

THE MORPHOLOGY AND RELATIONSHIPS OF THE CHLORANTHACEAE

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With three plates and sixty-four text-figures

INTRODUCTION

THE RECENT DISCOVERY of the retention of a primitive, vesselless xylem in *Chloranthus glaber* (Thunb.) Makino (= *C. brachystachys* Bl.) and *C. hainanensis* P'ei, of the Chloranthaceae raised the question whether these plants actually belong in the typically vessel-bearing genus *Chloranthus*. A totality of evidence obtained from a study of stem, node, leaf, bark, flower, pollen, etc., of the putative species of the genus strongly warranted the resurrection of the genus *Sarcandra* Gardn. to accommodate the two vesselless species (Swamy and Bailey, 1950). A detailed and intensive comparative study of the family Chloranthaceae as a whole has become necessary in order to determine whether *Sarcandra* should be retained within the family or excluded from it. Such an investigation is also very desirable for a clearer understanding of the relationships of the Chloranthaceae and its presumed allies.

With the segregation of the vesselless species in the genus *Sarcandra*, the family is at present constituted of three other genera — *Chloranthus*, *Ascarina*, and *Hedyosmum*. Herbarium specimens of 12 out of the nearly 16 species of *Chloranthus*, all 10 species of *Ascarina*, and 37 out of the approximately 45 species of *Hedyosmum* have provided material for observations on the early formed secondary xylem, bark, pith, node, leaf, floral structure, and pollen. Old wood samples of five species and nine collections of *Ascarina*, and of 20 species and nearly 40 collections of *Hedyosmum* were available for study.

A summation of morphological and anatomical data obtained through a careful re-examination of the type specimens indicates that *Chloranthus kiangsiensis* Metcalf and *Ascarina alticola* Schlechter should be excluded not only from the respective genera, but also from the family, and so these two species have not been considered in the present account. Detailed observations and arguments that have prompted the dissociation of the two plants from the Chloranthaceae will be presented in subsequent contributions.

A perusal of the literature reveals that the interests of earlier investigators on the anatomy of chloranthaceous plants were casual. Most of the accounts contain meagre references to only a few minor aspects of anatomy, and lack a comprehensive outlook. Solereder (1899) has brought together the salient observations of these authors, adding some of his own, in his admirable treatise, "Systematische Anatomie der Dicotyledonen." The

only important contribution subsequent to this publication is the observations of Thierry (1912), which are primarily concerned with the description of histological details of some species of *Chloranthus*, *Ascarina*, and *Hedyosmum*.

I am indebted to the following institutions for their cordial cooperation in sending herbarium specimens on loan: Arnold Arboretum and Gray Herbarium, of Harvard University, New York Botanical Garden, University of California (Berkeley), United States National Herbarium, and the Royal Botanic Gardens of Indonesia, Bogor, Java. To Drs. Robert W. Hess of Yale University, Theodore Just of the Chicago Museum of Natural History, and Mr. W. N. Watkins of the Smithsonian Institution, Washington, D.C., I am obliged for their courtesy in sending me cuttings of mature wood specimens from their respective collections.

It was a rare privilege to me to have initiated studies on the comparative morphology and relationships of ranalian families under the inspiring guidance of Prof. Irving W. Bailey of Harvard University. I have been greatly benefited by his stimulating discussions, cooperation and understanding. I am deeply grateful to him for the unending encouragement that I have been receiving from him.

I also wish to express my gratitude to the National Institute of Sciences of India, Prof. T. S. Sadasivan, and the Madras University for giving me opportunities to pursue this and other investigations.

VEGETATIVE STRUCTURES

Xylem: The outcome of surveys of anatomical characters of the xylary tissues of dicotyledons as a whole during the past 35 years clearly demonstrates, among other significant conclusions, that a complete series of stages in the origin and trends of specialization of vessels from a primitive vesselless condition are preserved in the representatives of extant floras, and that certain families or groups exhibit specific ranges of successive phylogenetic stages. Thus, families like the Monimiaceae and Icacinaceae provide an unusually wide spread of such stages, whereas some others show only specific restricted parts of the gamut. The family Chloranthaceae illustrates one such restricted part of the series — initial steps in the organization of vessels.

The genus *Sarcandra* (Swamy and Bailey, 1950; Swamy, 1953a) has preserved a type of vesselless xylem derived from a primitive cambium. The fusiform initials are pronouncedly elongated in a vertical direction and possess extensively overlapping ends. The fusiform cambial initials and their derivatives are nearly 2 mm. long during the fourth year's growth, and as may be seen in transections, conform to a relatively undisturbed radial seriation as in other living representatives of vesselless dicotyledons. The inter-tracheary pitting is confined to the radial facets and is typically uniseriate scalariform in the later formed elements of the primary xylem. A similar type of pitting occurs in the tracheids of the earlier formed secondary xylem of the first year and also in the first formed ones (about

three to five rows) of succeeding years. The remaining tracheids of the secondary xylem exhibit transitions to, and establishment of, uniseriate circular bordered pitting. The vascular rays are of two kinds, (i) uniseriate rays in the intra-fascicular parts, and (ii) multiseriate rays (four to five cells wide) radiating from the inter-fascicular parts of the primary xylem. Both kinds of rays are vertically extensive, and their constituent cells are elongated and upright. Wood parenchyma is distributed in a diffuse pattern and on the whole is rather scantily developed; it may be almost absent in some specimens.

The other genera of the family are all vessel-bearing. The majority of species of *Chloranthus* are perennial or annual herbs, only *C. officinalis* and *C. spicatus* being somewhat suffrutescent and having a vascular cylinder of three or four year's growth. *Ascarina* and *Hedyosmum* are generally large woody shrubs, often growing to the size of small trees. The tracheary elements of the metaxylem region of all the species of *Chloranthus* are very long and possess exclusively uniseriate scalariform pit-pairs on the lateral walls as well as on the steeply tapering overlapping facets. The pit-pairs retain full borders and pit membranes, that is, the pits are imperforate, and the cells typically tracheids. This character of the metaxylem in the vessel-bearing species of *Chloranthus* recalls that of the vesselless *Sarcandra*.

The primary xylem of *Ascarina* and *Hedyosmum* presents a more advanced evolutionary level than that of *Chloranthus*. The specialization pertains to the dissolution of pit membrane and to the complete elimination of the borders of pit-pairs that are distributed on the deeply inclined facets of the metaxylem elements. These changes result in the development of vessel members possessing pronouncedly inclined perforated facets with numerous slender transverse scalariform bars.

The tracheary derivative tissues of the cambium in the suffrutescent species of *Chloranthus* exemplify early steps in the organization of a vessel-bearing xylem, although the type of vessel-ray pitting indicates certain obviously precocious modifications as will be explained later. In conformity with the highly significant conclusion of Bailey (1944), the development of vessel-bearing xylem is promptly accompanied by an appreciable reduction in the length of vessel members as compared with that of their phylogenetically ancestral tracheids. It is obvious that the shortening of vessel members must have been foreshadowed in the fusiform initials of the cambium itself. The following measurements* of tracheary cells of the genera of the Chloranthaceae as given in TABLE I illustrate the point.

The vessels of *Chloranthus* are relatively long and possess extensively overlapping ends. The steeply inclined end walls of vessels bear very numerous (100–150) scalariform perforations that retain full borders

* The measurements were obtained where possible from cells in the 4th year's zone of growth. The oldest available specimens of *Sarcandra* and *Chloranthus* show a growth of about five years. In order to render the results comparable, figures for *Ascarina* and *Hedyosmum* were obtained from equivalent numbers of specimens of corresponding age.

Table I showing the average length of tracheids and vessel members

GENERA	AVERAGE LENGTH OF TRACHEIDS IN MICRA	AVERAGE LENGTH OF VESSEL MEMBERS IN MICRA
<i>Sarcandra</i>	1986	—
<i>Chloranthus</i>	922	856
<i>Ascarina</i>	954	823
<i>Hedyosmum</i>	947	834

(PLATE III, FIG. 9). The lumen of the vessels is only slightly larger than that of the tracheids in cross-sectional area and the outline conforms generally to that of a rectangle with slightly longer radial diameter and somewhat arched radial walls as seen in transection. The relatively undisturbed radial alignment of tracheary cells as in *Sarcandra* and other vesselless dicotyledons becomes less regular in the vessel-bearing *Chloranthus*, especially in the neighborhood of vessels, possibly due, among other factors, to the increase in the cross-sectional area of the vessel members however little it may be. The wood is typically diffuse porous (PLATE I, FIG. 2). The inter-vascular pit-pairs are extremely rare, due to the isolated distribution of vessels; however, in exceptional cases two longitudinal series of vessels do contact each other and the pitting on such walls is characteristically of the uniseriate scalariform type. The pit-pairs are large and retain full borders. When the radial wall of a vessel lies in contact with ray cells, the scalariform pits "break up" into circular bordered ones, and align themselves in two or three longitudinal series on the contacting facet. The pit-pairs are half-bordered, the overhanging secondary wall (constituting the pit border) having been retained by the vessel. The ray system closely parallels the condition of *Sarcandra*. However, the multiseriate rays of *Chloranthus* are less extensive vertically and the ends taper into one- to three-seriate "wings" as seen in tangisections. The constituent cells of the rays fluctuate in form from upright with narrow tangential diameter to almost cubical dimensions. The uniseriate rays consist exclusively of upright cells. The scantily developed parenchyma is apotracheal and occurs in a diffuse fashion. With the acquisition of a vessel-bearing xylem, the imperforate tracheary elements show a rather sudden morphological change. This consists in the development of pit-pairs on the tangential, as well as the radial, walls. The tracheidal wall in *Chloranthus* is slightly thicker than that of the vessel members, and circular bordered pit-pairs are scattered in a single series on all four longitudinal facets, although the number of pits per unit area is considerably greater on the radial walls. The pit aperture is largely "included," only occasionally extending beyond the limits of the border, which perhaps is due to the helical cracking of the secondary wall along the aperture. The over-all characters of the imperforate tracheary cells lean more toward that of a

fibre-tracheid, and this opinion is reinforced by the fact that a large percentage of the cells are septate.

The secondary xylem of *Ascarina* and *Hedyosmum*, as in the case of the primary xylem of these genera, shows slightly but definitely advanced trends of structural specialization over *Chloranthus*. Although the tracheary derivatives of the cambium tend to be nearly as long as those of the latter genus (see TABLE I), the vessels exhibit certain specific evolutionary modifications. Thus, the perforate tracheary cells of *Ascarina* and *Hedyosmum* exhibit conspicuously larger cross-sectional areas than those of *Chloranthus*. As between *Ascarina* and *Hedyosmum*, the latter genus exhibits a pronounced tendency to undergo a greater degree of radial and tangential expansion during ontogeny (TABLE II). The vessels of both of the genera possess relatively thin walls and those of *Ascarina* retain a

Table II showing the average cross-sectional area of vessels in square micra from comparable specimens

GENERA	4 YEARS OLD	10-15 YEARS OLD
<i>Chloranthus</i>	960	—
<i>Ascarina</i>	2640	3440
<i>Hedyosmum</i>	3420	16200

rather conspicuously angular outline in cross-section, while in *Hedyosmum* the contour is nearly circular or oval (PLATE I, FIGS. 1, 3). The pores in the earlier formed part of secondary xylem of both genera occur generally in radial chains, which arrangement soon shifts over to the diffuse porous type during subsequent ontogenetic stages. In the later formed secondary xylem of *Hedyosmum nutans* (PLATE I, FIG. 3) and *H. glabratum*, the pores sometimes exhibit a grouping in short radially oriented series and in that of *H. scabrum* in clusters of three or four. The perforated facets extensively overlap and contain very numerous (150-200) scalariform perforations that are totally devoid of borders; the intervening bars are rather tenuous (PLATE III, FIG. 8). The intervacular pitting (very rare in *Ascarina*) fluctuates between uniseriate scalariform (occasional) and transitional and opposite (frequent), the ratio of each type being variable often on the facets of a single cell; so also the size, shape, and degree of retention of the borders of pit-pairs. The vessel-ray and vessel-parenchyma pit-pairs present a similar range of form and distribution; the individual pit-pairs have reduced borders and are relatively widely spaced.

