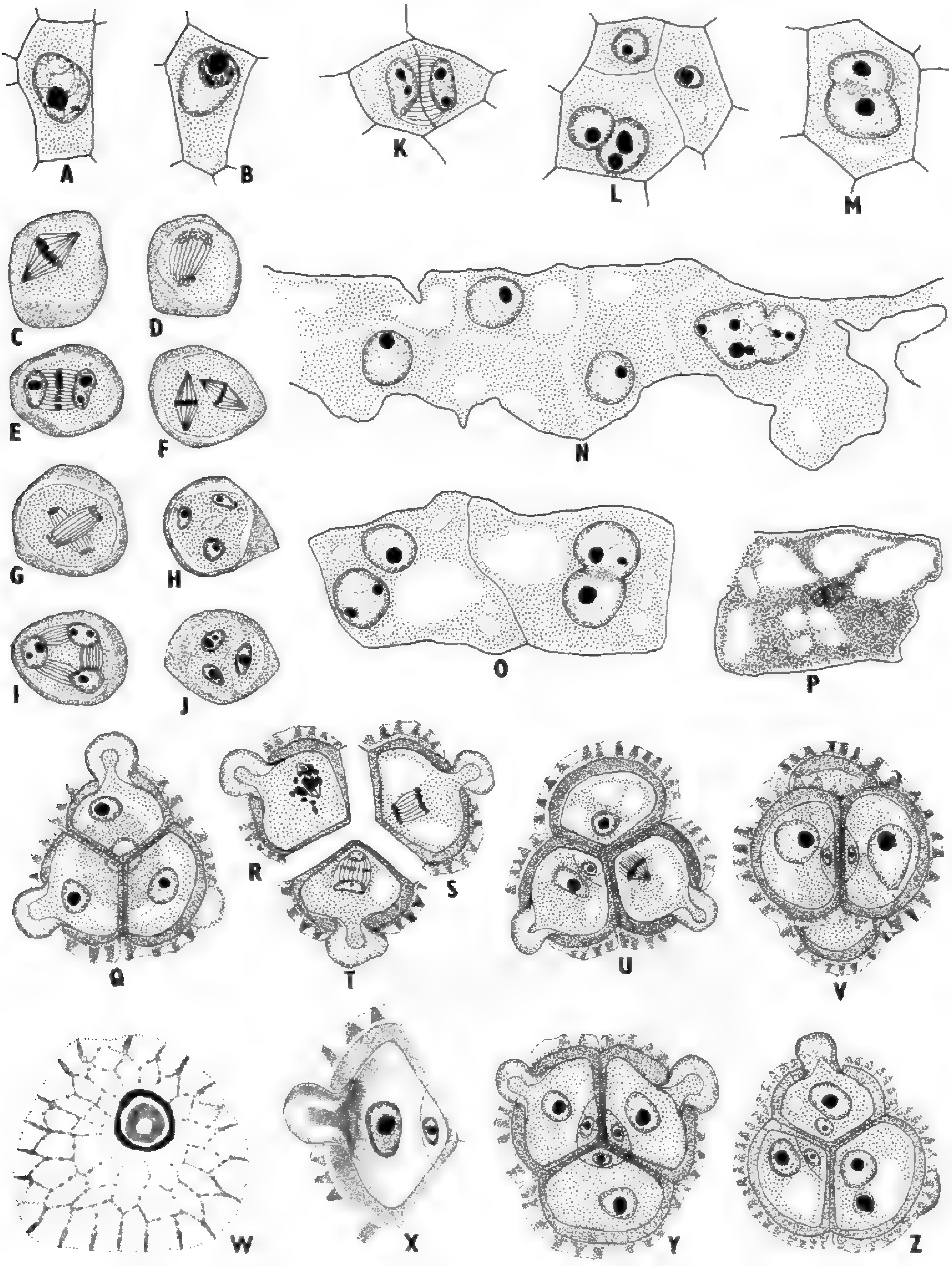


FIG. 2. *Drimys winteri*, microsporogenesis and male gametophyte. A–J, microspore mother cells showing different stages of meiosis, note that an incipient cell plate is formed after Telophase I in E; K–O, stages in the formation of occasionally bilayered tapetum with binucleate cells, the nuclei fuse to form polyploid masses in M and N; P, a degenerating tapetal cell; Q, a tetrahedral tetrad showing microspores with exine and intine, the intine much thickened at the region of germ pore through which it protrudes; R–T, three microspores showing different stages of division in the formation of the generative cell towards the proximal pole; U, single tetrad showing three microspores at different stages of division; V, a decussate tetrad with 2-celled pollen grains; W, polar view of a pollen grain showing the pattern of the exine, germ

xylene series and later embedded in paraffin. The seeds (mature seeds without seed coat) were run through the above or through the tertiary butyl alcohol series. Prior to sectioning, the embedded material (especially the seeds) was soaked in water or in 30 percent glycerine at room temperature for two weeks to facilitate microtomy. The sections were cut 6 to 14 microns thick and the preparations were stained with safranin-fast green, but those of seed development stained better with hematoxylin-eosin combination. Hand sections of mature seeds mounted in 15 percent glycerine were also examined to study the seed structure.

OBSERVATIONS

Microsporangium. The young anther is histologically undifferentiated with a well defined epidermis enclosing a homogeneous mass of cells. As the anther enlarges, in each of the four corners, a group of four or five hypodermal archesporial cells differentiates (Figs. 1A, I). The hypodermal cells divide periclinally to form the primary parietal layer and the sporogenous layer, while the subhypodermal ones directly form the sporogenous tissue (Figs. 1B, J). They divide mitotically to add to the sporogenous tissue (Fig. 1J). The primary parietal layer undergoes a periclinal division to form two layers (Figs. 1C, D, K, L). The outer forms the endothecium and middle layer I, while the inner gives rise to the tapetum and middle layer II (Figs. 1E, M, N).

The epidermal cells become tangentially compressed and highly vacuolated; their nuclei start degenerating but they stay as a thin layer of collapsed cells at the time of anther dehiscence (Figs. 1G, H, P, Q). During meiosis, the endothecial cells enlarge radially, develop strong fibrous thickenings (Figs. 1F–H, O–Q), and are persistent in the mature anther (Figs. 1H, Q). A few cells of the connective also develop such thickenings (Fig. 1Q). The middle layers remain healthy until the beginning of meiosis but soon after their cells become flattened. Consequently, the tapetum becomes detached and lies as an isolated layer inside the anther locule, surrounding the dividing microspore mother cells (Figs. 1F, O). The tapetal cells show high metabolic activity, become binucleate (Figs. 2K, L) and their nuclei fuse and form large polyploid masses (Figs. 2M–O). Soon the walls separating the adjacent tapetal cells become dissolved (Figs. 1O, 2N), and after the formation of microspore tetrads, the cells show signs of degeneration *in situ* (Fig. 2P). At a time when the exine is differentiating the tapetum gets absorbed completely.

Microsporogenesis and Male Gametophyte. Meiosis of microspore mother cells is non-synchronous. During heterotypic division (Figs. 2A–

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pore, and the dumbbell-shaped protrusion of intine; X, one microspore enlarged to show the protruding intine and the collar formed at the base of the protrusion due to thickening of the intine; Y, two-celled pollen grains in a tetrahedral tetrad; Z, pollen tetrad at the shedding stage. A–V, all × 780; W, X, both × 935; Y and Z, × 780.

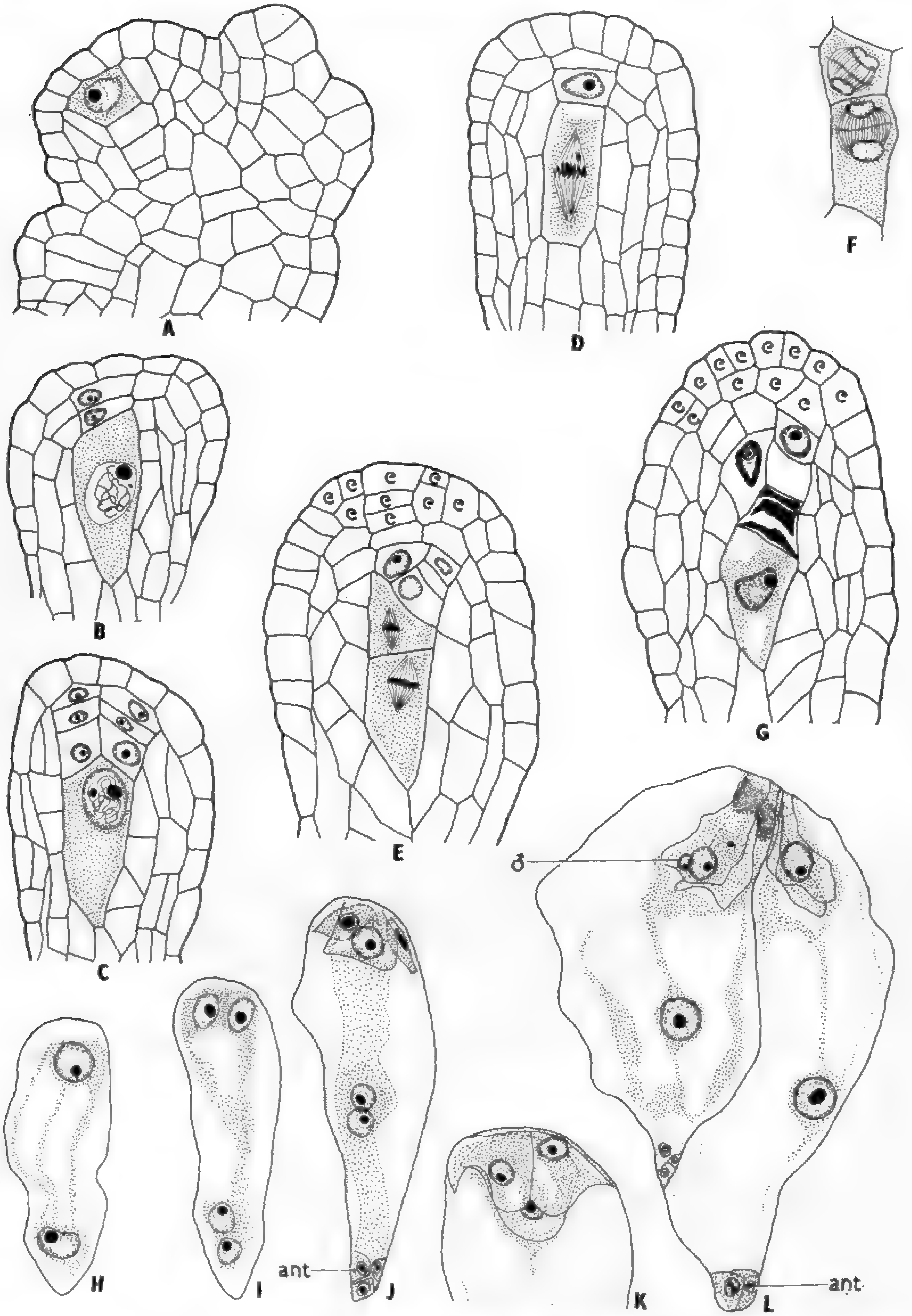

FIG. 3. *Drimys winteri*, megasporogenesis and female gametophyte (ant, antipodals; e, epidermis; ♂, male nucleus). A, longisection of ovular primordium showing a single-celled archesporium and primordia of two integuments; B, longisection of nucellus showing megaspore mother cell and two parietal cells; C, *the same*, megaspore mother cell and a 3-layered parietal tissue formed by the parietal cell; D, *the same*, megaspore mother cell at metaphase; E, longisection of nucellus, two dyad cells at metaphase II, the parietal