The ray systems of *Ascarina* and *Hedyosmum* belong to the same fundamental category — the so-called heterogeneous type I — as in the other genera already described. However, the two arborescent genera under consideration exhibit slightly divergent trends in ontogenetic sequences. In the earlier formed secondary xylem of *Ascarina* the uniseriate and multi-seriate rays (3-4 cells wide) are distinctly visible and the constituent cells are upright, although the average height of the cells composing the multi-

seriate rays is slightly lower than that of the uniseriate ones (PLATE II, FIG. 4). During later stages of ontogeny, the multiseriate rays widen (10–12 cells) * and the constituent cells attain a square or slightly procumbent form, appearing as isodiametric in tangisections (PLATE II, FIG. 5). Irrespective of these cellular modifications in addition to (i) the normal breaking up of the tall uniseriate and multiseriate rays into shorter ones, and (ii) the formation of secondary rays of both kinds, the mature wood retains relatively the same ratio of uniseriate and multiseriate rays as compared with the earlier formed part of secondary xylem. In the young secondary xylem of *Hedyosmum*, in relative contrast to the situation in *Ascarina*, the multiseriate rays are slightly wider (4–6 cells) and occur in a larger proportion in relation to the uniseriate rays (compare PLATE II, FIGS. 4, 6). Ontogenetic development does not disturb the shape of the constituent cells in any appreciable degree, thereby nearly all of the cells retain an upright form as seen in tangisections (compare the form of mature ray cells of *Ascarina* in FIG. 5 with that of *Hedyosmum*, in FIG. 7 of PLATE II), although the ray width may attain a diameter of nearly 1 mm. (width of 20–22 cells). The radial sections also reveal a larger proportion of upright cells as compared with the square ones. Again, unlike the old wood of *Ascarina*, that of *Hedyosmum* contains essentially multiseriate rays, the uniseriate ones occurring only sporadically.

As in the other genera of the family, the wood parenchyma is poorly developed in *Ascarina* and *Hedyosmum*. However, the amount developed fluctuates considerably not only between species but also between different specimens of the same species collected from diverse localities. In *Ascarina*, the parenchyma is apotracheal, and the cells are distributed in diffuse to diffuse-in-aggregate patterns (PLATE I, FIG. 1), with a tendency to form short tangential uniseriate rows of three to four cells in some specimens of *Ascarina lanceolata* collected from the Samoan Islands. The amount of parenchyma in the mature woods of *Hedyosmum* is much smaller than in *Ascarina*, and is paratracheal, being confined to a few cells abutting the vessel members (PLATE I, FIG. 3). In some specimens of *H. bonplandianum* and *H. glabratum*, parenchyma appears to be almost absent.

The imperforate tracheary cells of *Ascarina* in general exhibit more tracheid-like characters. The pitting is more numerous and the pit borders are larger on the radial than on the tangential walls; the apertures are "included." In contrast, the corresponding cells of *Hedyosmum* exhibit characters that are more nearly characteristic of fibers. Thus, although the cell wall remains as thick or sometimes slightly thicker than that of

* The number of cells that make up the width of a multiseriate ray, the upright or square form of the constituent cells, the relative proportions of these cell types in a single ray, etc., are factors that appear to vary considerably not only between species, but also in the different collections of a single species, and perhaps in different specimens obtained from diverse parts of a single tree. To determine these ranges of variability, an analysis of a vast quantity of adequately sampled material is necessary. This not having been accomplished at present, the morphological descriptions given here should be looked upon as being *general trends* rather than as distinctive characters.

Ascarina, the pitting is less frequent; the borders are conspicuously reduced and the apertures well "extended." *Hedyosmum calloserratum* and *H. glabratum* show abundant development of septate-fibers.

Bark: The material available for examination consisted of young twigs. In all genera the bark is relatively thin. Groups of sclerenchymatous fibers confront the fascicular parts of the xylem and the phloem ray cells become modified into heavily lignified and sclerosed stone cells in *Sarcandra*. Species of *Chloranthus* and *Hedyosmum* present a similar structure excepting for the absence or scanty development of sclerosis of the phloem ray cells. The bark of *Ascarina* is relatively thicker than in the other genera, a large proportion of the outer cortical cells being parenchymatous. The sclerenchymatous sheaths of cells confronting the fascicular parts are much dissected and more numerous, and the tissue between these and the secondary xylem shows incipient stratification of thin and thick walled cells as seen in transections. The multiseriate rays of the phloem undergo excessive "flaring" due to conspicuous dilation of the component cells, which remain thin walled.

Nodal anatomy: Two distinct strands of vasculature that are related to a single lacuna of the vegetative axis are concerned in supplying the leaves of *Ascarina* and *Hedyosmum* (TEXT-FIGS. 1, 3), and therefore the nodal anatomy is typically of the *unilacunar* type. The primary vascular system as seen in the internodal regions of *Ascarina*, *Hedyosmum*, and *Chloranthus* consists of four vascular strands (see the bottom ends of TEXT-FIGS. 2, 4, 6). In *Ascarina*, each strand bifurcates* at the subnodal level into larger and smaller strands. The two pairs of smaller strands are opposite to each other and subtend the opposite leaves at the nodal level. The remaining four larger strands continue through the succeeding internode and at the next node undergo similar behavior (TEXT-FIG. 2).

The young stems of *Hedyosmum* exhibit a basically similar plan of vasculature, with a slight modification in the behavior of the leaf traces. In the subnodal region, the two pairs of leaf traces bifurcate. The two smaller branches of the bifurcation soon fuse to form a single intervening strand between the two larger branches, which in turn split into two (TEXT-FIG. 4). Thus, in transections taken at upper levels of the node, the "foliar buttress" as well as the petiole shows five vascular strands (TEXT-FIG. 5), the slender one occupying a median position with a pair of larger strands on either side.

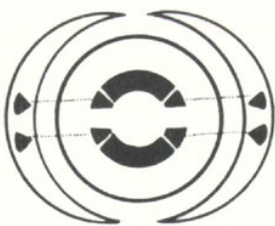
The vasculature of the stems of *Chloranthus*, as also of *Sarcandra* (Swamy and Bailey, 1950; Swamy, 1953a), is of a modified unilacunar type. In these genera, the internodal vasculature of the stem also consists of four bundles (TEXT-FIG. 6). At the subnodal level each of these gives off two branches so that the stem at this level contains 12 vascular strands, — four larger and eight smaller, the latter being placed one on either side of the

* The terms "bifurcates," "runs," "continues," "splits," etc., in connection with the vasculature of vegetative or reproductive structures have been employed in this paper only to describe the pattern of behavior of vascular strands as seen in serial transections, and *do not* involve any ontogenetic implications.

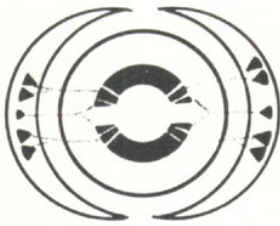
larger bundles. The two smaller bundles that are subjacent to the subtended leaves above bifurcate, the median two branches unite into one, and the resulting three strands form the median vein of the corresponding leaf (TEXT-FIGS. 5, 6). The remaining four smaller strands, placed at right angles (as seen in transection, TEXT-FIG. 5) to the petiolar axis of the opposite leaves, constitute the marginal veins, two veins entering each of the corresponding foliar appendages (TEXT-FIG. 5). It is usual for the two adjacently placed lateral veins, however, to exhibit fusion to varying distances during their course through the preceding internode, and in TEXT-FIG. 6, the fused condition is shown to extend throughout its length. Thus, the median vein (constituted of two larger strands and an intervening smaller one) of the leaf is related to one "gap" and the four marginal veins (two for each of the oppositely arranged leaves) arise from two "common gaps," in contrast to the typical trilacunar nodal situation where the four marginal strands (of two leaves) confront a corresponding number of independent "gaps." Therefore, the type of nodal structure in *Chloranthus* and *Sarcandra* (as also in the representatives of the family Calycanthaceae among the Ranales) cannot be assigned either to a strictly unilacunar type or to a typically trilacunar one. However, it appears reasonable to consider the nodal structure of *Chloranthus*, *Sarcandra*, and the like, as being a modification of the unilacunar type on account of their sporadic occurrence always among representatives that possess predominantly unilacunar nodal anatomy.

Leaf: The leaves of all four genera of the family are simple with varying types and degrees of serrated margins, and are penninerved. As mentioned above, transections taken nearer to the basal end of the petiole show two leaf strands in *Ascarina* (TEXT-FIG. 1), five (two pairs of larger strands with an intervening smaller one) rather closely aggregated strands in *Hedyosmum* (TEXT-FIG. 3), and again five (two larger strands and three smaller ones) in *Chloranthus* and *Sarcandra*; in the latter two genera, three of the strands (two larger and an intervening smaller one) occupy a median position and the remaining two smaller ones are on either lateral extremity of the petiole (TEXT-FIG. 5). During their course through the petiole to the base of the lamina, no significant changes are encountered either in regard to orientation of the individual strands or to their splitting. Thus, transections towards the distal end of the petioles reveal approximately similar configuration of vasculature as compared with sections from basal levels. The medianly situated groups of strands of the petiole (two in *Ascarina*, five in *Hedyosmum*, and three in *Chloranthus* and *Sarcandra*)

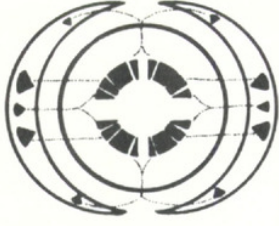
TEXT-FIGS. 1-9. FIGS. 1-6. DIAGRAMS TO ILLUSTRATE NODAL ANATOMY: FIGS. 1, 2. *Ascarina*; FIGS. 3, 4. *Hedyosmum*; FIGS. 5, 6. *Chloranthus*. FIGS. 1, 3, and 5 are diagrammatized from transections at nodal levels; FIGS. 2, 4, and 6 illustrate the vasculature of two successive nodes as split longitudinally and spread in one plane. FIGS. 7-9. TRANSECTIONS OF STOMA. FIG. 7. *Ascarina lanceolata*, $\times 400$. FIG. 8. *Chloranthus officinalis*, $\times 400$. FIG. 9. *Hedyosmum racemosum*, $\times 400$.



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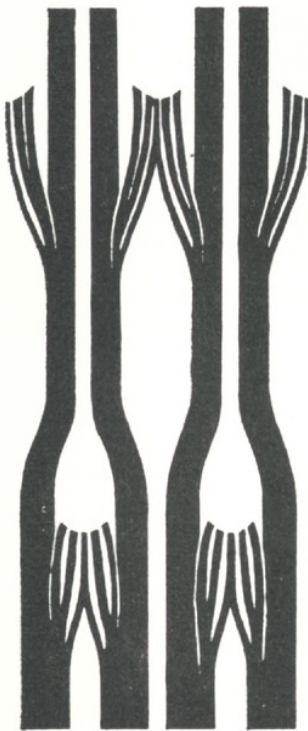
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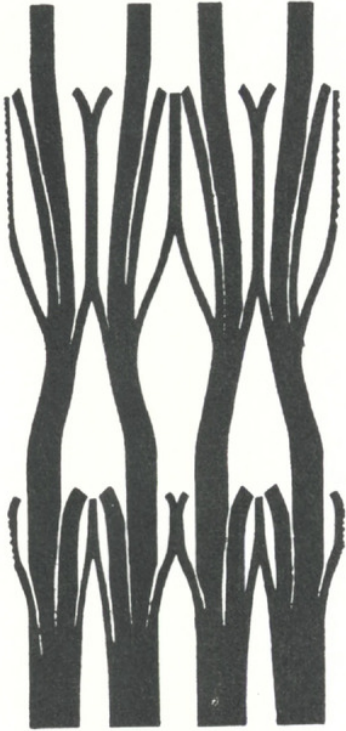
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constitute the midrib bundles of the leaves of the respective genera. In the earlier stages of ontogeny, the larger bundles of the midrib generally remain distinct throughout the length of the lamina, but in later stages they appear to have undergone approximation or fusion at varying distances from the apex of the leaf. Particularly in *Ascarina* the two bundles maintain distinctiveness for a greater distance in the leaf, and in such instances it is very clear that each longitudinal half of the leaf is vascularized by ramifications derived from the individual bundle lying on the corresponding side. In *Hedyosmum*, the basal half of the blade derives its vasculature from the branches of the outermost larger bundles, and the distal half from the two centrally located ones. The small central strand remains rather slender and disappears after traversing about half of the costa. The larger bundles of the midrib strand in the leaves of *Chloranthus* and *Sarcandra* take part in organizing the major vasculature of the blade; the intervening smaller bundle of the costa as well as the laterally situated weakly developed bundles proceed into the blade only for a short distance and finally disappear or undergo fusion with one of the adjacently situated bundles.

The pattern of smaller veins and veinlets of the leaf is typically reticulate. In texture, the lamina fluctuates between chartaceous and coriaceous, depending upon factors such as the thickness of cuticle, the number of layers and the size of component mesophyll cells, the degree of reticulation of the veinlets, the coarse or slender character of the veinlets, the occasional occurrence of sclerenchymatous cell clusters in the mesophyll (species of *Hedyosmum*), etc. Although these characters, in varying proportions and combinations, are subject to variation often among the leaves of the same species (for example, as between sun-leaves and shade-leaves, or between specimens obtained from lower altitudes and higher altitudes, etc.), a generalized statement may be made to the effect that: (i) the foliage of *Chloranthus* and *Sarcandra* tends to be thin with a rather loosely reticulated venation; (ii) the leaves of a few species of *Ascarina* and several of *Hedyosmum* are relatively thicker with a comparatively denser reticulation of the veinlets; and (iii) the lamina of certain other species of *Hedyosmum* exhibits a system of relatively coarser veinlets with generally dilated endings and denser reticulation. In some species, the toughness becomes exaggerated due to the presence of isolated or clustered groups of stone cells in the epidermis and subjacent mesophyll tissues.

The lamina of several species of *Ascarina* and *Hedyosmum* possesses a hypodermal layer; in a few other species of these genera, as also in some species of *Chloranthus*, the distribution of such a layer tends to be restricted to the neighborhood of veins. A hypodermis may be absent in *Sarcandra*. As observed by Solereder (1899), Thierry (1912), and others, a morphologically typical palisade tissue is characteristically wanting in all the genera. Its place and function, however, is taken over by muricate cells. Relatively large secretory cells, the "ethereal oil cells," are freely scattered throughout the mesophyll tissues of the leaves, as also generally in young cortex, pith, and in floral appendages. Mucilage ducts are present in *Hedyosmum arborescens* (see also Skutch, 1927) and a few allied but

as yet unidentified species. Crystals occur only occasionally — as small, solitary bodies in the epidermal cells of some specimens of *Chloranthus spicatus*, and as druses in the cortex of *Hedyosmum brasiliense*.

In general, the cell walls of dorsal and ventral epidermal layers are uniformly straight in *Ascarina*, wavy in *Chloranthus*, and straight in some species of *Hedyosmum* but wavy in others. The subsidiary cells of the stomata in *Sarcandra* and *Chloranthus* are oriented parallel to the guard cells (the so-called "rubaceous type"); one or both guard cells occasionally show a septation at right angles to the longer axis, thereby indicating a division having taken place. This type of stomatal structure is specific for the above two genera. On the other hand, *Ascarina* and *Hedyosmum* are characterized by stomata that are surrounded by a varying number (between four and six) of ordinary cells forming a rosette. In *Chloranthus* and *Sarcandra*, the guard cells rest partially on the subtended parts of constituent epidermal cells (TEXT-FIG. 8), whereas in *Ascarina* and *Hedyosmum* they are set more or less in line with the epidermis (TEXT-FIGS. 7, 9). In all four genera, the cuticle is excessively thickened around the stomatal opening to form a vestibule-like structure with overhanging borders (TEXT-FIGS. 7-9).

REPRODUCTIVE STRUCTURES

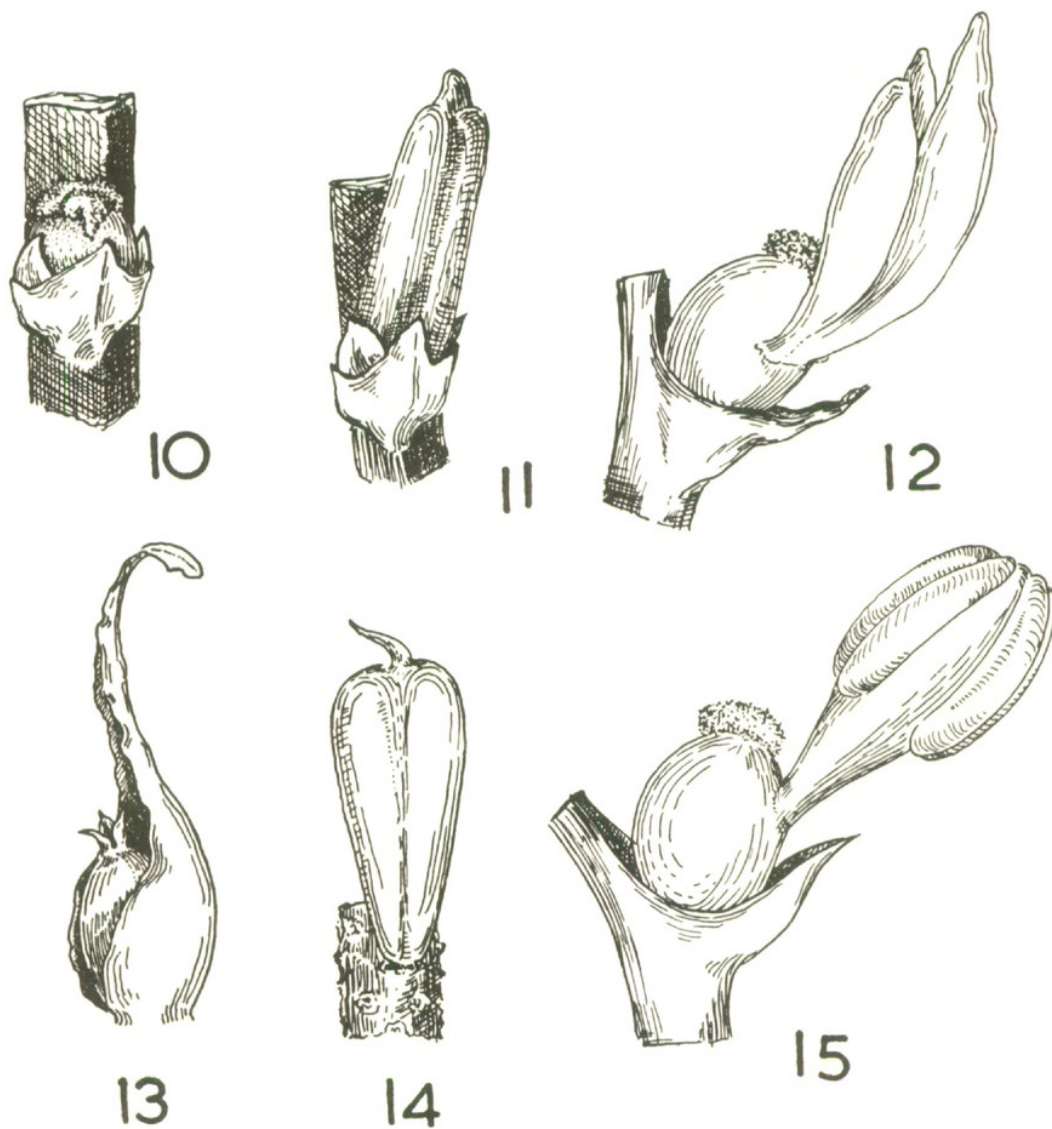
External morphology: In all four genera of the family, the flowers are borne on compound spikes that are axillary or terminal. In *Hedyosmum Artocarpus*, the individual flowers are so closely approximated and partly fused, not only among themselves but also with the axis, that they appear as an aggregated structure.

The flowers of *Sarcandra* and *Chloranthus* are bisexual; those of *Ascarina* and *Hedyosmum* unisexual. Furthermore, the former genus is dioecious while the latter often bears distinctly male and female inflorescences on one and the same plant. Although the flowers of these genera have received elaborate descriptions in taxonomic papers, a comparative summary of salient features is given below to enable the reader to get a clearer picture of the interrelationships of individual floral parts as well as of the flowers of different genera.

The individual flowers of *Sarcandra* and *Chloranthus* are subtended by a single, somewhat keel-shaped, lanceolate bract. A solitary pistil with a capitate, tufted stigma and no style is inserted in the axil of the bract (TEXT-FIGS. 12, 15). In *Sarcandra*, a single fleshy stamen with a quadri-locular anther is attached at the middle height of the pistil on the abaxial side (TEXT-FIG. 15). In *Chloranthus* (TEXT-FIG. 12), it suffices at present to note that the attachment of the tripartite androecium to the pistil has the same relation as in *Chloranthus*, but that its form, number and degree of development of the thecae, etc., are variable in different species. A detailed treatment of these structures will be found on a subsequent page.

The unisexual flower of *Ascarina*, in some species, is subtended by three deltoid bracts, a larger outer and two smaller inner ones (TEXT-FIGS. 10,

11); in the remaining species, the bract is single and nearly of the same size and form as that of the outer bract of the former set of species. This feature, in association with others, forms a very significant criterion in recognizing two distinct groups of species within the genus (Swamy, 1953b). The styleless solitary pistil with an unequally bilipped tufted



TEXT-FIGS. 10-15. FIG. 10. *Ascarina lanceolata*, female flower. FIG. 11. Same, male flower. FIG. 12. *Chloranthus Henryi*, flower. FIG. 13. *Hedyosmum orientale*, female flower. FIG. 14. Same, male flower. FIG. 15. *Sarcandra glabra*, flower.

stigma occupies the axil of the bract or bracts (TEXT-FIG. 10). In the male flower of the three-bracteate species a single stamen is present, while in the one-bracteate species, a single flower bears two stamens. In either case, the stamen is sessile, cylindrical, with four longitudinally extensive thecae (TEXT-FIG. 11).

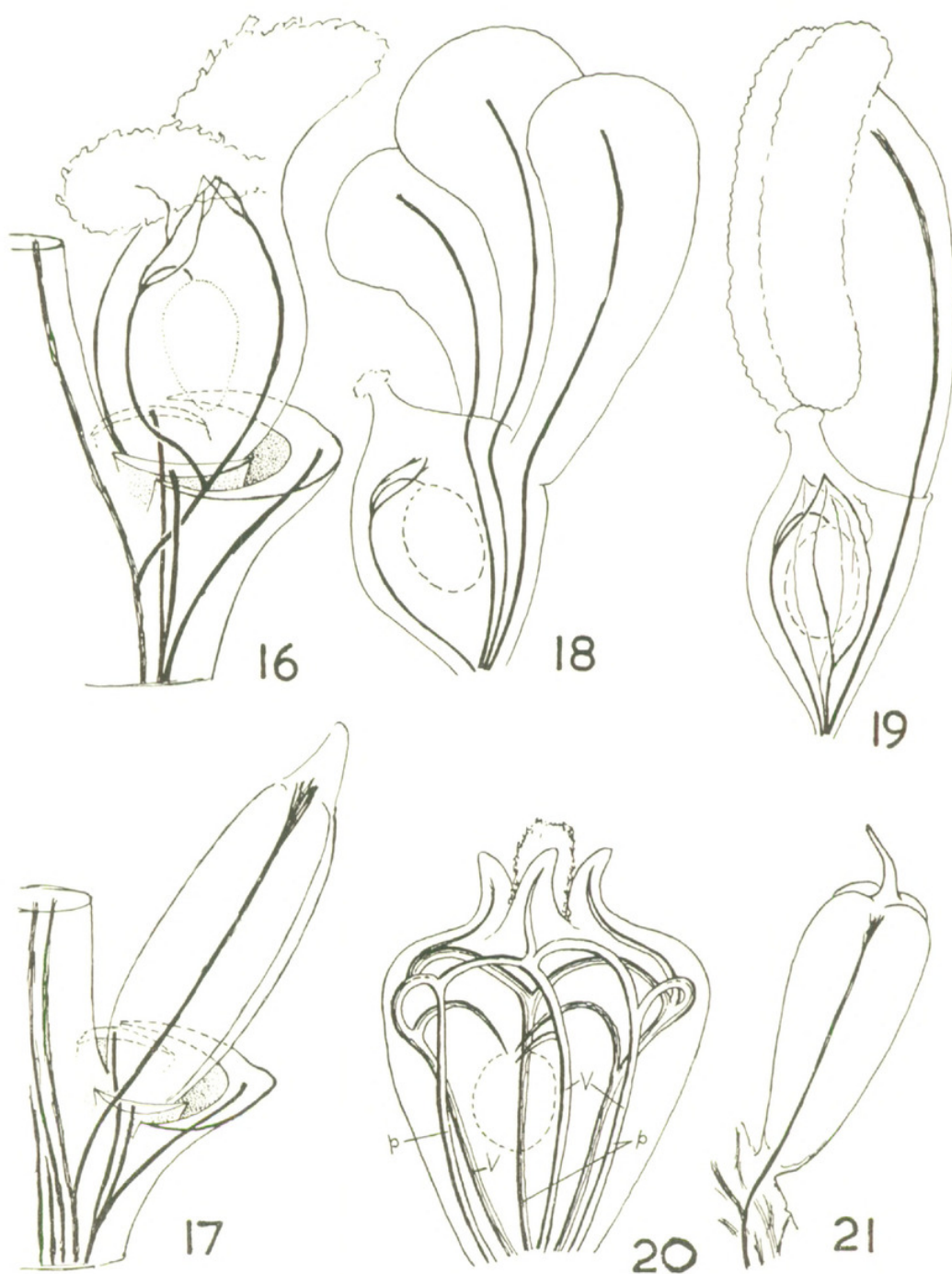
The flowers of *Hedyosmum* differ from those of the other three genera