E) an evanescent cell plate is sometimes formed at Telophase I (Fig. 2E). At the end of homotypic division (Figs. 2F–J) simultaneous quadripartitioning occurs by furrowing. The microspores remain in permanent tetrads which may be tetrahedral or decussate (Figs. 2Q, U, V). At the beginning of gametogenesis, the nucleus of the microspore moves towards the proximal pole of the tetrad where it divides (Figs. 2R–T). The four microspores in a tetrad may show different stages in the formation of the generative cell (Fig. 2U). The wall between the two cells degenerates so that the generative cell, surrounded by a hyaline cytoplasmic sheath, comes to lie free within the cytoplasm of the vegetative cell (Fig. 2Z).

The pollen grains are monoporate and the pore is developed towards the distal end. The intine protrudes through the pore and shows maximum thickening in this region (Figs. 2Q–Z). As stated by Bailey and Nast (1943a) for *Drimys* section Wintera, here also a collar is present at the base of protruding intine (Figs. 2W, X). The pollen grains are shed in tetrads at the 2-celled stage (Fig. 2Z).

Megasporangium, Megasporogenesis and Female Gametophyte. The young carpel resembles a conduplicately folded leaf. The two approximated margins of the carpel are firmly concrescent except at the stigmatic region where the epidermal cells interlock. There are 15 or 16 anatropous, bitegmic and crassinucellate ovules. A single hypodermal archesporial cell differentiates in the nucellus (Fig. 3A) and divides transversely to form a primary sporogenous cell and a parietal cell. The latter undergoes repeated periclinal and anticlinal divisions to form a 2- or 3-layered parietal tissue (Figs. 3B–E). Meiosis I in the megaspore mother cell (Figs. 3C, D) results in a dyad, of which the micropylar cell is smaller (Figs. 3E, F). Both of the dyad cells divide simultaneously to form a linear or a T-shaped tetrad (Figs. 3E, F). The chalazal megaspore functions and the other three megaspores degenerate (Fig. 3G). Three successive mitoses result in a 2- (Fig. 3H) 4- (Fig. 3I) and 8-nucleate embryo sac (Figs. 3J–L). Thus, the development conforms to the Polygonum type. Occasional instances of twin embryo sacs were also observed (Fig. 3L).

Fertilization and Endosperm. Syngamy and triple fusion have been observed (Fig. 4A). The pollen tube is sometimes persistent during early stages of the endosperm development. The endosperm is *ab initio* cellular. The primary endosperm nucleus migrates towards the center of the embryo sac before its division (Figs. 4B, C) which is followed by the formation of a transverse wall (Fig. 4D). The next division in the two unequal cham-

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tissue is being contributed by both the parietal layer and the nucellar epidermis; F, two dyad cells showing telophase spindles indicating the formation of a T-shaped tetrad; G, longisection of nucellus showing tetrad with the chalazal functional and the other three degenerated megaspores; H, I, two- and four-nucleate embryo sacs; J, organized 8-nucleate embryo sac showing egg apparatus, two polar nuclei and three uninucleate antipodal cells; K, micropylar end of an embryo sac enlarged to show egg apparatus with hooked synergids; L, twin embryo sacs. A–E, and G, all × 465; F, H–L, all × 610.

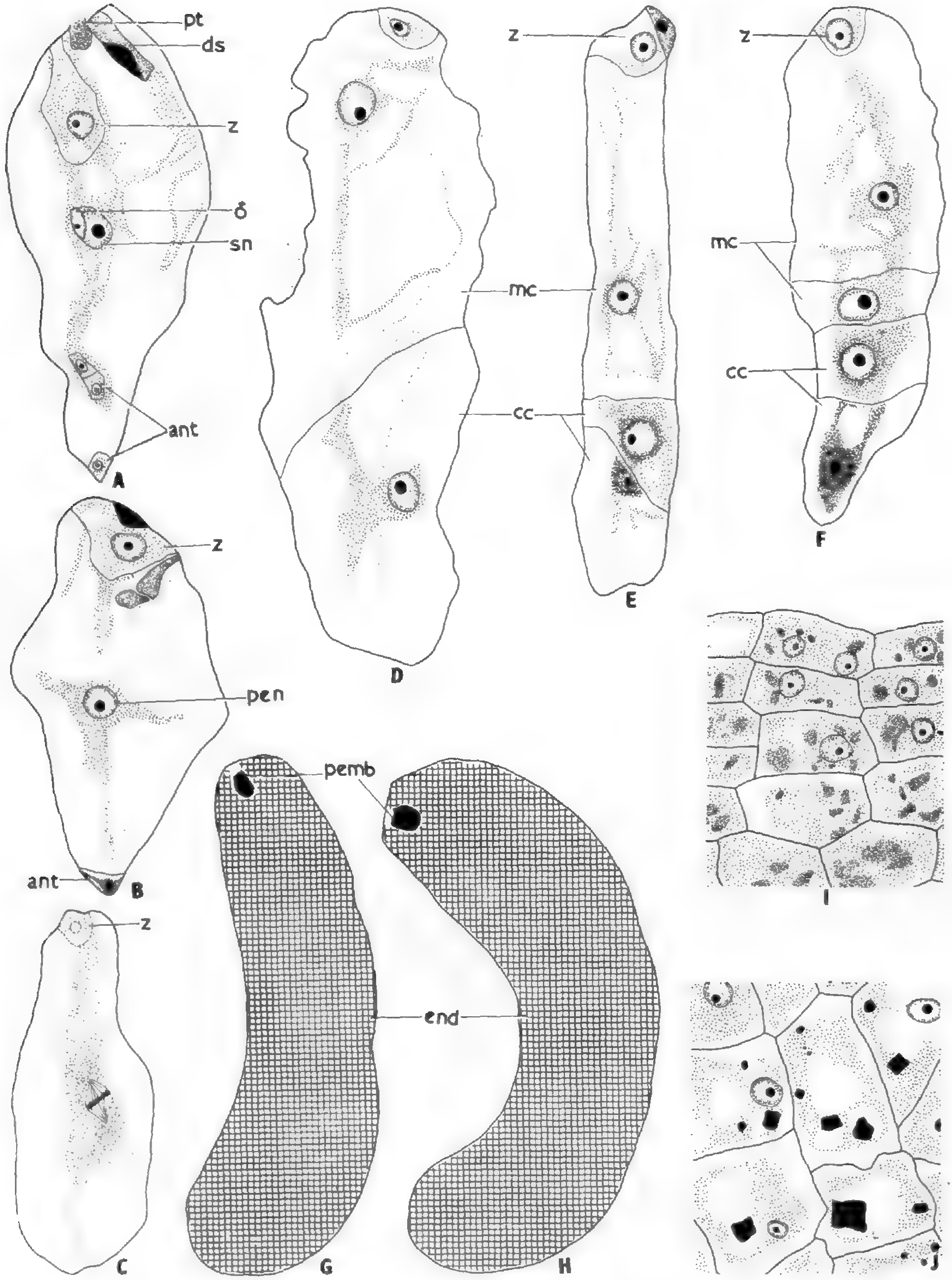

FIG. 4. *Drimys winteri*, endosperm (ant, antipodal cells; cc, chalazal chamber; ds, degenerated synergid; end, endosperm; ♂, male nucleus; mc, micropylar chamber; pemb, proembryo; pen, primary endosperm nucleus; pt, pollen tube; sn, secondary nucleus; z, zygote). A, embryo sac showing triple fusion, note the persistent remnants of pollen tube; B, *the same*, showing primary endosperm nucleus, zygote, remnants of degenerated synergids and antipodal cells; C, embryo sac with the primary endosperm nucleus in division; D–F, two-, three-, and four-celled endosperm stages, the chalazal chamber has divided into two cells of which the lower cell is degenerating; G, H, longisections of mas-

bers is transverse but the division in the chalazal chamber precedes that of the micropylar (FIG. 4E). The two cells formed in the micropylar chamber are again unequal, the smaller cell being towards the chalazal end (FIG. 4F). It appears that the chalazal chamber does not contribute much to the formation of the endosperm proper.

The endosperm soon becomes massive and at the 10-celled stage of the embryo it is made up of cells having prominent nuclei and dense cytoplasm. Later, the endosperm cells become packed with small round or oval brownish particles of unknown nature which did not give any positive test for starch, oil or proteins (FIGS. 4G, I). In mature endosperm the cells are large with little cytoplasm but are packed with bodies which stain darkly with hematoxylin (FIGS. 4H, J).