in two important respects: (i) the male flower has no subtending bract or any other corresponding structure (TEXT-FIG. 14), and (ii) the female flower shows the presence of a cupuliform structure that encloses the solitary pistil and slightly projects beyond in the form of three deltoid emergences which have been generally believed to represent a perianth (TEXT-FIG. 13). The cupuliform perianth is free from the ovary wall for the most part, but is fused with the carpel along the three ridges and also at the substigmatic level. Such a flower is subtended by a relatively conspicuous bract, whose shape and size are subject to considerable variation; in some species it undergoes profound modifications into a tubular structure that almost completely envelops the flower (e.g. *H. calloserratum*); in *H. Artocarpus*, the bracts become distinguishable only with difficulty due to the extreme concrescence or fusion between the adjacent flowers and inflorescence axis. The pistil is sessile, styleless with a short, stumpy, tapering, hairy stigma. However, the characters of the latter structure generally vary between species. Unlike the other genera, the stigma is caducous in *Hedyosmum*.

Vasculature: The vascular anatomical features of the flowers of *Sarcandra* having already been described elsewhere (Swamy and Bailey, 1950), they will be referred to at present only when needed for comparison with the situation in other genera. In all the genera, the bract is vascularized by a single bundle that remains unmodified within the structure.

In *Chloranthus*, four bundles commonly traverse the flower — three on the abaxial side and one on the opposite side. The latter constitutes the ventral bundle, the extremity of which trifurcates, the median branch supplying the ovule and the other two diverging in the apical tissues of the pistil beneath the stigma; the former three abaxially disposed bundles run in the wall of the carpel, and at the point of attachment of the androecium deviate into the corresponding lobes and traverse almost the entire length of the structures (TEXT-FIG. 18). There is no vasculature corresponding to a dorsal bundle (Armour, 1906; Swamy and Bailey, 1950).

The pattern of vasculature in the flowers of *Chloranthus multistachys* deserves consideration here because of the presence of a single stamen with a quadrilocular anther as in the vesselless *Sarcandra*, in contrast to the trilobed staminal appendage with one quadrilocular anther and two bilocular ones as in the other species of *Chloranthus*. The dorsal bundle in this species also is absent; the stamen is supplied with just one bundle. The origin and behavior of the ventral bundle and the mode of vascular supply to the ovule conforms to the same pattern as in the other species of the genus. But the ovary contains two other bundles, each occupying a position in the wall between the bundle that supplies the stamen and the ventral bundle (TEXT-FIG. 19). These additional bundles soon bifurcate and the branches reach the apical extremity of similar branches of the ventral bundle and form anastomoses. In occasional cases, the flowers of this species bear a pair of small degenerate anthers one on either side of the larger median one (TEXT-FIG. 36). In such cases the median lobe is supplied with a single bundle as in the normal flowers, and two weakly de-



TEXT-FIGS. 16-21: GENERALIZED RECONSTRUCTIONS ILLUSTRATING PATTERNS OF VASCULATURE OF: — FIG. 16. Female flower of *Ascarina lanceolata*. FIG. 17. Male flower of the same. FIG. 18. Flower of *Chloranthus Oldhami*. FIG. 19. Flower of *Chloranthus multistachys*. FIG. 20. Female flower of *Hedyosmum nutans*. FIG. 21. Male flower of the same.

veloped bundles traverse the degenerate lobes to varying distances; and significantly, the lateral bundles in the ovary of such flowers are characteristically absent. This situation suggests, in all probability, that the lateral bundles in the ovary of normal flowers of *C. multistachys* may indeed represent the vasculature of the lateral lobes of the stamens which now, however, have been eliminated in this particular species, but are present in all the remaining species of the genus.

In the flowers of *Ascarina*, the bract or bracts (depending upon the species) receive(s) a single bundle each. A vascular strand of the inflorescence axis enters the female flower, and at the base of the pistil splits into two. One of the branches constitutes the dorsal bundle which generally exhibits a slender forking beyond the upper level of the locule. The other branch forms the ventral bundle whose behavior is similar to the situation in *Chloranthus*. At the base of the stigma, the branchlets of the dorsal and ventral bundles undergo anastomoses (TEXT-FIG. 16). In the male flower, the single stamen is supplied with one bundle that traverses the entire length of the connective and in the region of the conical apex, undergoes slight widening (TEXT-FIG. 17). In those species of the genus where the male flower bears two stamens, the strand for each stamen is independent and does *not* arise as a branch of any single strand of the inflorescence.

The female flowers of *Hedyosmum* exhibit a range of variability in structure, not only in relation to those of the other genera, but also among different species of the genus. The material that was available for present study consisted of only six species and no specimens of highly modified flowers, as those of *H. Artocarpus*, could be secured. Even the small number of species studied was enough to indicate that the number is inadequate as a basis for reliable conclusions in view of the variations shown by the vascular pattern. Therefore, the observations recorded here are of a provisional nature.

Transections at the base of the flower show six equidistantly arranged bundles in the form of a ring. As shown by Edwards (1920), three of these traverse the three corners of the so-called perianth (*p* in TEXT-FIG. 20). The remaining set of three occupies an alternating position with the outer set and run in the wall of the carpel (*v* in TEXT-FIG. 20). These are probably homologous with the ventral bundles of the carpels in other genera. At the fused level of the perianth (with the ovary wall) each of the six bundles bifurcates and the branches diverge to anastomose with similar adjacent members. From the point of bifurcation of the carpellary bundles, a short branch enters the deltoid apex of the perianth. The ovule receives three traces, one from each of the carpellary bundles (TEXT-FIG. 20), in sharp contrast to the single-trace situation in the other genera. The vascularization of the male flower closely parallels that of *Ascarina* — a single bundle traversing the entire length of the connective (TEXT-FIG. 21).

The salient trends in the floral vasculature of the four genera may be summarized as follows:

1. In the flowers of *Sarcandra*, the stamen is supplied with two bundles that originate *not* as a result of a dichotomy of a single strand, but independently of each other. Such an origin may be traced even from the lowest levels of floral axis, and often from a considerable distance in the inflorescence axis. Likewise, the ventral bundle of the carpel also has a "double" origin and similar course throughout the length in *S. glabra*; in *S. hainanensis*, however, the ventral bundle is single from the beginning (FIGS. 5–8, in Swamy and Bailey, 1950). The ovular supply is derived directly from the ventral bundle. The dorsal bundle of the carpel is also "double."

2. In the flowers of *Chloranthus*, the carpel does not possess a dorsal bundle; a single ventral bundle is present which trifurcates at the extremity, the median branch supplying the ovule. Each of the three lobes of the androecium receives a single bundle; these again are *not* the products of splitting of any single vascular strand of the inflorescence axis, but have independent origins.

3. In the female flower of *Ascarina*, the vasculature consists of a dorsal bundle and a ventral one, both arising by a simple forking of a strand from the inflorescence axis. The ventral branch, as in *Chloranthus*, splits into three at its apex, the median branch supplying the ovule. In the male flower the stamen receives a single bundle.

4. The stamen of *Hedyosmum* is supplied only with a single bundle much in the same manner as in *Ascarina*. The vasculature of the female flower is slightly complicated, obviously in conformity with the floral structure. The gynoecium is triangular in cross-section and receives three bundles, each running in a flat side of the wall; the ovule receives a small branch from each one of these bundles. Three bundles traverse the corners of the cupuliform structure (external to and partly fused with the gynoecium) that has been interpreted to be the perianth. The corners of this structure and of the gynoecium are opposite to each other but their respective bundles occupy alternating positions.

Such a situation in *Hedyosmum* raises two important considerations:

1. The morphological nature of the external cupular covering of the gynoecium. Clarke (1858), Solms (1869), Eichler (1878), Bentham and Hooker (1880), and others contend that this structure is of perianthial nature. Baillon (1871), while referring to the deltoid lobes as "wings," feels that their true nature is by no means decided. Edwards (1920) postulates that this whorl may represent three modified stamens, in view of the alternating arrangement of the vascular bundles belonging to the two categories of structures; but he himself rejects this hypothesis saying that "there is no definite evidence in favor of this view, since the earliest phases of the developing perianth show no essential peculiarities common to the perianth and to the stamens." It must be emphasized here, in view of the considerable range of morphological variability of floral structure evidenced in the genus as a whole, that the homology of this structure

cannot be clearly understood by the study of a limited number of species. An intensive investigation of wider representative material, both from ontogenetic and comparative aspects, may yield valuable data that would help towards a clearer understanding of the concerned structure.

2. The three corners of the gynoecium as well as of the enclosing cupular sheath have a corresponding number of vascular bundles in each; the ovule also receives three traces. Could these facts be employed to suggest a basically trimerous plan of construction of the flower? The floral structure in the other genera of the family does not provide evidence either for or against such a suggestion. It is interesting to note in this connection that the androecial structures in *Chloranthus* are also three. A study of families as Lauraceae, Gomortegaceae, Hernandiaceae, etc., may yield useful data towards a cogent explanation.

Have the flowers of *Chloranthus* a perianth?: Eichler (1878) claimed to have seen a small scale at the base of the insertion level of the staminal structure in some species of *Chloranthus*, and interpreted the scale as a perianth. Later, Čelakovsky (1900) expressed a similar view, however, adding that the structure was incomplete and reduced. Armour (1906) has identified a similar structure in *C. chinensis* (= ?*C. officinalis*) and believes it to be just a short outgrowth of the carpellary wall itself. She aptly observes that "in the structure of this minute scale nothing appears to justify giving it such importance." In the numerous specimens of almost all of the putative species of *Chloranthus* examined in the course of this investigation, no structure similar to a *scale* on the carpel or anywhere else on the flower has been observed. Some species that bear a relatively large staminal appendage (e.g. *C. Fortunei*, *C. angustifolius*, *C. multistachys*, etc.) often show a slight abaxial deformation of the carpel in the form of a minute projection or fold beneath the point of attachment of the stamen. This feature is seen in an exaggerated degree in *Sarcandra Irvingbaileyi* (Swamy, 1953a), where the wall of the carpel surrounding the base of the large stamen appears as a cushion. When such flowers are subjected to drying, the deformed part becomes much more pronounced and at times may appear as a small protuberance. The structures reported by Eichler and Čelakovsky are obviously such "artifacts." The features in the vascular anatomy of the flowers also fail to provide evidence for the presence of a rudimentary perianth. Therefore it becomes obvious that the existing flowers of *Chloranthus* do not bear any structures that could be identified or interpreted as perianth.