Embryogeny. The earlier stages observed were a zygote (FIG. 5A) and a nearly 20-celled proembryo which is rather irregularly organized (FIG. 5B). Perhaps the divisions do not correspond to any of the known types of embryogeny. From the globular stage onwards the embryo development is regular (FIGS. 5C–G) with a prominent suspensor and well demarcated protoderm. During late embryogeny periclinal divisions in the 6th or 7th subprotodermal layer begin the demarcation of the embryonal pith, procambium, and cortex in a globular proembryo (FIGS. 5H, I). The suspensor cells are filled with starch grains. In the oldest seed that we examined the embryo was at a pre-heart-shaped stage (FIGS. 5H–I). No more details could be obtained due to paucity of material.

Seed coat. At the megaspore mother cell stage the outer and inner integuments are 3-layered for the greater part of their length (FIG. 6A). During megasporogenesis brownish substances accumulate in some cells of both the integuments. Just after fertilization the cells of the outer integument and those of the inner epidermis of the inner integument at the micropylar region become packed with substances which stain dark red with safranin. Subsequently, the space between the outer and the inner integument becomes almost obliterated (FIG. 6B).

In a mature seed the testa is formed by the outer integument. The cells of the outer epidermis elongate radially, become thick walled, extremely hard, and packed with brownish contents (FIGS. 6C–E). Next to this are two layers of cells filled with tannin and the inner epidermis, which remains thin-walled with small nuclei and large vacuoles (FIG. 6C). The inner integument becomes almost crushed and is represented by one or two layers of compressed thin-walled parenchymatous cells.

An interesting feature is that in the mature seed the outer surface of

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sive endosperm at globular and post-globular stages of the embryo, respectively; I, part I in G enlarged to show a few cells of the endosperm which are densely cytoplasmic with prominent nuclei and filled with oval or globular particles; J, portion J in H enlarged to show a few endosperm cells, the cells are highly vacuolate and contain dark squarish particles of reserve food materials. A–C, × 550; D–F, × 440; G, H, × 30; I, J, × 360.

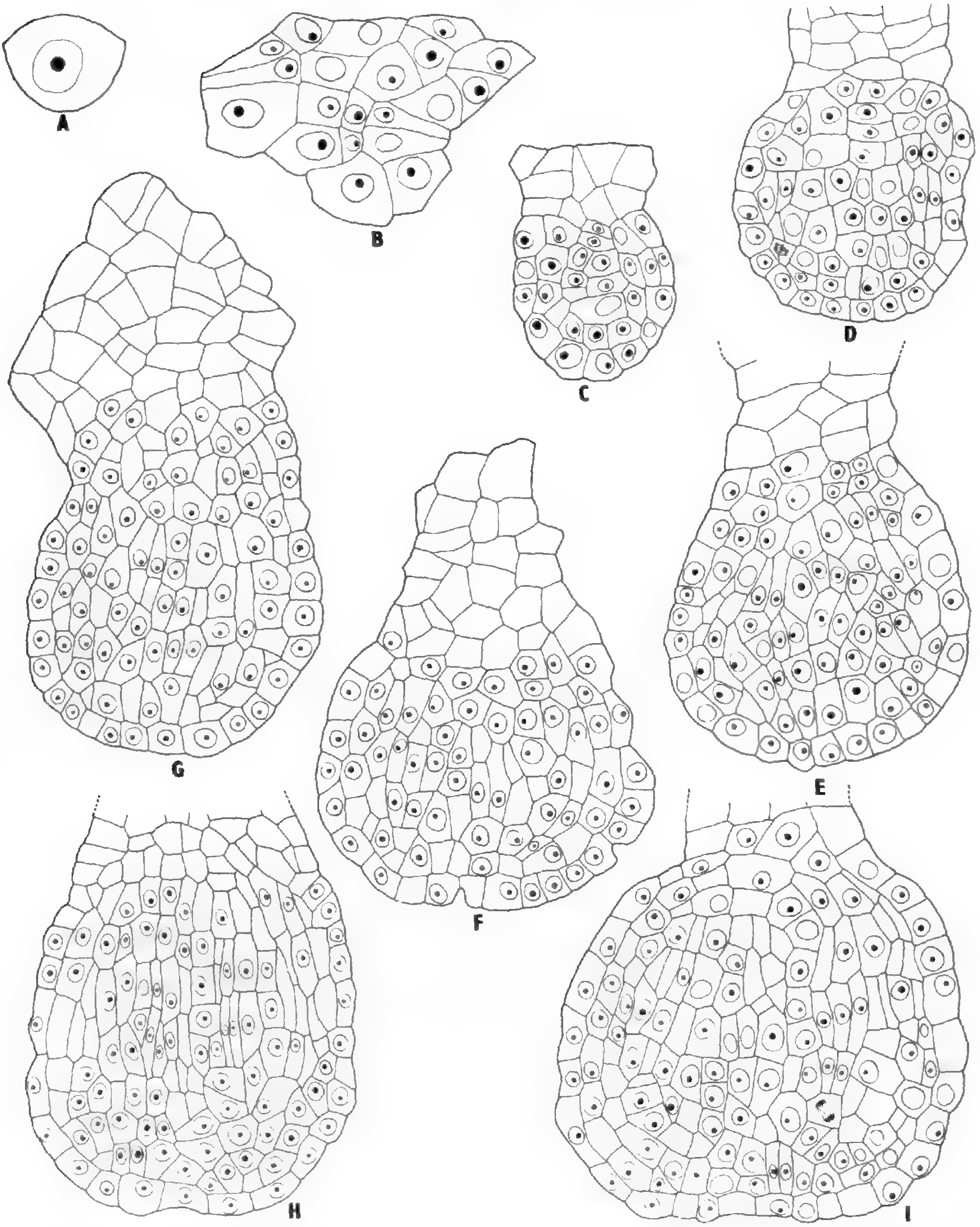

FIG. 5. *Drimys winteri*, embryogeny. A, zygote; B, an irregularly organized nearly 20-celled embryo; C–G, stages in the development of a globular embryo with a conspicuous suspensor; H, I, an undifferentiated heart-shaped embryo contained in a seed obtained from a mature fruit. A, B, × 600; C–G, × 325; H, I, × 265.

the seed coat is thrown into three or four ridges. The endosperm, however, is not ruminate (FIGS. 6D, E).

Pericarp. At the megaspore mother cell stage the ovary wall consists of ten to twelve layers of parenchymatous cells (FIG. 6F). Two or three inner and outer layers are filled with brownish phenolic compounds. Numerous ethereal oil cells having a vacuolated cytoplasm and prominent nuclei are interspersed within the pericarp (FIG. 6F). During post-fertilization stages the wall becomes 20- to 25-layered. The number of ethereal oil cells and tannin cells also increases (FIG. 6G). When the embryo is at the globular or post-globular stage the pericarp becomes nearly 30-layered and the outer and inner epidermis are greatly flattened. The number of tannin cells increases and they become completely filled with such substances. The parenchymatous cells become greatly stretched and break down (FIG. 6H). No meristematic activity of the pericarp as has been observed in *Pseudowintera* (Bhandari, 1963) is seen here.

DISCUSSION

Embryological observations on the Winteraceae are rather meager and are confined to *Drimys*, *Pseudowintera*, and *Zygogynum*. These are discussed in the light of the present work on *Drimys winteri*.

The anther tapetum is glandular in *Pseudowintera axillaris* (Sampson, 1963) and *Zygogynum* (Swamy, 1952) and amoeboid in *P. colorata* (Bhandari, 1963). Bhagavathi Kutti Amma's (1938) report of amoeboid tapetum in *Drimys* is doubtful since the present investigation has clearly established its glandular nature. In *Zygogynum* the nuclei in the tapetal cells divide and fuse to become polyploid but in *Pseudowintera* they remain binucleate. In *Drimys*, however, the tapetum becomes irregularly bi-layered with binucleate cells which often become polyploid.

In *Zygogynum baillonii* (Swamy, 1952) a centripetal furrow is formed after Meiosis I. Rarely an incipient equatorial cell-plate is also laid down at the end of heterotypic division but quadripartitioning of the microspores is completed only after homotypic division. Contrary to this, in *Pseudowintera colorata* (Bhandari, 1963) the division is simultaneous without any evanescent cell-plate while in *P. axillaris* (Sampson, 1963) and *Drimys* (present investigations) it is formed after Telophase I. The phylogenetic implication of the presence of such an evanescent cell-plate in these and some other primitive genera (*Magnolia*, cf. Farr, 1918) is not clear, although it might perhaps represent the relics of an ancestral feature. The pollen grains are monoporate and are shed at the 2-celled stage. The generative cell is cut off towards the proximal end. In *Zygogynum* (Swamy, 1952) and *Pseudowintera colorata* (Bhandari, 1963) the divisions of the microspore nucleus in a tetrad are simultaneous. In *Pseudowintera axillaris* (Sampson, 1963) and *Drimys winteri* (present report) the microspores in the same tetrad show different stages of division.

The embryo sac is of the Polygonum type in all three genera. The synergids and antipodal cells degenerate soon after fertilization in *Zygogynum* (Swamy, 1952) but in *Pseudowintera colorata* (Bhandari, 1963) and *Drimys winteri* (present work) they persist for a few divisions of the endosperm. A twin embryo sac has been observed in *D. winteri* (present work).