Are the flowers of *Chloranthus* and *Sarcandra* reduced inflorescences?: Cordemoy (1863) considered that a single flower of *Chloranthus* is in reality an inflorescence, in which the axis bears at its extremity a single female flower composed of a naked ovary, and laterally in the axil of the bract a little glomerulous (biparous sessile cyme) of male flowers, represented by a bilocular stamen, or by unilocular stamens. An essentially similar view has been maintained by Hooker (1890), but in a slightly

modified version — that the male inflorescence is reduced to a single flower (in contrast to a biparous sessile cyme of Cordemoy). As long ago as 1869, Solms ascribed a hermaphroditic nature to the flowers of *Chloranthus* (in which was included *C. brachystachys* = *Sarcandra glabra*), a view which was accepted by Baillon (1871) and by a number of later botanists.

It may be pointed out here that, if the individual flower represents an extremely reduced inflorescence, the axis of the flower (which should be homologous with the inflorescence axis itself) often reveals the presence of either modified supernumerary structures externally, or abnormal behavior in the course of vascular bundles, or various combinations of these features. For example, the view that the so-called male and female flowers of *Cercidiphyllum* (Swamy and Bailey, 1949) as found today are, in reality, vestiges of once elaborate inflorescences is amply supported not only by data provided by comparative morphology, but also by the invariable presence of supernumerary vasculature; furthermore, additional confirmatory evidence has come from palaeobotanical findings. In *Chloranthus*, one fails to see any arguments for upholding the views of Cordemoy and Hooker. Although it is true that the vasculature of the flowers is, in general, much reduced and simplified — as also external floral structures which have disappeared — this does not necessarily imply that a single flower should represent the sole vestige of an inflorescence; nor that the flower is a fused product of highly reduced male and female inflorescences. Therefore, in the absence of critical and convincing evidence in favor of Cordemoy's interpretation, and in light of the presence of a well organized compound spike type of inflorescence in the extant representatives, it appears rational to consider (as a majority of botanists do) that the existing flowers are individual bisexual flowers, which of course have undergone reduction with reference to the perianth whorl, but are not reduced or composite inflorescences.

Pollen: The pollen grains of *Chloranthus* are subspherical, measuring on an average $22.5 \times 30.0 \mu$ along the shorter and longer diameters. The grains of the other genera are mostly spherical, 28μ in diameter in *Sarcandra*, 30μ in *Ascarina* and 35μ in *Hedyosmum*. The grains of *Sarcandra* have no special germinal areas, and hence are acolpate. Those of *Ascarina*, on the other hand, show a typically monocolpate structure. The germinal furrow or colpa extends to the poles and is of a rather uniform width throughout with bluntly rounded off polar extremities. The pollen grains of *Chloranthus* show a polycolpate condition with considerable modifications. The number of colpa per grain varies between three and five in *C. serratus* and six and eight in *C. angustifolius*. The extent of furrow is rather restricted both in longitudinal and latitudinal dimensions. Although in a few instances the furrows may reach the polar regions (e.g. *C. Fortunei*) they often stop short at varying distances, appearing as slender, unsculptured, wavy, meridional streaks. In some species as *C. serratus*, the furrows can be distinguished only as very faint, tenuous,

short zig-zag lines. In *Hedyosmum* also the grains are generally polycolpate, the characters of the germinal furrows resembling those of *Chloranthus*. However, modifications appear to have progressed along two lines: (i) localization of furrows towards either one pole whereby often the ends become contiguous, or towards a restricted facet of the sphere whereby the furrows place themselves close together (e.g. *H. domingense*, *H. calloseratum*, etc.); and (ii) reduction in the number and size of the furrows resulting in acolpate grains (e.g. *H. nutans*, certain collections of *H. arborescens*). The intine of *Ascarina* pollen is relatively thick excepting at the region of the furrow. The exine exhibits a minute, faint, rather uniformly distributed pitted-reticulate sculpturing; the external surface of the furrow (intine) shows mildly speckled protuberances. The grains of *Sarcandra* possess a coarsely reticulate pattern of sculpturing on the exine; those of *Chloranthus* (see illustrations in Swamy and Bailey, 1950) and *Hedyosmum* show successively finer grades of reticulate-pitted sculpturing.

THE ANDROECIUM IN CHLORANTHUS

The possession of vessel-bearing xylem, of bisexual flowers, and of a three-partite androecium distinguish *Chloranthus* from the other generic units of the family. As mentioned on a previous page, the androecial appendage is subject to considerable morphological variability, the types of variations being one of the major criteria in segregating the species. Detailed accounts of these structures are contained in taxonomic or regional monographs issued from time to time, the most recent one being that of P'ei (in *Sinensia*, IV [1935] 665) wherein he has included all of the Chinese representatives of *Chloranthus*. Therefore, only the salient points of structure will be mentioned here.

In general, the androecium is essentially a three-lobed structure, the median lobe bearing a "full"-anther (four-celled when young and bilocellate at maturity) and each lateral lobe a "half"-anther (two-celled when young and unilocellate at maturity). The lobes are placed adjacent to one another on the abaxial side of the carpel. Variations of this norm are brought about by one or several of the following factors: (i) the mature length and shape of the individual lobe; (ii) the degree of cohesion of the basal region of the lobes; (iii) the width between the pairs of sporangia on the median lobe; (iv) the location of sporangia on the lobe; (v) the degree of fertility of the sporangia on the median or on the lateral lobes; and (vi) the fleshy or foliose character of the lobes, etc.

The individual lobes of the androecium in *C. Oldhami* and *C. Henryi* (TEXT-FIGS. 44, 45, 22, 23) are completely free from one another and each lobe, although differing in general outline in the two species, bears a striking resemblance to a stamen of *Austrobaileya* (Bailey and Swamy, 1949). Thus, the microsporophyll is ovate or broad-lanceolate in outline, somewhat fleshy, and the slightly protuberent sporangia are situated nearer to the base; the median lobe in particular shows a greater degree of similarity to the stamen of *Austrobaileya* in possessing two pairs of sporangia. In *C.*

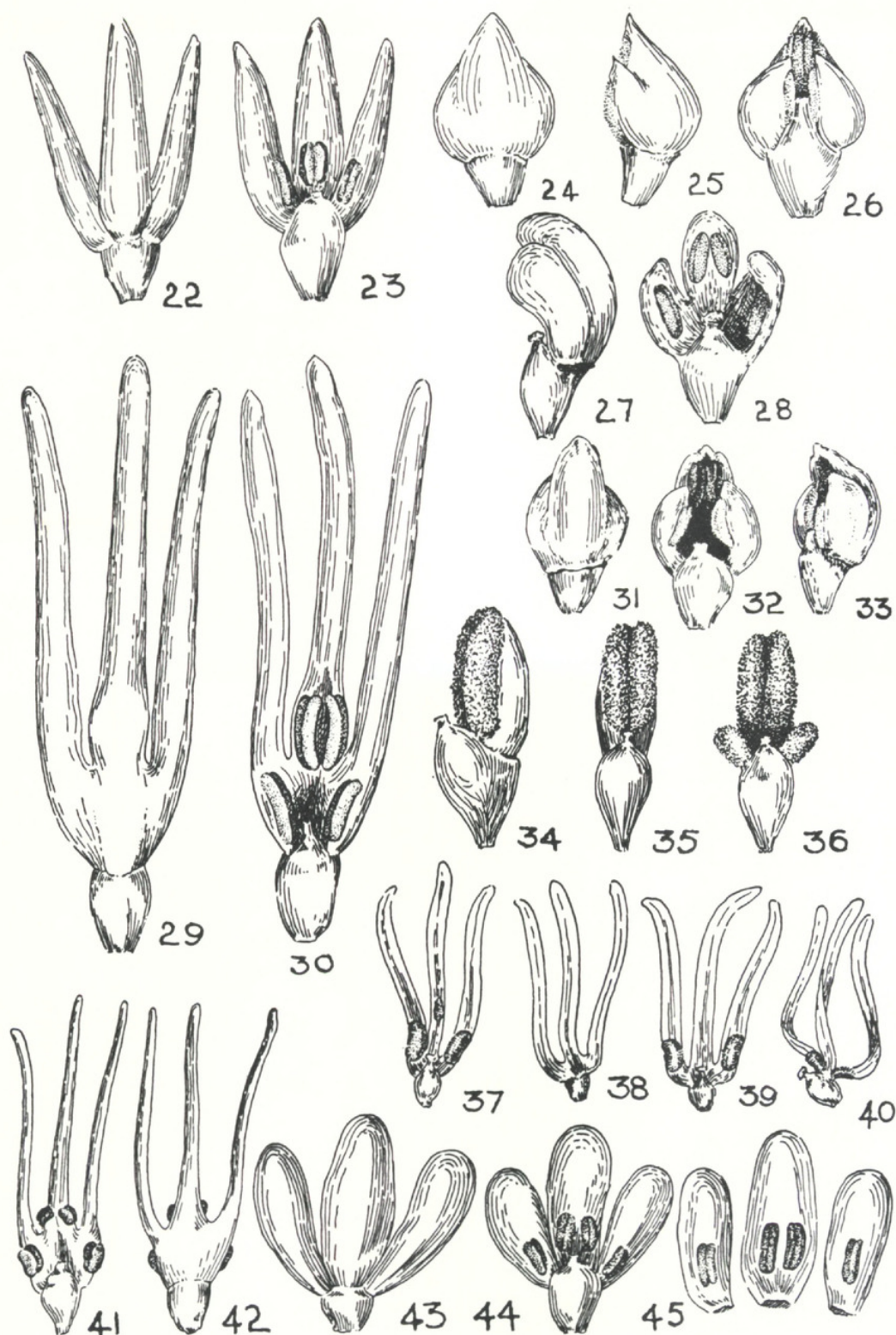
Henryi all the four sporangia lie close together (TEXT-FIG. 23) and in *C. Oldhami* (TEXT-FIGS. 44, 45) the two pairs are slightly separated.

The staminal appendages of *C. serratus* (TEXT-FIGS. 27, 28) exhibit an early step in the cohesion of the adjacent lobes. The individual lobes have the same general form as that of the two species just mentioned, but the two pairs of sporangia on the median lobe occupy a position nearer to the apex of the microsporophyll (TEXT-FIG. 28). The lobes have concave adaxial and convex abaxial surfaces and all the three lobes together form an incipient hood over the pistil (TEXT-FIG. 27). A much more important modification lies in the cohesion of the basal parts of the three lobes (TEXT-FIG. 28). This tendency finds an extreme expression in the androecial structures of *C. officinalis* (TEXT-FIGS. 24–26) and *C. spicatus* (TEXT-FIGS. 31–33). Here, the anthers of the middle lobe are disposed nearer to the apex, and although the basal cohesion has not progressed much farther, the hood-formation has reached such a pronounced development as to envelop the distal half of the pistil almost completely. In *C. officinalis*, the median lobe has a single pointed apex, while that in *C. spicatus* has a mildly tridentate apex (compare text-figs. 26 and 32) — only a small difference morphologically, but a major criterion in the segregation of the two species.

The androecium of *C. multistachys* appears to illustrate the end product of another trend of modification. The median lobe alone is represented normally (TEXT-FIGS. 34, 35) and the microsporophyll is extremely reduced, being restricted only to the abaxial side and delimited by the outline of the sporangia. The anther, however, is quadrilocular as in the median lobe of other species. The lateral lobes develop only occasionally (TEXT-FIG. 36), but remain free, insignificant, and sterile. Another minor trend associated with the anther of this species is the possession of a papillate epidermis over the sporangia.