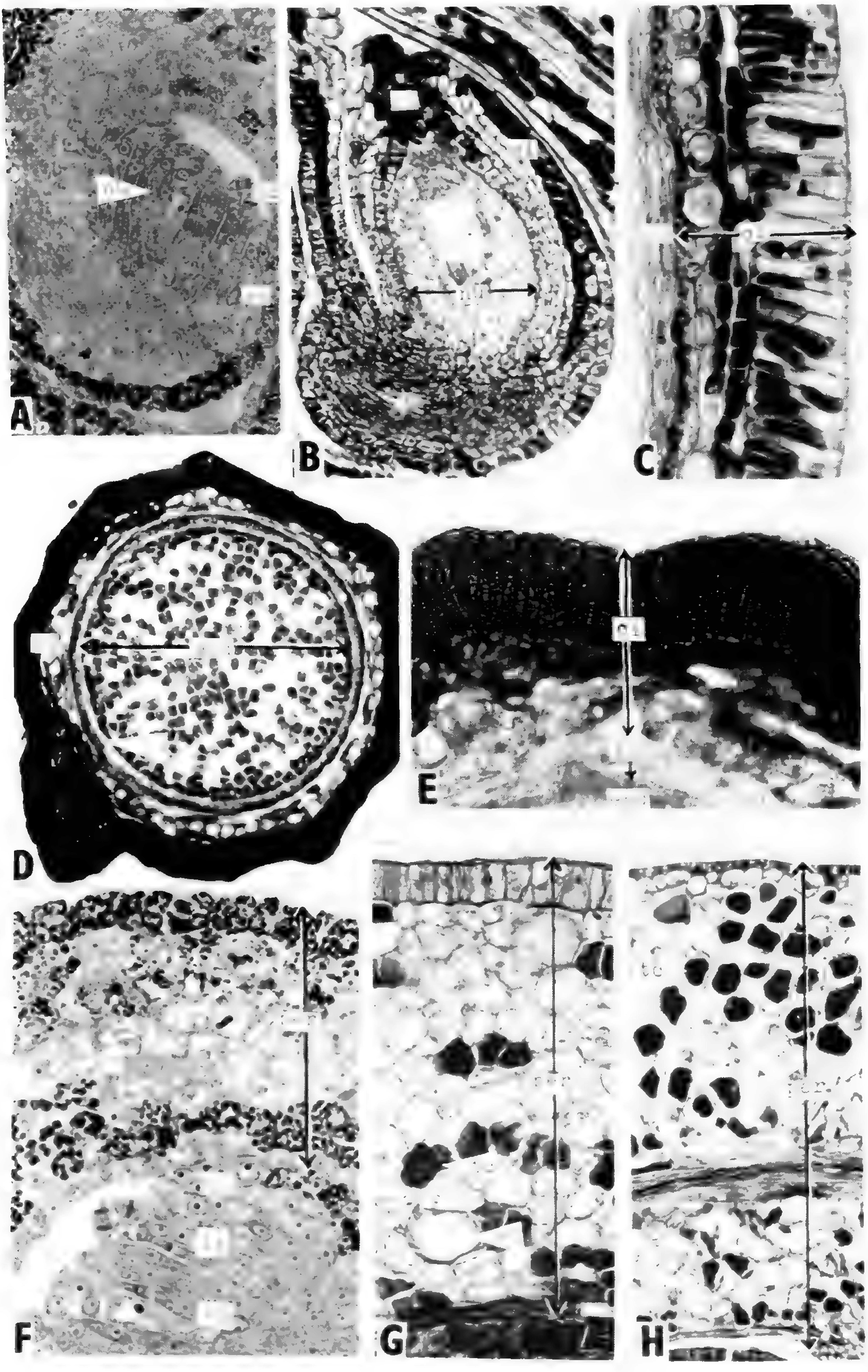

FIG. 6. *Drimys winteri*, seed coat and pericarp (ec, ethereal oil cells; end, endosperm; ii, inner integument; ie, inner epidermis; nu, nucellus; oi, outer integument; per, pericarp; tc, tannin cells). A, longisection of ovule at mega-

Triple fusion precedes syngamy in *Pseudowintera colorata* (Bhandari, 1963) and *Drimys winteri* (present work). In *Zygogynum baillonii* (Swamy, 1952), *P. colorata* (Bhandari, 1963) and *Drimys winteri* (present work) the endosperm is cellular. The division of the primary endosperm nucleus is invariably transverse in *Zygogynum* (Swamy, 1952), but may be transverse or longitudinal in *P. colorata* (Bhandari, 1963). In *D. winteri*, Strasburger (1905) reported nuclear endosperm. A reinvestigation (present observations) of this species, however, has shown this to be erroneous. The endosperm, therefore, is *ab initio* cellular in all the genera so far investigated.

The present investigation is the only record of embryogeny indicating that the earlier divisions of the developing embryo are irregular. However, from the globular stage onwards the development is regular. In *Pseudowintera colorata* (Bhandari, 1963) the embryo is dicotyledonous but in *Drimys winteri* it remains undifferentiated.

In *Pseudowintera colorata* (Bhandari, 1963) and *Drimys* (present work) the seed coat is formed by elongated tannin-filled cells of the outer epidermis, along with two or three hypodermal layers of thick-walled cells of the outer integument. In *Drimys*, however, (present work) the outer epidermis of the outer integument is variously ridged.

The pericarp is composed of 20 to 25 layers of parenchymatous cells with interspersed ethereal oil cells in both *Pseudowintera colorata* (Bhandari, 1963) and *Drimys* (present work). In *P. colorata* the unilocular ovary becomes chambered during the maturation of fruit because of meristematic activity of pericarp between the ovules. No such meristematic activity has been observed in any other winteraceous member.

Systematic position. Bentham and Hooker (1862–67) included *Drimys* together with *Illicium* in the tribe Wintereae of the Magnoliaceae.

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spore mother cell stage to show the two integuments which are 3- or 4-layered; B, *same* at the zygote stage, the outer integument is 4-layered at the tip and 5-layered below with outermost 2 layers completely filled with tannin, inner is 5- or 6-layered only in the micropylar region, these cells are packed with tannin; C, a magnified part of the seed coat at the preglobular stage of the embryo, the outer integument has elongated cells completely filled with tannin, the innermost layer consists of large parenchymatous cells, the inner integument persists as a thin layer of compressed parenchymatous cells; D, transection of mature seed to show the ridges on the hard seed coat (hand section); these ridges are restricted only to the outer epidermis of the outer integument; E, a part of D magnified to show the details of the seed coat; F, transection of a carpel at the megaspore mother cell stage of the ovule showing the 10 to 12 parenchymatous layers of the pericarp, the outer and the inner two or three layers are filled with tannin; a few ethereal oil cells are also seen; G, a magnified part of transection of post-fertilized carpel, the pericarp is 15 or 16 layers thick, the epidermal cells are radially elongated and prominent, a number of tannin cells and ethereal oil cells are interspersed in the rest of the parenchymatous tissue; H, *same* at the globular stage of embryo, the outer and the inner epidermal layers are compressed, between these are 20 to 25 layers of parenchymatous cells with numerous tannin cells and empty ethereal oil cells. A, × 225; B, × 100; C, × 110; D, × 100; E, × 200; F, × 435; G, × 140; H, × 35.

Van Tieghem (1900) grouped all the members with vesselless xylem under Homoxylées. He placed five winteraceous genera (*Drimys*, *Bubbia*, *Belliolum*, *Exospermum* and *Zygogynum*) in this group whereas Dandy (1933) later added the sixth genus, *Pseudowintera*, from New Zealand. Barkley (1966) has recognized three more genera, namely, *Tetrathalamus*, *Wintera*, and *Lassonia* in this family but includes *Belliolum* with *Drimys*. Hutchinson (1959), too, considers *Tetrathalamus* a distinct genus of the Winteraceae although Smith (1943) merges this genus with *Bubbia* as *B. montana*. Embryological information on *Tetrathalamus*, *Lassonia* (=*Magnolia*, see Willis, 1966) and *Wintera* is wanting and any consideration regarding their taxonomic position must await such data.

Hutchinson (1959) also believes that *Degeneria* is related to *Exospermum* and *Zygogynum* and should, therefore, be included in the Winteraceae. Bhandari (1963) has compared the embryological features of the Winteraceae and *Degeneria* and supported the conclusions of Bailey and Smith (1942) that *Degeneria* be assigned to a separate family, the Degeneriaceae. However, no light has yet been thrown, embryologically, on the relationship of Winteraceae with the Illiciaceae. The morphological and embryological characters of these families are compared in the following table:

Table 1

	WINTERACEAE	ILLICIACEAE
HABIT	Trees and shrubs.	Shrubs and trees.
*WOOD ANATOMY	Vesselless, heterogeneous ray structure. Tracheary pitting scalariform.	Vessels present, multiseriate ray structure. Tracheary pitting scalariform to opposite.
*NODAL ANATOMY	Trilacunar.	Unilacunar, single-traced
FLOWERS	Actinomorphic to zygomorphic, bisexual or unisexual, hypogynous.	Actinomorphic, bisexual, hypogynous.
*CALYX	Calyptrate; sepals bract-like, connate.	No differentiation into calyx and corolla; tepals numerous.
*COROLLA	Petaloid to scale-like, reduction from many to 2.	
*ANTHER	Microsporangia subterminal, or lateral, protuberant or embedded.	Microsporangia lateral, protuberant.
*ENDOTHECIUM	Endothecium extends towards the connective region.	Endothecium does not extend towards connective region.

* Points of difference.

Table 1. (*Continued*)

*TAPETUM	Amoeboid or secretory, cells binucleate, parietal in origin.	Glandular, irregularly 2-layered, cells binucleate, originates from sporogenous tissue.
TETRADS	Tetrahedral, tetragonal, or decussate.	Tetrahedral.
*POLLEN GRAINS	In permanent tetrads, monoporate, generative cell cut off at proximal end, intine comes out of the germ pore.	Individual, tricolpate, isopolar.
*CARPEL	Open or closed, conduplicate, sessile or stipitate.	Closed, sessile.
OVULE	Anatropous, bitegmic, crassinucellate.	Anatropous, bitegmic, crassinucellate.
FEMALE GAMETOPHYTE	Polygonum type, antipodals degenerate after fertilization.	Polygonum type, antipodals ephemeral.
ENDOSPERM	Cellular.	Cellular or nuclear?
*EMBRYOGENY	Irregular.	Asterad type.

* Points of difference.

It is clear from the above Table that *Illicium* differs from *Drimys* and allied genera in numerous embryological and morphological features which negate its relationship with the Winteraceae and support its inclusion in a separate family, the Illiciaceae (cf. Eames, 1961; Hayashi, 1960, 1963; Kapil & Bhandari, 1964; Smith, 1947). However, at the same time it has certain features which indicate its ranalian affinities.

We are grateful to the late Professor P. Maheshwari F.R.S. for suggesting the problem and procuring the material for us, to Professor B. M. Johri for his keen interest, and to Dr. A. C. Smith for reading the manuscript.

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THE DIRECTOR'S REPORT

THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1968

AN UNUSUAL early and temperate spring season produced a spectacular flowering display, and the living collections were particularly beautiful, drawing larger numbers of visitors than have been seen in the experience of the current staff. Spring, 1968, can be considered one of those rare and enjoyable spring seasons in New England which permit the public to enjoy the grounds to their fullest and the staff to make observations through long periods of flowering. The lilacs, for example, were at their best for two weeks from May 12 to 25, while last year the short and belated display period occurred between June 3 and 10. In contrast was the unexplained severity of winter damage to many plants in the nursery areas. Severe losses of young plants occurred in January when a normally adequate snow cover was on the ground. The same pattern was also seen in commercial nurseries and on private grounds throughout the northeastern part of the United States, with the most severe losses of plant materials occurring in areas on Cape Cod.

An item of major construction completed during the year was the new garage and storage building for mechanical equipment used on the grounds. Ever since the construction of the herbarium addition to the Administration Building in 1905, mechanical equipment and tools had been kept in the basement, with access through a narrow ramp. Although in earlier days the grass in the Arboretum was permitted to mature and was, in fact, cut by scythe and stacked in mounds, in recent years mowing has been a continuous operation through the growing season, and the cut grass has been retained as a mulch. The tractor-drawn mowers and similar power devices to cut grass or to care for the living collections fitted like pieces of a jig-saw puzzle in the basement. With funds accumulated from the bequest of Martha Dana Mercer a new garage was planned and constructed and was officially accepted on March 1, 1968. Built into a bank area, the one-story structure, 44 by 105 feet, is of reinforced concrete faced with brick. Adequate storage at ground level for all vehicles and grounds equipment is supplemented with special storage rooms for parts, tools, fertilizers, and sprays. Four electrically operated overhead metal doors permit easier access. The $145,000 budget for this building included a grease pit, overhead lift, 1000-gallon gasoline storage tank, and additional essential equipment, such as a hydraulic press, steam cleaner, air compressor, electric welder, and electric grinder. A paved parking area for twenty-one staff cars removes them from the front of the administration building and permits easier parking for visitors. The whole

The newly completed garage and vehicle-servicing facility constructed adjacent to the Administration Building. Climbing plants have been planted along the end walls of the building and near the fence and these will soon soften the lines of the addition.

garage area is enclosed by a chain-link fence topped by barbed wire. Nineteen different kinds of climbing plants have been started near the garage and along the fence to beautify the area.

Staff:

Again this year the Arboretum staff lost by death one of its valuable members. Dr. George Konstantin Brizicky died on June 15, 1968, after a heart attack. Dr. Brizicky joined the staff in 1960, initially on a joint appointment with the Gray Herbarium, and worked with Dr. Wood as a botanist on the *Generic Flora of the Southeastern United States*. His careful bibliographic and taxonomic work is exemplified in more than 80 scientific papers. His unusual career will be reviewed in a biographical sketch planned for a later issue of the Journal.

Two staff members retired at the end of the year: Mrs. Margaret C. Lefavour, as herbarium secretary, and Mr. Henry Draper, as superintendent of the Case Estates in Weston. New appointees will take their places, but it will be difficult to equal their loyal contributions to the development of the Arboretum during the years they have served on the staff.

Resignations were received from Mr. Andrey Baranov, Herbarium Assistant, who will do botanical consulting, and Dr. Harrison Flint, Associate Horticulturist, who will join the faculty of the Department of Horticulture of Purdue University.

New appointments to the staff included Dr. Paul Davidsen Sorensen, as Assistant Horticultural Taxonomist, and Mr. George Howard Pride as Associate Horticulturist. Dr. Beryl Simpson Vuilleumier was appointed as Botanist on the Flora of the Southeastern United States project. Mr. Thomas Matthew Kinahan, of the Arboretum grounds staff, was promoted to be Superintendent of the Case Estates.

The members of the staff serve the broad fields of systematic botany and horticulture in many ways, both nationally and internationally. These are often through various committees, and new assignments accepted during the year include the appointment of Dr. DeWolf to an advisory panel of the National Science Foundation; Mr. Fordham as chairman of the International Plant Propagators Society's committee to evaluate woody plant cultivars; Dr. Howard as chairman of the Plant Records Center Committee of the American Horticultural Society; Mr. Pride to the Garden and Grounds committee of Old Sturbridge Village; and Dr. Wyman to the Board of Directors of the Roxbury-Dorchester Beautification Project.

Dr. Howard was elected an honorary foreign member of the Royal Danish Academy of Science and Letters and the Honorary President-at-large of the Herb Society of America. He also received the distinguished citizen citation for 1968 issued by the Metropolitan Area Association of Warren, Ohio.

Horticulture:

The activities of the staff in the field of horticulture involve the maintenance and care of the living collections of woody plants; work in plant

The several planted terraces for genetic dwarf conifers below the slat house holding the *bonsai* collection. The Dana greenhouses appear in the background.

propagation; and the operation of nursery areas and display plantings established at the Case Estates in Weston.

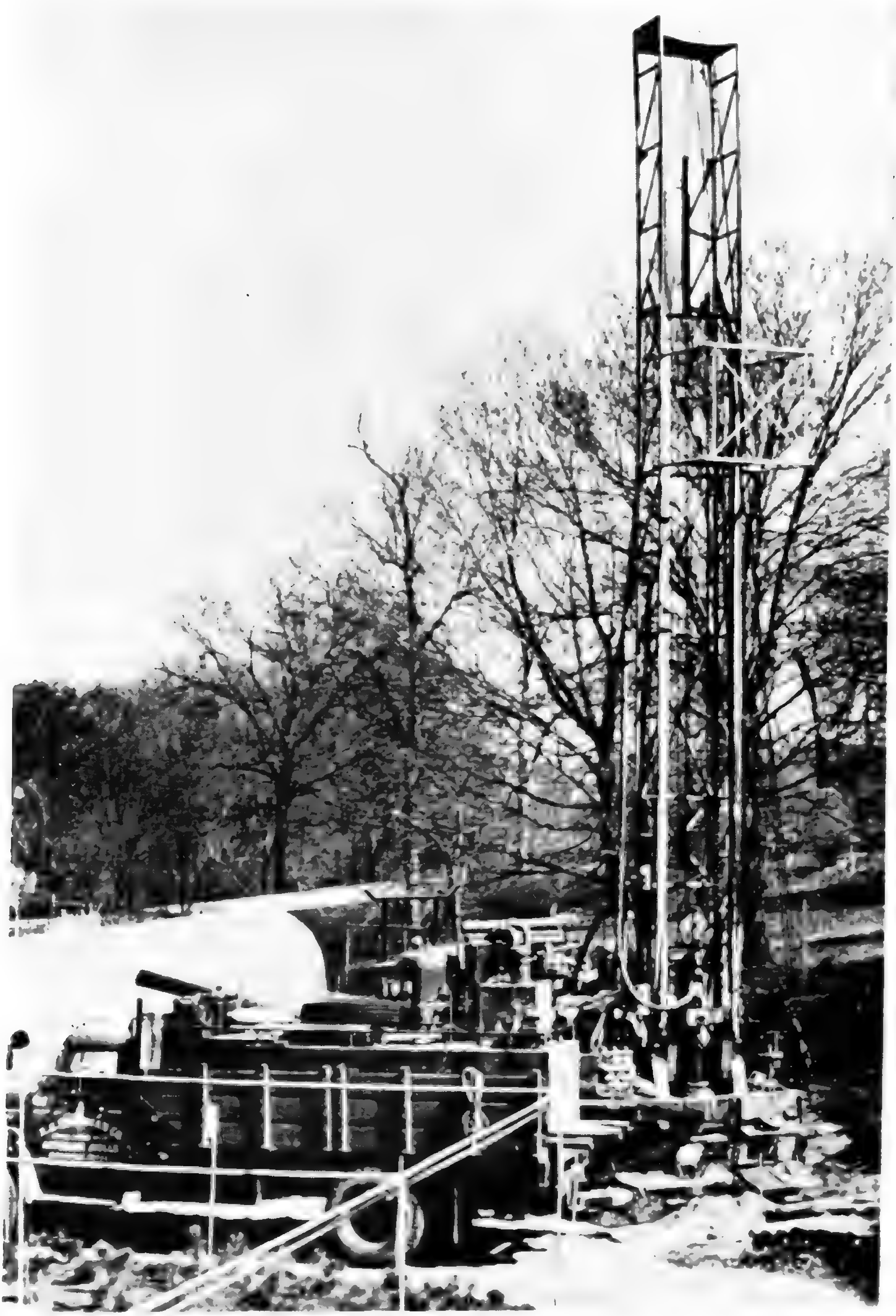
In Jamaica Plain, work continued on the old road bed along Centre Street recently acquired from the City of Boston. The road surfacing material was removed and replaced with soil and mulching materials. Grass was sown and some coniferous species planted. This area, although small, will permit an expansion of the pinetum and the development of attractive plantings of crab apples visible from the heavily travelled U.S. Route 1.

With construction of the new garage adjacent to the administration building, new entrances were constructed to the basement and to the first floor of the herbarium, the latter in association with a loading platform which will facilitate delivery of supplies. The ugly ramp to the basement was replaced with a bulkhead. The lawn in front of the building, which was ruined by the installation of water pipes and by the construction equipment, was completely renovated; it will soon look better than before.

The collection of genetic dwarf conifers was enlarged by the addition of 177 taxa planted on two additional levels of the terraces below the *bonsai* house. Around the nursery, the collection of ground cover plants especially suited for bank planting was increased by 24 taxa. During the fall and spring 375 taxa were added to the general collections of living plants.

Shortages of water during past years have had accompanying city restrictions on the outdoor use of water, even in our nursery areas. To counter this problem a well 115 feet deep was drilled this spring, with the pleasing result of a supply of 50 gallons per minute. This quantity will be sufficient to supply five sprinklers in the greenhouse area through the use of an electric pump and will be adequate for greenhouse and nursery needs during periods of future restrictions on city water. A new overhead irrigation sprinkler system was also installed by the staff for the nursery area. Included in the system is an automatic timing device permitting a sequence of watering in various areas and an intake system so liquid fertilizers can be applied through the water flow.