Chloranthus angustifolius, *C. Fortunei*, and *C. japonicus* reveal still another line of morphological modification. The androecial lobes become comparatively much more elongated than in other species, and their confluent base becomes rather pronounced (TEXT-FIGS. 29, 30, 41, 42). In *C. Fortunei*, the pairs of sporangia on the median lobe occupy a position

TEXT-FIGS. 22–45. ILLUSTRATIONS OF FLOWERS OF *Chloranthus* SPECIES WITH PARTICULAR REFERENCE TO ANDROECIAL STRUCTURES. FIG. 22. *Chloranthus Henryi*, abaxial view. FIG. 23. Same, adaxial view. FIG. 24. *C. officinalis*, abaxial view. FIG. 25. Same, side view. FIG. 26. Same, adaxial view. FIG. 27. *C. serratus*, side view. FIG. 28. Same, adaxial view. FIG. 29, *C. Fortunei*, abaxial view. FIG. 30. Same, adaxial view. FIG. 31. *C. spicatus*, abaxial view. FIG. 32. Same, adaxial view. FIG. 33. Same, side view. FIG. 34. *C. multistachys*, side view. FIG. 35. Same, adaxial view. FIG. 36. Same, adaxial view of an abnormal flower with additional sporangia. FIG. 37. *C. japonicus*, adaxial view of a flower with sterile sporangium on the median lobe. FIG. 38. Same, abaxial view. FIGS. 39, 40. Same, with sporangia only on the lateral lobes, adaxial view. FIG. 41. *C. angustifolius*, adaxial view. FIG. 42. Same, abaxial view. FIG. 43. *C. Oldhami*, abaxial view. FIG. 44. Same, adaxial view. FIG. 45. Same, individual lobes.



on the adaxial surface (TEXT-FIG. 30); all the four pairs of sporangia are of the same size, develop to maturity, and produce fertile pollen. The two pairs of sporangia on the median lobe of *C. angustifolius* are small, degenerate, and sterile, only the larger "half"-anthers being functional (TEXT-FIG. 41). This tendency attains a further degree of accentuation

in the androecium of *C. japonicus*. Thus, the median lobe bears a single pair of degenerate sporangia only occasionally (TEXT-FIG. 37), the general condition being its total absence; the sporangia borne on the lateral lobes are the functional ones (TEXT-FIGS. 37, 39, 40).

The androecial structures of other species of the genus not mentioned here fit into one or other of the modifications mentioned above.

Whether the androecium of *Chloranthus* represents a single stamen with four pairs of sporangia or three independent stamens that have undergone fusion with one another towards their base, has remained a major controversial issue. A critical perusal of taxonomic descriptions of the different species (which is the only source of information available on this topic) clearly demonstrates that the words stamen and anther have been employed in highly ambiguous and indiscriminate usages. Understanding *stamen* to mean "one of the pollen-bearing . . . organs of the flower," and *anther* to mean "polliniferous part of a stamen" (as defined by Asa Gray in his "Elements of Botany," 1877, and by many other classical writers), there appear to be the following opinions expressed in regard to the morphological nature of the androecium:

(1) that it consists of a *single stamen* which has developed three lobes, the median lobe bearing two pairs of sporangia and each of the lateral lobes a single pair (Nakai, Fl. Sylvat. Koreana, XVIII [1930] 16; and others).

(2) that it consists of *three stamens* that are connate towards the base, the number and distribution of sporangia similar to the above condition in (1) (Bentham and Hooker, Gen. Pl. III [1880] 134; Cordemoy in Adans. III [1863] 296; Hemsley in Jour. Linn. Soc. Bot. XXVI [1891] 367; Asa Gray in Perry, Jap. Exped. II [1857] 318; etc.).

(3) that it consists of *three anthers* (= a single stamen as in (1) ?) fused at the base; the median one is bilocular and the lateral ones unilocular (Hamilton in Edinb. Jour. Sci. II [1825] 11; Solms, in DC. Prodr. XVI [1869] 476; etc.).

(4) that it consists of a *single tripartite anther* (= one stamen as in (1) ?) (Oliver in Hook. Ic. XXII [1886] t. 1580; Pampanini in Nuovo Giorn. Bot. Ital. N.S. XXII [1915] 272; etc.).

(5) that it consists of a *three-lobed filament* (= of a single stamen as in (1) ?) (Wight, Ic. IV [1853] t. 1945).

Merrill (Philipp. Jour. Sci. Bot. VII [1912] 259; *ibid.* X [1915] 3) uses the non-committal term "*anther scale* . . . divided nearly to the base into three lobes" or "antheriferous scale 3-partite," possibly implying that the androecium is made up of a single stamen. P'ei (Sinensia, IV [1935] 666) uniformly designates the male structures by the phrase, "anthers connate by connectives." This epithet is rather unfortunate (from the morphological point of view) as there is no certainty as to the number of stamens involved.

However, leaving aside the ambiguous instances as in the preceding paragraph, as well as the clauses (3) to (5) above, the consensus of

opinion is divided between two schools that deserve further consideration. The first school contends that the androecium is represented by a single stamen (see (1) above) bearing four pairs of sporangia, two on the median lobe and one on each of the lateral lobes. According to this postulate, it is necessary to assume that the immediate ancestral type of stamen (whatever its exact shape might have been) possessed four pairs of sporangia, that the trifurcation commenced at the apex, that the cleavage progressed basipetally and between the lateral pairs of sporangia to result in a median quadrilocular and one bilocular lobe on either side (see the upper series of diagrams in text-fig. 46). According to the second school (see (2) above), the starting point would be an androecium consisting of three independent stamens, the median one lodging a quadrilocular anther and the lateral ones bearing bilocular anthers; during phylogeny, the bases of the stamens have become fused to result in the existing form (see the lower series of diagrams in text-fig. 46).

Both these views leave certain points unanswered. For example, how did the eight-locular stamen — the ancestral form according to the first school, or the two two-locular stamens — the starting point for the second school originate? Are these necessarily the true ancestral norms or do they in reality represent products of preceding phylogenetic changes? An answer to such questions would be only futile speculation. Of course, the advocates of the "Telome theory" may come forward with a ready explanation for the origin of the eight-locular stamen, that it represents a sort of a syntelomic modification which has resulted in response to the interplay of one or several of the principles that have been believed to be the operating factors in phylogenetic specialization, perhaps planation and fusion of two or more basic telomes in the present case. It is obvious that we do not have any evidence to make an *a priori* assumption of this nature, particularly where angiosperms are involved. It must be observed that the supposed existence of three independent stamens as the starting point (as envisaged by the proponents of the second school) obviously does, in all probability, represent a derived stage of preceding evolutionary modifications. The evidence for this statement is exemplified in the lateral stamens each of which bears only a bilocular anther, the other counterpart having become eliminated. It must be emphasized in this connection that such a tendency towards the degeneration or elimination of anthers is seen also among some living species of *Chloranthus* (e.g. *C. angustifolius*, *C. japonicus*, etc.).

Now, in regard to the actual steps involved in the derivation of the extent situation either from an eight-locular stamen (first school) or from three independent stamens (second school), let us consider the available evidence: —

First school: There are several serious obstacles to acceptance of such a method of derivation:

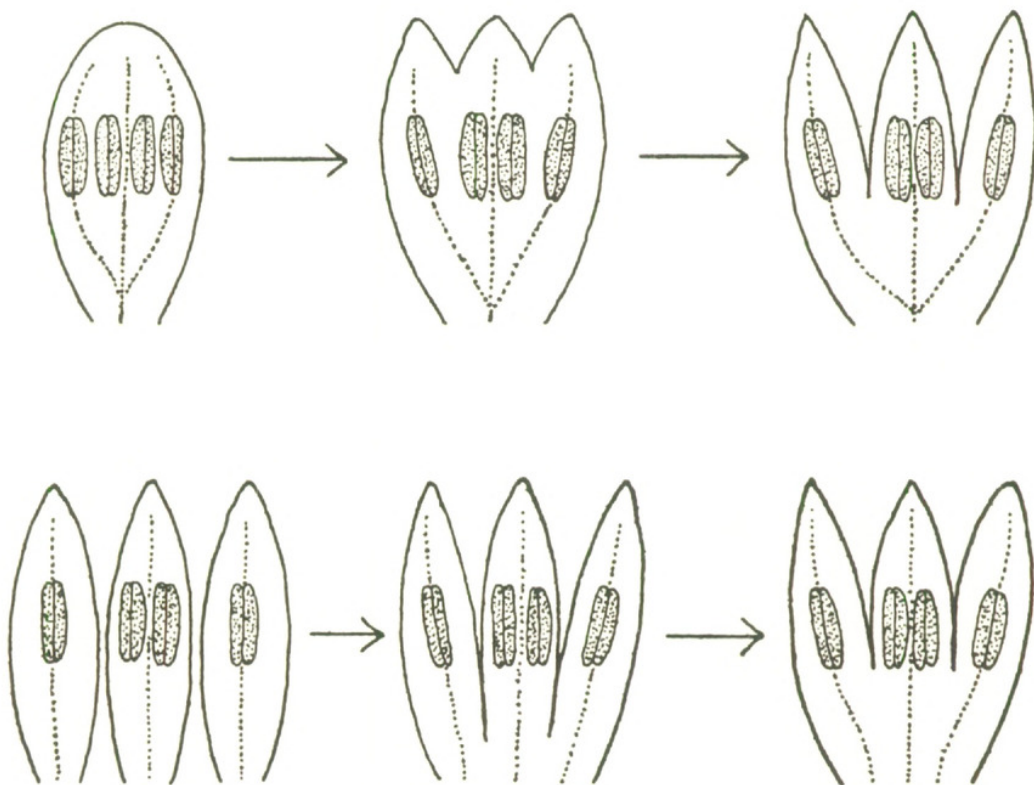
(i) The starting point as well as the second stage (see the upper series of diagrams in text-fig. 46) are purely hypothetical.

(ii) The trend of development does not explain why the cleavage should have taken place only between the lateral pairs of sporangia.

(iii) The pattern of vasculature of the androecium is not in keeping with the "split" or "partite" nature of a single stamen.

(iv) Ontogenetically, the androecial primordium does not start out as a single growing point and trifurcate at a later date,* as one may reasonably expect to be the situation according to this school of thought.

(v) The sequence of events is rather complicated and illogical.



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FIG. 46. Diagrams to illustrate the derivation of the androecium of *Chloranthus* according to the two current schools of thought. For explanation, see text.

Second school: There appear to be a number of features in favor of this type of derivation:

(i) All the stages depicted in the lower series of diagrams in text-fig. 46, are actually the existing conditions among the several species of the genus, and no hypothetical steps are involved.

(ii) The trilobed appearance can be easily explained as being a resultant of lateral fusion of the bases of the three stamens.

* Payer, 1857, p. 422; also unpublished observations by the author on *C. spicatus* and *C. japonicus*.

(iii) Each of the three stamens receives one vascular bundle; the bundles have independent origins in the eustele of the inflorescence axis, and are not branches of any one single "fascicular strand."

(iv) Ontogenetically, the primordia of the three stamens are separate from the beginning, the basal cohesion becoming apparent only during later stages.*

(v) The sequence of events is relatively simple, direct, least involved and in harmony with other types of evidences.

Thus, a totality of available evidence appears to afford considerable support for the second school of thought, — that is, to regard the androecial structure of *Chloranthus* as being constituted of three stamens. Whether this interpretation would help towards an understanding of the morphological nature of the "stamens" and "staminal appendages" that are encountered in the families Monimiaceae, Gomortegaceae, and Lauraceae, or whether the so-called appendages of the stamens in these families are "*de novo*" structures as proposed by Kasapligil (1951) for *Umbellularia* and *Laurus* of the latter family, will be discussed in future contributions.