The work of the greenhouse staff includes a consideration of needed additions to our collections through seeds and the propagation of plants on the grounds needing replacements. During the year 401 taxa were propagated to prepare replacements for specimens which appeared to be failing or which were insufficiently represented within our collections. One hundred fifty-five shipments of plant materials, comprising 649 taxa, were received from the United States and nine other countries. Seeds of 339 taxa either for germination and addition to the collections, or for experimental studies in germination, or for staff research were included in 86 shipments from the United States and 25 other countries. Requests for materials, seeds, or propagating material from our collection were filled when possible. Although material which can be procured from commercial sources is rarely distributed in response to nonprofessional requests, legiti-



The well drilling operation adjacent to the greenhouses struck water at less than 100 feet. A flow of 50 gallons per minute will solve some watering problems in the nursery area.

mate requests for documented material are honored, and during the year 214 shipments of plant materials comprising 1146 taxa were sent to coöperating scientific institutions or nurseries or for individual research projects in 17 countries.

The program of distribution in a plant hardiness test begun last year by Dr. Flint was expanded this year with the coöperation of Mr. Fordham and the plant propagation staff. Twenty-five coöperating stations from western Massachusetts to Presque Isle, Maine, and areas in northern New Hampshire and Vermont were selected, and more than 1500 container-grown woody plants of 41 taxa were distributed. Uniform methods of culture have been suggested for these plants, as well as systematic observations which can be correlated to increase our knowledge of hardiness of species and of the nature of winter damage.

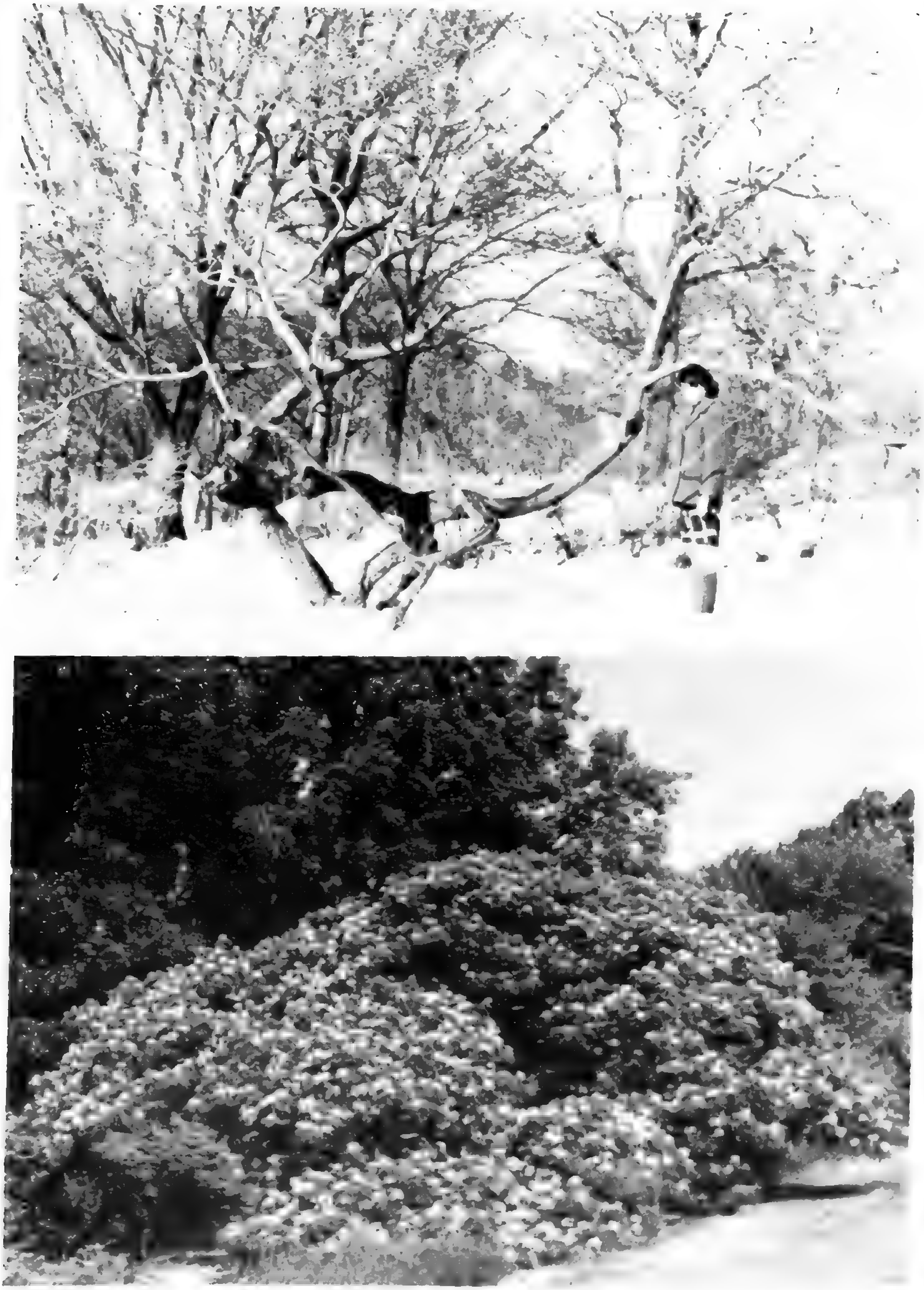
Surplus plants from the Arboretum nursery areas were given as usual to the Department of Buildings and Grounds at Harvard and to neighboring institutions in adjoining states. These materials correctly identified and properly labelled and documented increase the value of campus plantings as teaching aids to departments of botany and horticulture. We have also coöperated with the City of Boston in programs for beautification of depressed areas. Two truck loads of plants were given to the Roxbury-Dorchester Beautification Project, and over one thousand rhizomes of surplus *Iris* were made available for distribution.

Activity in the registration of new cultivars of woody plants continued during the year. A registration list of cultivars in *Lantana* is nearing completion, and progress is being made on one for *Philadelphus*. An issue of *Arnoldia* was devoted to the publication of new names submitted for registration. From our own collections *Albizia julibrissin* cultivar ERNEST WILSON, introduced from Korea by E. H. Wilson in 1918 and now considered to be sufficiently distinctive to merit formal recognition, was described.

The staff is also coöperating with a national committee in re-evaluating the species and cultivars of lilacs grown in the United States. After a three-year study the committee plans to reissue its analysis of "Lilacs for America," which was first published in 1953.

A mail survey of American colleges was conducted to determine the number of campus floras and the frequency of their documentation. Local lists prepared by taxonomists and properly documented by herbarium specimens can be used for information on the distribution and hardiness of cultivated taxa with greater reliability than can data obtained from nursery catalogues.

The staff is also coöperating with the American Horticultural Society in the establishment of a Plant Records Center. Dr. Howard serves as chairman of a committee which will coördinate the gathering of information on the holdings of various botanical gardens and arboreta. An ultimate goal is a data processing system permitting quick recovery of information on the source and location of important plant materials. No up-to-date system for the location of particular plants needed for scien-



Albizia julibrissin 'Ernest Wilson', a new cultivar status for an old tree. The hardiness in the New England climate and the spreading habit distinguish this selection from the more southern plants.

tific studies exists today. A grant to the American Horticultural Society from the Longwood Foundation will initiate this work. Administrative procedures are being worked out at the present time, with compilation of information to begin as soon as possible.

A program of collecting herbarium specimens from plants in the Arboretum collections which are the sources of type material is under way. Although such specimens exist in our own herbarium, the increased interest on the part of others in vouchers and the possibility of obtaining equally valuable material from other institutions makes this a project of particular value. When the size of the plant permits, twenty specimens are collected for future exchanges.

The research program of Dr. Owen Rogers, of the University of New Hampshire, as a Mercer Fellow during the past year is of special interest. His work during the spring involved controlled crosses of many taxa of *Syringa* using plants in the living collections and those from his plots in New Hampshire. Time is required for an analysis or evaluation of the seeds obtained and seedlings developed. It is of interest to record that, although many seeds were obtained from crosses of *Syringa velutina* and *S. meyeri*, only albino seedlings developed, a result similar to that obtained earlier by Karl Sax from crosses involving *Syringa pubescens*.

Case Estates:

The Case Estates, comprising 110 acres of land in the town of Weston, serve both as the nursery area for the Arboretum and for display plantings open to the public. The land also provides room for specimens which cannot be accommodated in the plantings in Jamaica Plain.

A generous gift of 575 *Rhododendron* seedlings and over 100 rooted cuttings of cultivars of *Ilex* was made by Mr. Josiah K. Lilly, III, of Sandwich, the owner of the Dexter Estate. These plants will be grown to larger size, tested for hardiness, and evaluated at the Case Estates.

Through the efforts of Mr. George Pride and members of the New England Wild Flower Society a collection of wild flowers also is being developed. Since the natural areas of the Case Estates are used by the public schools of Weston and are visited by many interested organizations, a small collection of wild flowers will enhance the educational value of this area.

The extensive collection of crab apples planted on the Newton Street tract flowered profusely this year, drawing the attention of commuters and visitors. An additional roadside planting on Wellesley street of 32 varieties of *Rhododendron* will add to the attractiveness of this land in the center of Weston.

Herbarium:

The problem of adequate space continues in the herbarium of spontaneous plants housed in Cambridge. The University is coöperating in a study of means of obtaining increased space either by the addition of a fifth floor to the present building or by the addition of a wing. Studies of space needs for laboratories, staff offices, and herbarium storage, and methods of financing construction are ahead.

A total of 31,750 specimens was mounted during the year and added to the herbarium, bringing the holdings to 881,730, of which 132,750 specimens are housed in Jamaica Plain and are from plants in cultivation.

These additions are from collections on hand from past years, and only in small part from those received during the current one. During 1967–1968, 13,234 specimens were received in exchange, 562 as gifts, 4,886 from the subsidy of expeditions, 4,118 from staff collections and 1,363 in exchange for identifications. These ranked in order of magnitude from Papuasia, the West Indies, Africa, Mexico and Central America, Western Malaysia, and the United States, with lesser numbers from the rest of the world. Our holdings from Africa are inadequate for reference and teaching purposes, and we value the coöperation of colleagues in Berlin and South Africa who have supplied selected African material. A total of 8,867 specimens was sent as exchange, with 112 additional ones sent for identification or as special gifts.