COMPOSITION OF THE FAMILY

The exomorphic and endomorphic characters of both vegetative and reproductive structures in the family exhibit diverse levels of evolutionary modifications. Thus, while the xylem of *Sarcandra* has retained a vesselless nature and that of other genera a decidedly low level of structural specialization, the reproductive structures of all four genera illustrate in general advanced stages of phylogenetic modifications involving a total loss of perianth whorls (excepting perhaps in *Hedyosmum*), and a reduction in the number of essential organs per flower. The rather lax arrangement of flowers on the inflorescence axis in *Sarcandra*, *Chloranthus*, and *Ascarina* has shifted over to a more compact aggregation in *Hedyosmum*, and in some species of this genus this tendency culminates in the fusion of individual flowers with one another and with the inflorescence axis. In all the genera, the gynoecium is represented by a single pistil, and the androecium, by three stamens (*Chloranthus*), or two (species of *Ascarina*), or one (species of *Ascarina*, and *Hedyosmum*). The flowers of *Chloranthus* and *Sarcandra* are bisexual, whereas those of the other two genera are unisexual. Although the pollen grains of *Sarcandra* are acolpate with a coarsely reticulate sculpturing of the exine, a tendency towards the elimination of the germinal furrows and towards the development of finer grades of similar sculpturing are strongly seen in *Chloranthus* and *Hedyosmum*; *Ascarina* possesses typically monocolpate pollen. Structural characters of the vegetative parts of the different genera also exhibit several trends of modification. The leaves of *Ascarina* are supplied with two strands of vascular tissue from a single "gap"; in *Hedyosmum*, the two strands undergo precocious splitting and recombination so that there are five leaf-

* See foot-note on the preceding page.

strands at the nodal level; in *Chloranthus* and *Sarcandra*, not only this tendency is present, but also the addition of marginal strands originating from two "common gaps." The stipules of *Sarcandra*, *Chloranthus*, and *Ascarina* are small and denticular, whereas those of *Hedyosmum* are comparatively larger and variously fringed. The stomata of *Sarcandra* and *Chloranthus* have their subsidiary cells oriented parallel to the guard cells, while those of *Ascarina* and *Hedyosmum* have a rosette of ordinary epidermal cells. Although the evolutionary gap between the vesselless xylem of *Sarcandra* and the vessel-bearing xylem of the other genera is considerable, in the latter group the general level of specialization of the tracheary cells has remained relatively primitive. Among the many tissues of the xylem also there are minor divergences; for example, the retention of essentially erect cells in the mature multiseriate rays and the vasicentric distribution of wood parenchyma in *Hedyosmum*.

Furthermore, there are the following characters or trends shared by all the four genera: decussate phyllotaxy; petiolar bases of opposite leaves fused to form a vaginate sheath; serrate-dentate leaf margin; absence of typical palisade tissue in the leaf; unilacunar node or a type derived therefrom; an essentially "double" median strand of the leaf; presence of "ethereal oil cells" in the parenchymatous tissues of stem, leaf, and flower; a fundamentally similar type of inflorescence with little or no variation; highly reduced floral parts with a single pistil of a uniform shape and construction; absence of perianth; single orthotropous ovule with two integuments and massive nucellus, hanging from the apex of locule; seed with a relatively small embryo and abundant endosperm.

It will be clear from the account in the preceding two paragraphs that the relative rates of specialization of the different organs and tissues in the four genera are by no means synchronized. Every one of the genera exhibits a combination of most of the characters or trends as mentioned above; also, it often happens that one or two characters or trends may be lacking in any one genus while they are always, either as such, or with slight modifications, present in the other genera. This situation is indicative of a relatively intimate reticulate relationship among the generic units. Therefore any attempt to remove from the Chloranthaceae either *Sarcandra* solely upon the basis of its having a vesselless xylem, or *Hedyosmum* on account of its possession of a so-called perianth, or any other genus upon some other slender basis, would be unwarranted. Nor is it justifiable to arrange the genera in a definite sequence to imply that one is directly derived from the other. In other words, all the available evidence emphasizes the desirability of treating the four genera as members of a single family.

Whether the genera should be further classified under sectional heads within the family, or should be left as such depends largely upon the degree of emphasis given to the taxonomic characters employed by the proposer. It should be noted, however, that there are several characters that may be employed as sectional criteria, if one is intent upon such a classification. But any such classification is bound to be artificial, because

the relative rates of evolutionary modifications in the different parts and tissues of the four genera are at variance, and the interrelationships of the genera are profusely reticulate. Furthermore, the number of genera in the family being small, there do not appear to be cogent reasons for recognizing categories within the ranks of the family.

However, an artificial key for the ready identification of the genera is by no means undesirable. Four examples are given below, which further exemplify the reticulate nature of the interrelationships:

I. Key based on the type of sex-expression and on floral structure.

Flowers bisexual.

Stamen 1. *Sarcandra*.

Stamens 3. *Chloranthus*.

Flowers unisexual.

Male flowers bracteate. Female flowers naked. *Ascarina*.

Male flowers ebracteate. Female flowers enveloped by a cupule.
..... *Hedyosmum*.

II. Key based on the habit and characters of the xylem.

Habit suffrutescent, or herbaceous.

Xylem vesselless. *Sarcandra*.

Xylem vessel-bearing. *Chloranthus*.

Habit arborescent or shrubby.

Cells of mature multiseriate rays square to procumbent, appearing as somewhat isodiametric in tangisection. *Ascarina*.

Cells of mature multiseriate rays upright to square, appearing vertically elongate in tangisection. *Hedyosmum*.

III. Key based on the characters of the androecium and the pollen.

Stamens 1, club-shaped or discoid; anther quadrilocular.

Pairs of sporangia separated by connective; pollen acolpate with a coarsely reticulate exine. *Sarcandra*.

Pairs of sporangia close together, latrorse; connective ending in a conical or pointed apex.

Pollen grains monocolpate. *Ascarina*.

Pollen grains polycolpate to acolpate. *Hedyosmum*.

Stamens 3, basally connate; median one bearing two pairs of sporangia, and each of the laterals a single pair; pollen polycolpate. *Chloranthus*.

IV. Key based on the nodal anatomy and characters of the pith.

Nodes typically of the unilacunar type.

Vascular strands of the leaf two, of equal size (at the nodal level). ...
..... *Ascarina*.

Vascular strands of the leaf five, lateral pairs larger, median strand smaller (at the nodal level). *Hedyosmum*.

Nodes of a modified unilacunar type.

Clusters or diaphragms of stone cells absent in the pith. . *Chloranthus*.

Clusters or diaphragms of stone cells present in the pith. . . *Sarcandra*.

The distinctive combination of characters of each genus may be briefly mentioned as follows:

1. *Ascarina* Forst. Trees, dioecious; xylem vessel-bearing, but retaining a relatively unspecialized level; node unilacunar and related to two

leaf strands; no stone cells in pith; flowers subtended by 1 or 3 bracts; perianth absent; male flower: stamen 1; female flower: pistil 1, with an unequally bilipped sessile stigma; pollen monocolpate with minutely reticulate-pitted exine and warty-papillate intine in the region of colpa.

GEOGRAPHICAL DISTRIBUTION: The Philippines, Malaysian and Polynesian Islands.

2. *Chloranthus* Sw. Suffrutescent or perennial to annual herbs; xylem vessel-bearing, but retaining a relatively unspecialized level; node of a modified unilacunar type, the marginal strands of opposite leaves originating from two "common gaps"; three leaf strands related to the median "gap"; no stone cells in pith; flower bisexual, subtended by a single bract; pistil 1, stigma capitate and sessile; stamens 3, basally confluent and partly adnate to pistil; median stamen with two pairs and lateral ones each with a single pair of sporangia; pollen polycolpate with ill-defined, irregularly distributed, and somewhat reduced germinal furrows; sculpturing of exine finely reticulate-pitted.

GEOGRAPHICAL DISTRIBUTION: Essentially in South-eastern China, two or three species extending eastwards into Japan and southwards into the Philippines, Burma and Indonesia.

3. *Hedyosmum* Sw. Trees or shrubs; xylem vessel-bearing, but retaining a decidedly low level of specialization; node unilacunar, related to five leaf strands; flowers unisexual; subtending bract in the male flower absent; stamen 1; female flower: "perianth" cupular, adnate at the neck of the pistil; pistil 1, style absent, stigma short, tail-like, papillose; pollen polycolpate to acolpate; colpa ill-defined and reduced; sculpturing on the exine finely reticulate-pitted.

GEOGRAPHICAL DISTRIBUTION: Essentially in Central and Latin America, only one species in the Far-east.

4. *Sarcandra* Gardn. Suffrutescent; xylem vesselless; nodal structure as in *Chloranthus*; subtending bract of flower 1; flower bisexual; pistil 1; stigma sessile, capitate; stamen 1, quadrilocular, partly adnate to pistil; pollen acolpate; exine with a coarsely reticulate sculpturing.

GEOGRAPHICAL DISTRIBUTION: Southern China, Japan, the Philippines, Malay Peninsula and Archipelago, Assam, Indo-China, South India, Ceylon.

AFFINITIES OF THE FAMILY

An historical resume of the family with particular reference to its presumed relationships suggested from time to time has been given by Thierry (1912). A synoptic review of literature reveals that prior to the establishment of the family Chloranthaceae by Bentham and Hooker (Gen. Pl. [1880] 134), *Chloranthus* was relegated to the Loranthaceae by Jussieu, and to the Caprifoliaceae by Sprengel; and that after the creation of the family to accommodate the three genera, *Ascarina*, *Chloranthus*, and *Hedyosmum*, the following views have been expressed as to the relationships of the family:

(1) Brongniart placed it in his Santalinae, stressing the similarity be-

tween the two groups as evidenced in the absence of corolla, single ovary, calyx adnate to ovary, and suspended ovules. The last character is obviously unfortunate because, in the Santalales, the ovules are suspended from the apex of a basal pillar-like placental column, whereas in the Chloranthaceae the ovules arise directly from the roof of the locule.

(2) Endlicher, because of the presence of naked flowers, unilocular ovary with an orthotropous ovule, and drupaceous fruit treated the family as being related to the Ceratophyllaceae. Cordemoy also agreed with this view.

(3) Van Tieghem classified the family (together with the Ceratophyllaceae) among the apetaleae, distinguishing the Platanaceae and Chloranthaceae only on the possession of an achene in the former family and of a drupe in the latter.

(4) Lindley placed the family in his 39th group, the Piperales, the segregation being based upon the possession of erect ovule and of opposite or alternate leaves with or without stipules in the "Piperinae," and the possession of suspended ovule and opposite leaves with intermediate stipules in the Chloranthaceae. *This view has been universally maintained ever since by botanists in general.*

(5) Hallier also first (1905) followed Lindley, but in a later contribution (1912) suggested a relationship to the Monimiaceae.

Almost all proposals mentioned above in regard to the affinities of the family are based upon characters obtained through a study of specific selected parts of plants, and with an especial emphasis on similarities of such parts between the groups concerned. It is becoming increasingly evident that any proposal involving the phylogeny of an individual or of a group not based upon a summation of evidence from *all* parts of the plant in the first case, or in addition, from at least a majority of representatives in the second case, is unreliable. Likewise, an excessive emphasis on mere resemblances between two groups in attributing natural relationships deliberately ignores the fact that similarities commonly are due to parallel evolutionary trends.

It is true that specific parts of the chloranthaceous genera bear similarities to homologous parts of the families that are suggested to be its nearest relatives. But a totality of evidence fails to support such proposals. The possession of monocolpate pollen or of types phylogenetically derived therefrom, and of "ethereal oil cells" by the representatives of the Chloranthaceae rule out the possibility of bringing the family in relationship with any of such families as the Loranthaceae, Caprifoliaceae, Santalaceae, Ceratophyllaceae, or the families of the Urticales. At the same time, this combination of features of the Chloranthaceae speaks of a decidedly ranalian affinity. Within the Order Ranales (*sensu lato*), the Chloranthaceae may be associated with the Piperaceae, Saururaceae, and Lactoridaceae, implying a rather intimate phylogenetic bond among the families.

Whether these four families really represent as natural an assemblage

as has been assumed to be until now — or to be more specific, does the Chloranthaceae fall in line with the other three families — remains to be critically examined. The Chloranthaceae exhibits, in addition to the vesselless xylem in one genus, a decidedly primitive cambium composed of very long fusiform initials with extensively overlapping ends in the other three genera; the derivative tissues of the cambium on the xylem side show comparatively slight phylogenetic specialization. Thus, the vessels are long with steeply inclined end walls that bear very numerous scalariform perforations, and the other xylary tissues, on the whole, also exemplify a relatively unmodified primitive condition. The xylem of the Piperaceae, Saururaceae, and Lactoridaceae, on the other hand, bears distinct evidences of a rather highly evolved type: the fusiform initials of the cambium as well as their derivatives are comparatively very short, as also the vessel members that have conspicuously truncated ends with typical porous perforations; there is a predominant tendency for the almost complete elimination of the uniseriate rays; the imperforate tracheary cells are of the fiber or of the libriform type; in the Piperaceae, cortical and medullary bundles and anomalous secondary growth are of very general occurrence; and in the woody representatives of this family the cambium and one or more of its derivative tissues are often stratified. Such a conspicuously wide gap existing between the over-all primitive organization of the cambium and xylem of the Chloranthaceae on the one hand, and the general highly advanced situation of the corresponding tissues of the Piperaceae, Saururaceae, and Lactoridaceae on the other, serve to question the wisdom of including the Chloranthaceae in alliance with the latter families.