The combined herbaria of the Arnold Arboretum and the Gray Herbarium sent 18,050 specimens on loan for scientific studies. There were 168 loans to 84 institutions, 54 in the United States and 30 in 16 other countries, For our staff and students we borrowed 13,139 specimens in 80 loans from 35 institutions, 29 in the New World and 5 in the Old.

Herbarium specimens are borrowed for monographic studies or to aid floristic work. These represent the primary scientific studies of the systematic botanists on the Arboretum staff which are possible only with the use of a major herbarium and its supporting library. The resident staff and some of the Mercer Fellows have the advantage of these important collections in their work. Our materials are also consulted by numerous visiting scholars. Unfortunately, working space for these scientists is minimal, and additional work space and housing area for specimens and books must be provided in the very near future.

Although the published bibliography indicates the completed scientific contribution much significant work is in progress. The Southeastern Flora project under the supervision of Dr. Carroll Wood is financed by a grant from the National Science Foundation. Dr. Beryl Vuilleumier and the late Dr. George Brizicky have coöperated with him in the studies of plant families in this flora. Visiting collaborators appointed as Mercer Research Fellows during the past year have included Dr. John Thieret, of the University of Southwestern Louisiana, working on the Scrophulariaceae and Orobanchaceae; Dr. Robert Long, of the University of South Florida, the Acanthaceae; and Sister Mary Victoria Hayden, of Catherine Spalding College, genera of the Rubiaceae. An important paper on the genera of the Euphorbiaceae by Dr. Grady L. Webster, University of California, Davis, was published in the *Journal of the Arnold Arboretum*. Reflecting Dr. Webster's long-standing interest in this complex family, this account deals with many problems far beyond the geographic borders of the *Generic Flora*. Ten additional families are currently under study, by various botanists. Mention should also be made of the work of the artists associated with this project. Mrs. Sydney B. DeVore, who replaced Miss Rachel A. Wheeler during the year, is continuing the critical illustrations of genera. Each illustration is based on living or recently preserved material and represents an original study. Many genera are being illustrated for the first time. Errors in fact and interpretation which have been long perpetuated are revealed and corrected in the course of the art work. Detailed illustrations have been prepared for 205 genera of 105 families.

The staff wishes to express a special word of appreciation for the work of Dr. George Brizicky who died during the year. His fluency in Slavic languages was a particular asset to the project, for he was most generous with his time and assistance. At the time of his death Dr. Brizicky was working on the genera of the Malvaceae, and he had completed a manuscript on the general problem of subgeneric and sectional names, their starting points and early sources, subjects which had interested him for a number of years.

Dr. Thomas Hartley has continued his work in the identification of personal collections of plants made in Papua and New Guinea between 1961 and 1965. The 3700 numbers represent one of the largest recent collections from the area, and they are specially significant in supporting phytochemical studies. The final study will be a check list published in collaboration with chemists of the Commonwealth Scientific and Industrial Research Organization in Melbourne, Australia, documenting the chemical analyses which came from field and laboratory studies. Dr. Hartley's monographic studies in the family Rutaceae are continuing with an investigation of the genus *Flindersia*.

Dr. Howard completed the field studies of an elfin forest on the top of Pico del Oeste, in the Luquillo Mountains of eastern Puerto Rico. This project, supported by a grant from the National Science Foundation, was an ecological study of a peculiar environment and forest type. The collaboration of many scientists from other institutions made possible studies on the weather, soils, and root and anatomical characteristics of the vascular plants, as well as on the non-vascular plants. The study documents the unusually high and persistent humidity associated with a nearly continuous cloud cover and places greater significance on the air-borne moisture of clouds than on the prevailing winds. Studies of composition of the forest compared the frequency of species with the occupancy of the canopy surface and revealed that species infrequent in number in the total flora dominated the canopy. The unusual habits of constituent plants included the development of prop roots, as well as branched and unbranched aërial roots, the high frequency of long-shoot–short-shoot growth patterns, and a candelabra branching system, all of which contribute to the contorted stem structure and low growth aspect of the elfin forest. Since liverworts proved to be more abundant than mosses, the commonly used term "mossy forest" is a misnomer for this area. Algal studies by a collaborator showed an unexpectedly high number of species, not only on the ground, but on the trunks of the trees, in the gelatinous sheaths of adventitious roots, and in the liquid held by epiphytic bromeliads.

Chemical studies showed a low percentage of plants with alkaloids and related chemicals but an unexpectedly high number of plants containing chemicals showing biological activity in relation to animal tumors. The results of the study will be published in subsequent issues of this Journal.

Dr. Hu spent four months in the territory of Hong Kong developing her studies of the flora of that area. Her field work has greatly increased the collections of specimens including plants under cultivation in Hong Kong in our herbarium. The courtesies extended to her by the staffs of Chung Chi College and the Herbarium of the Urban Council and Urban Services Department, Hong Kong, are greatly appreciated.

Dr. Nevling, representing the staffs of both the Arnold Arboretum and Gray Herbarium, is participating actively in investigations on the vegetation of the state of Veracruz with Dr. Arturo Gómez-Pompa and members of the Instituto de Biología, Universidad Nacional Autónoma de México. Two field trips during the year permitted quick surveys and selected collecting of native and cultivated plants. The staff of the Instituto de Biología is continuing collecting efforts subsidized in part by the Arboretum. Dr. Nevling is assisting in the identification of specimens and in research necessarily based at Harvard's more complete libraries. This study continues the traditional interest of Harvard's botanists in the flora of Mexico. Dr. Nevling's monographic interests continue in the family Thymelaeaceae.

Dr. DeWolf and Mr. David Hall, a Mercer Fellow, are collaborating on a study of the genus *Ficus* in Venezuela for a national Flora of that country being prepared by the staff of the Instituto Botánico in Caracas. A similar treatment of *Ficus* in Suriname prepared by Dr. DeWolf will be published by the State University of Utrecht, Netherlands. Detailed studies of the misunderstood *Ficus dicranostyla*, a species of western and central Africa, have shown that this belongs to a small group of species the nearest member of which is restricted to a small area of northern Madagascar. This is an unusual distribution pattern for species of *Ficus*, but is another example of the phytogeographic patterns previously reported for other genera.

Dr. Schubert has worked towards completing floristic treatments for *Desmodium* and *Dioscorea*. Requests for accounts of *Desmodium* in the Galapagos islands, Texas, Panamá, and tropical East Africa are all associated with floras in preparation at other institutions. Her field work in Mexico has permitted a special investigation of several small-statured species of *Dioscorea* which have not been adequately represented by herbarium material.

Dr. Sorensen has continued his broadly based study on the genus *Dahlia* and is currently tracing the introduction of species into cultivation and their subsequent selection and breeding. Cytological work on plants grown at the Arnold Arboretum has yielded original chromosome counts for 16 species and hybrids. Coöperative phytochemical and anatomical studies of *Dahlia* materials are being undertaken by scientists from the University of California and the University of Massachusetts.

Miss Powell, in coöperation with Dr. Howard, has undertaken special historical studies of plant introductions to and from the West Indies. With the collaboration of Mrs. Brigid Sturrock, resident in St. Lucia, a renewed study of the plants of that island is under way. Studies of the phenology of plants from St. Lucia can be correlated with ecological studies based in Puerto Rico and St. Kitts.

Each of these staff projects demonstrates the unique contribution possible from a major herbarium and library of world wide concern.

Library:

The problem of available space for growth of collections referred to in connection with the herbarium is also of concern within the library. Studies for an addition to the Harvard University Herbaria building in Cambridge will involve the nature of growth and the increased use of the library collections. Currently, 90 per cent of the available shelf space is filled, which is beyond the recommended maximum of 70 to 85 per cent, the remaining unoccupied space being needed to avoid unnecessary shifting of books.

The library of the Arnold Arboretum grew by the addition of 491 volumes and 219 pamphlets and reprints to totals of 54,267 and 21,098, respectively, or a total holding of bound books and periodicals and unbound reprints and pamphlets of 75,365.

The regularly issued additions of the Gray Herbarium Index, the Index Nominum Genericorum, and the Torrey Index were filed. Thirty-six hundred sixty new catalog cards were added during the year, and the Rehder Index of important information on cultivated plants maintained in Jamaica Plain received an additional 625 cards. Until the end of last year reports of our holdings as duplicates of catalogue cards were sent to the National Union Catalog at the Library of Congress and to Widener's Union Catalog at Harvard. Now an additional record will be sent to the new undergraduate science library at Harvard, which will also hold general card indices.

Miss Sutton continues her work on the biography of Charles Sargent and on the cataloguing of manuscripts and letters of historical interest at the Arnold Arboretum.

During the year an inventory was made of the publications of the Arboretum, including the accumulations of reprints of articles by former staff members. The reprints were arranged in sets, and a list of these and available publications was prepared and distributed to libraries and members of the American Society of Plant Taxonomists. The collections of reprints offered at cost were quickly sold and the number of publications on hand significantly reduced, not only making the volumes available to interested persons, but freeing useful space.

Comparative Morphology:

The wood collection received normal curatorial care during the year.

Additional specimens of wood and slides were received, including sets of prepared slides associated with Project 1, School of Forest Resources of the North Carolina State University, a study of the woods of the United States. Requests for wood samples or for the loan of slides were handled when possible. Active use of the collections involved the work of Dr. William Theobald and Mrs. Helen Roca-Garcia in investigations on the woods, stems, and leaves of plants of the dwarfed forest on Pico del Oeste, Puerto Rico, while Dr. Alfred Linn Bogle continued his studies of the Hamamelidaceae and allied families.

Education:

No formal courses were taught in the Department of Biology by members of the Arboretum staff during the year, but active instruction to graduate students and participation in seminar programs continued as usual. Dr. Schubert conducted the seminar program in systematic botany during the fall term. Dr. Hartley again offered the Harvard University Extension Commission course in general botany.

Field courses were offered to Friends of the Arboretum during the fall by Dr. Wyman and by Mr. Pride, in Jamaica Plain and Weston, respectively. Mr. Fordham offered a discussion of methods of collecting and treating seeds of woody plants. During the winter a series of lectures on Caribbean botany was given at the Case Estates by Dr. Howard. The regular spring class in ornamental plants was offered by Dr. Wyman in Jamaica Plain, and Dr. Owen Rogers taught a class on hybridization and breeding of ornamental plants. Mr. Pride presented a course entitled "Beginning Botany for Gardeners" at Weston during the spring.

Staff members are frequently requested to speak to various organizations on the work of the Arnold Arboretum or on subjects of their research interests. A new brochure facilitates the handling of these requests. In addition, the staff participates in seminars and similar programs of other scientific organizations. Dr. Harrison, Mr. Fordham, and Mr. Williams all participated in the lecture discussions sponsored by the Massachusetts Horticultural Society during the annual spring flower show. Mr. Fordham also talked on the Members' Monday programs of that organization as well as at the Regional Meeting of the American Rhododendron Society, the Connecticut Nurserymen's Short Course, and the annual meeting of the International Plant Propagators Society. Dr. Flint spoke at the same meeting of the Plant Propagators Society and at the annual meeting of the Vermont Plantsmen's Association. Mr. Pride was on the winter program of the Worchester County Horticultural Society.

Dr. Howard was sponsored by the American Institute of Biological Sciences at the University of Maine for two talks. He appeared on the regular programs of the Pennsylvania Horticultural Society, the Barnes Arboretum, Connecticut Nurserymen's Short Course at the University of Connecticut, the Horticultural Society of New York, and gave seminar talks at the botany department of the University of Connecticut and at Clark University. He was the banquet speaker at the Clara B. Ford

Garden Forum in Michigan and the annual meeting of the American Association of Botanical Gardens and Arboreta at Hamilton, Ontario.

Dr. Wood participated in a two-day Science Seminar as part of the 125th anniversary celebration of Roanoke College in Salem, Virginia. He represented the field of biology on a panel including two chemists, a physicist and a mathematician. His talk on the subject of "Biology or Oblivion" commented on the population crisis and man's destruction of his environment.

Dr. Wyman spoke at meetings of the Garden Club Federation of Maine and the Massachusetts Garden Club Federation. He took part in the Longwood Gardens Symposium held jointly with the University of Delaware. He was on the program of the New York Botanical Garden and of the University of Georgia short course for nurserymen.

Again this year the Arboretum staff coöperated with the science teaching program in the elementary schools in Weston. The students were encouraged to study the plants and plantings of the Case Estates in Weston and to prepare competitive reports. The participants were divided into two groups: first prizes were awarded to Kenneth Leghorn and John Algird, with second and third prizes also cash awards; as honorable mention recognition, etchings were presented to each group. The prize papers concerned descriptions of the grounds, the plants or the activities there, an historical study of the Case family and the property, a special study of crab apples, one of the bristle-cone pine, and a report including a tape recording of the behavior of a family of grackles. The interest of the students and their parents resulted in larger attendance on the grounds and perhaps greater awareness and appreciation of the activities of the staff.

A special gift was received to establish an Arnold Arboretum Achievement Award for Botanical or Horticultural Excellence to be given to a student in a high school in Jamaica Plain. The award consists of a certificate, the student's selection of books of a stated value, and a gift from the Arboretum of a tree or shrub from the available duplicate plants within our nurseries. The first award was made to George B. Ransom, a senior in the Agricultural Department at the Jamaica Plain High School.

The Arboretum donated 10 units of plant material for the annual auction held by Channel 2, WGBH, Boston's educational television channel, to raise unrestricted funds for the station. Most of the plants offered for auction were unavailable through commercial sources and had been introduced and grown by the Arboretum. All plants drew bids in excess of the approximate commercial cost of such material. The commentators who offered the plants to the wide New England audience did justice to the Arboretum in their comments.

The staff coöperated with the Worcester County Horticultural Society and the Weston Garden Club in preparing and presenting two displays at the fall and spring flower shows of each organization. A display of mulch materials and berried or fruiting plants was prepared for Worcester, and an exhibit of methods of plant propagation and a collection of edible and poisonous wild plants of New England were offered at the Weston shows.

Travel and Exploration:

Members of the staff traveled less than usual during the year, although one trip was of extended duration. Dr. Hu spent four months in Hong Kong and offered lectures in plant taxonomy at Chung Chi College. She collected where possible in the territory from the coastal mangrove area at Tai Po Kau to the mountain vegetation at Ma An Shan. Dr. Nevling and Dr. Schubert made independent trips to Mexico, the former in association with the American Institute of Biological Sciences meetings in Texas and in coöperation with the University of Mexico. Mr. Pride visited Morocco, obtaining photographs of the vegetation, as well as seeds and specimens, and continued his trip to Teneriffe, Madeira, and "Les Cèdres" at Cap Ferrat, France. He visited gardens and established contacts for the Arboretum in each area. We are grateful for the many kindnesses and the hospitality extended to him during this trip by so many people, particularly Dr. Andres García Cabezon, Director, Jardín de Aclimatación de la Orotava; Mr. and Mrs. P. Graham Blandy; and Mr. and Mrs. Julien Marnier-Lapostolle.

The field study of the dwarfed mountain top forest in Puerto Rico enabled many staff members to take part for short periods of time and to learn of the tropical vegetation in the process or continue their own studies of taxa represented in that flora. Misses Powell and Sutton and Messrs. DeWolf, Nevling, Wyman, and Howard participated. Drs. Howard and Nevling visited a comparable site on the island of St. Kitts, where studies were made with the permission of the governor, Sir Fred Philipps, and the coöperation of Mr. Campbell Evelyn. En route from St. Kitts to Puerto Rico, they spent a short time on St. Thomas for observations on the dryland vegetation.

Dr. Flint visited research stations in Minnesota, North Dakota, and Manitoba in connection with his studies of plant hardiness.

The Arboretum has also been able to support the work of other botanists collecting in areas of particular interest to the staff or of value to our collections. The field work of Dr. L. Bernardi, of the Conservatoire Botanique, Geneva, Switzerland, extended from Madagascar through Malaysia and to New Caledonia where he is making botanical collections to be shared with us. More recently, the threat of the complete destruction of the vegetation on the inadequately known island of Anegada in the West Indies was called to our attention. A special gift permitted support of collecting in this area with the specimens to be identified and distributed by the Arboretum staff. As a comparable example, Dr. Wood collected material of *Drosera* in a unique bog on the Gaspé Peninsula in August, 1967. The bog has since been destroyed but the plants now growing in the Arboretum greenhouses represent at least three species, one of which appears to have originated by hybridization of the other two followed by chromosomal doubling. There are also back-cross hybrids with both parental species. Regrettably the botanist cannot act with sufficient speed and interest to stay ahead of the world wide destruction of essentially scientifically unknown plant material.

Gifts and Grants:

The many friends of the Arboretum renewed their support during the year with most gifts being without restrictions for use in the general work of the Arboretum. We were pleased to accept memorial gifts in honor of Mrs. John S. Ames and Mrs. Alice Hoagland and several gifts specified for the care of the *bonsai* and/or the genetic dwarf conifers.

Many persons have been generous in donating special plant materials, and we particularly value the collection of *Rosa* species and ecotypic material of *Rosa wichuraiana* from Mr. Seizo Suzuki and of *Rhododendron* and *Ilex* selections from Mr. Josiah K. Lilly, III.

A display case in the entrance hall of the Arnold Arboretum holds a collection of indian artifacts gathered from the grounds of the Arnold Arboretum by the late Ernest J. Palmer and by Alfred Fordham. Mr. Palmer bequeathed the collection to Mr. Fordham who has now officially given the display to the Arboretum. We are grateful for these evidences of former use of the land occupied by our collections.

Through the kindness of Dr. George T. Jones, of Oberlin College, the Arboretum received residual materials from the estate of Franklin P. Metcalfe, formerly of our staff. These included field books and numerical listings of his and other collections from China, as well as a smaller number of books of unusual historical interest.

Publications:

Dr. Bernice Schubert continued to edit the *Journal of the Arnold Arboretum* during the past year when four numbers, totalling 675 pages and including 20 articles, were issued. Dr. Harrison Flint served as editor of *Arnoldia*, which comprised 9 issues, totalling 91 pages.

The early volumes of the *Journal of the Arnold Arboretum* have long been out of print, as have several numbers of more recent dates. The Kraus Reprint Company, of New York, has been authorized to reproduce back issues and now volumes 1 to 20 of the *Journal of the Arnold Arboretum* are available in the reprint edition and volumes 21–40 are being prepared for reprinting.

Mercer Fellows:

The appointment of Mercer Fellows to the staff of the Arnold Arboretum was begun in 1961 following Mrs. Martha Dana Mercer's bequest to the Arboretum. Individuals are selected from candidates who request consideration for support of their program of work or study of the Arboretum collections or with the staff. As the awards have been made in the past no academic credit is given, but Fellows may audit Harvard classes with permission of the particular instructor and have full access to libraries, collections, and receive other benefits. Recipients have been at all academic levels, from those without college background to postdoctoral scholars and those on sabbatical leaves from their home institutions. Mercer Fellowships have been awarded to scholars from Argentina, Belgium, England, Finland, Jamaica, Mexico, the Philippines, South Africa, and the United States.

The largest number of short term appointments to date was made during 1967–1968. Recipients of Mercer Fellowships for all or part of the past year and their fields of interest are indicated below.

ARTHUR CHARLES GIBSON, Miami University (Systematic botany).
MAXINE GLICKMAN, Stockbridge School, University of Massachusetts (Horticulture).
DAVID W. HALL, University of Florida (Systematic botany).
SISTER MARY VICTORIA HAYDEN, Catherine Spalding College (Systematic botany).
SYED MOHAMMED ANWARD KAZMI, Peshawar University, Pakistan (Systematic botany).
ROBERT WILLIAM LONG, University of South Florida (Systematic botany and floristics).
JOHN O'CONNOR, Wolverhampton, Technical Teachers College, England (Plant propagation).
FREDERICK E. ROBERTS, University of Connecticut (Horticulture).
OWEN MAURICE ROGERS, University of New Hampshire (Cytology and cytogenetics).
ARLON LEE SLAGH, Michigan State University (Horticulture).
JOHN WILLIAM THIERET, University of Southwestern Louisiana (Systematic botany).

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† Died June 15, 1968.
* Appointed jointly with the Gray Herbarium.
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