The occurrence of conspicuously wide rays in the Chloranthaceae has been frequently mentioned as an evidence of relationship of this family to the Piperaceae. This character by itself does not provide a reliable basis, as such rays are known to occur sporadically throughout the dicotyledonous families (Dadswell and Record, 1936); furthermore, a strong tendency towards excessive widening of rays characterizes certain genera of the Lauraceae, Monimiaceae, Berberidaceae, etc., in the Order Ranales itself.

The nodal anatomy in the Chloranthaceae (as also in the Lactoridaceae, the morphology and relationships of which will be discussed in a future contribution) is of the unilacunar type or of a derived pattern of this category; in sharp contrast, the situation in the Piperaceae and Saururaceae is typically of the multilacunar type. Furthermore, the median leaf strand in the Chloranthaceae (and Lactoridaceae) is invariably "double" in origin, although the two strands may subsequently dichotomize and reunite to result in an odd number of bundles. But, in the other two families, the corresponding strand shows specialized trends of modification resulting in a single strand that splits into three bundles in the base of the petiole.

The pollen of the Piperaceae and Saururaceae appear to have undergone a particular trend of specialization that has resulted in the formation of uniformly small-sized grains with very faint or no sculpturing on the exine, and with a single germinal furrow. Although the pollen grains of *Ascarina* are monocolpate, those of the other genera show a polycolpate condition

with a strong tendency towards the elimination of germinal furrows. This trend has culminated in the acolpate grains of *Sarcandra* and of some species of *Hedyosmum*; the exine in all genera exhibits a reticulate-pitted sculpturing of varying grades; the grains in general are relatively large.

Undue emphasis has been given in the past to certain similarities in the floral structure of the Chloranthaceae and Piperaceae. The most important of such characters are the apetalous nature and the presence of a single orthotropous ovule. That an apetalous nature of flowers is not always a trustworthy and decisive criterion in determining natural affinities is becoming more and more obvious by detailed investigations of all parts of plants and by critical evaluation of summations of the data thus obtained. To mention an example from the Ranales itself: "such strange bedfellows as *Eucommia*, *Cercidiphyllum*, *Euptelea*, and *Trochodendron*" were included by a large number of botanists in the Trochodendraceae, the decision to do so being "based largely, if not entirely, upon the absence of a perianth" (Nast and Bailey, 1946). But a careful analysis of all pertinent characters has emphasized the high degree of diversified evolutionary modifications among these genera and has yielded convincing evidence to establish independent families to accommodate the respective genera. In regard to the presence of an orthotropous ovule, it must be admitted that this feature need not necessarily indicate a true relationship. The very fact that orthotropous ovules occur in many unrelated families suggests that its development may as well be due to parallel evolutionary trends.

Unfortunately, the utilization of such characters as the opposite or alternate phyllotaxy, presence or absence of stipules, pinnate or palmate venation of the leaves, "haplocheilic" or "syndetocheilic" type of stomata, differentiation of a hypodermis, etc., in phylogenetic considerations is at present handicapped by a lack of proper understanding in regard to their evolutionary trends of specialization. Instances are numerous where pairs of such differential characters are present in one and the same family or even in the same genus. For example, in the Monimiaceae (Money, Bailey and Swamy, 1950) both types of stomata and also some intergrading conditions occur; a hypodermis of one, two, or three layers is differentiated in some, but not in other genera. Until extensive surveys of such features are accomplished on angiosperms *as a whole*, and information obtained as to the probable phylogenetic tendencies in the modification of these characters, it is inadvisable to employ indiscriminately such features in discussions of putative relationships.

Although the available embryological information on the Chloranthaceae is rather meagre to allow detailed comparisons with the Piperaceae and Saururaceae, it provides certain significant points of differences that merit consideration. The female gametophyte in the Chloranthaceae develops according to the *Polygonum*-type (Armour, 1906; Edwards, 1920), whereas in the Piperaceae, the development follows the tetrasporic types. The endosperm in the latter family fluctuates between nuclear (in *Piper*, *Hackeria*) and cellular (in *Peperomia*) types; that in the Chloranthaceae is cellular. Furthermore, the first and next few divisions of the primary

endosperm nucleus in *Hedyosmum* result in wall formation that are predominantly transverse, while in the Piperaceae (*Peperomia*) the first division results in the formation of a vertical wall. Again, in the Piperaceae, the first wall in the zygote is vertical, and that in the Chloranthaceae transverse. A much more consistent and reliable point of difference between the Chloranthaceae on the one hand, and the Piperaceae and Saururaceae on the other, occurs in the mature seed. In the seeds of the Chloranthaceae, the endosperm is abundant, the embryo being embedded in this tissue; and there is no perisperm. In the seeds of the Piperaceae and Saururaceae, the embryo is embedded in a relatively insignificant quantity of endosperm; and the major bulk of the seed cavity is filled with perisperm.

As suggested in a previous paper (Money, Bailey and Swamy, 1950), the ranalian families possessing monocolpate pollen and phylogenetically derived dicolpate, polyporate and acolpate pollen, and having "ethereal oil cells" fall into two distinct categories:

Category I: NODES UNILACUNAR

Austrobaileyaceae	Hernandiaceae
Trimeniaceae	Chloranthaceae
Amborellaceae	Calycanthaceae
Monimiaceae	Lactoridaceae
Gomortegaceae	

Category II: NODES TRILACUNAR OR MULTILACUNAR

Winteraceae	Myristicaceae
Degeneriaceae	Eupomatiaceae
Himantandraceae	Canellaceae
Magnoliaceae	Piperaceae
Annonaceae	Saururaceae

A summation of cumulative evidence — in particular, a decidedly low level of structural specialization of the cambium and xylem, the essentially unilacunar nodal anatomy, and the nonperispermous seeds — not only provides valid negation to aligning the Chloranthaceae with the Piperaceae and Saururaceae, but also affords positive evidence for placing the family in category I.

CONCLUSIONS

Morphological:

(1) The general level of structural specialization of the cambium and the tissues of the xylem derived therefrom is relatively primitive

(2) The nodal anatomy is of the unilacunar type or a modification therefrom.

(3) The flowers in general appear to have undergone reduction both in regard to the number of floral parts and vasculature.

(4) Pollen of the monocolpate type and two of its derived types — polycolpate and acolpate — occur in the family.

(5) There is no evidence at present either to regard the flowers of *Sarcandra* and *Chloranthus* as possessing a reduced perianth or to interpret the individual flowers as reduced or composite inflorescences.

(6) Conclusive evidence is wanting to attribute a perianthial nature to the cupular envelope of the gynoecium in *Hedyosmum*.

(7) Available evidence appears to afford considerable support to the view that the androecium of *Chloranthus* is constituted of three stamens, rather than that it represents a single stamen split into three parts.

Systematic and phylogenetic:

A totality of evidence obtained through a study of exomorphic and endomorphic characters warrants the following observations:

(8) The included genera — *Ascarina*, *Chloranthus*, *Hedyosmum*, and *Sarcandra* — of the family exhibit profuse reticulate interrelationships, and as such there are no valid reasons to remove any of them from the family.

(9) The Chloranthaceae exhibit significantly diverse trends of phylogenetic modification as compared with the Piperaceae and Saururaceae. Therefore, the Chloranthaceae deserve to be dissociated from their present piperaceous alliance.

(10) The nearest relatives of the Chloranthaceae are those families of the ranalian affinities that possess monocolpate pollen, "ethereal oil cells," and unilacunar nodes.

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- PRESIDENCY COLLEGE,
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EXPLANATION OF PLATES

PLATE I

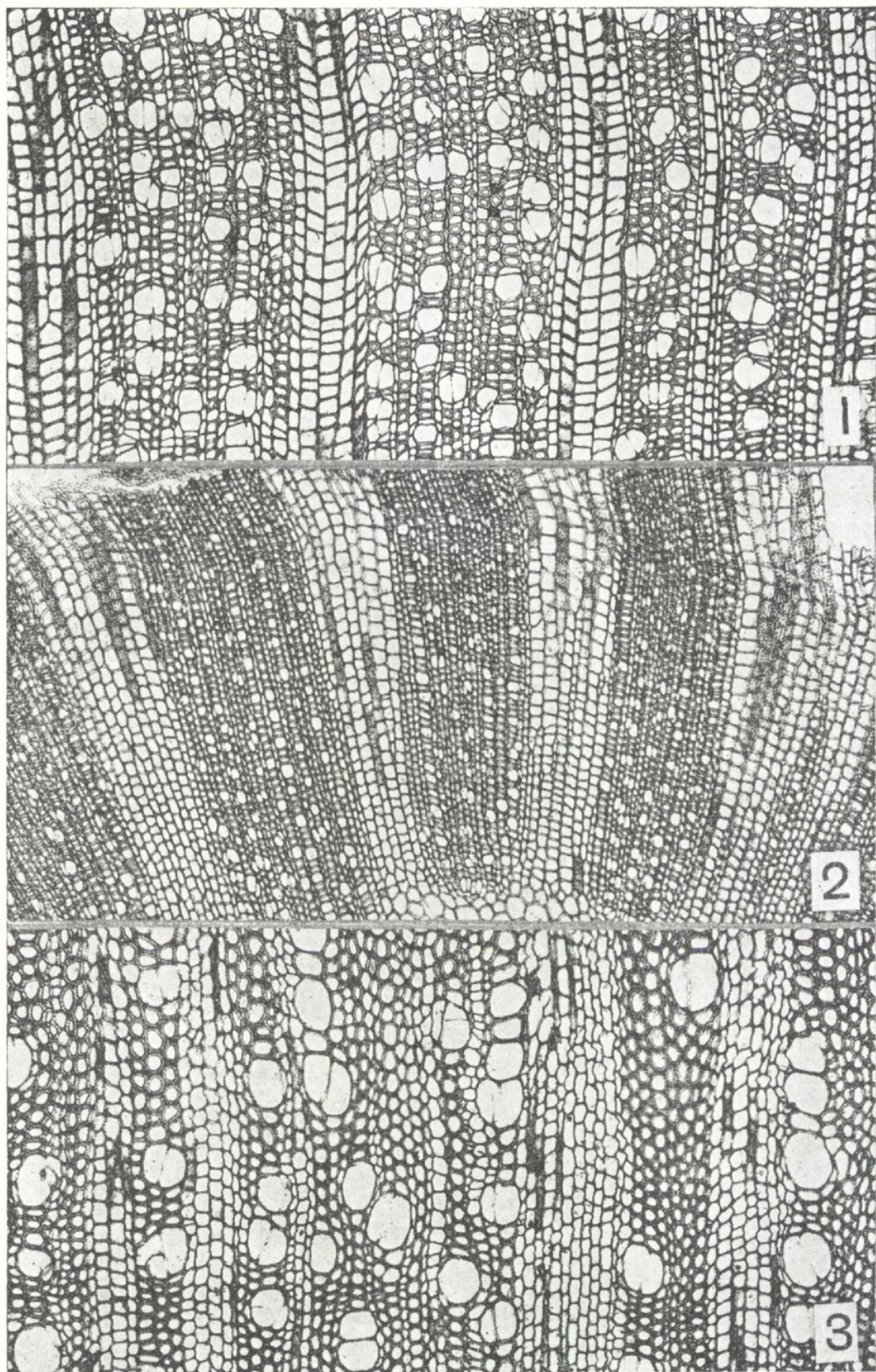
FIG. 1. Transection of secondary xylem of *Ascarina lanceolata*, $\times 50$. FIG. 2. Transection of secondary xylem of *Chloranthus officinalis*, $\times 50$. FIG. 3. Transection of secondary xylem of *Hedyosmum nutans*, $\times 50$.

PLATE II

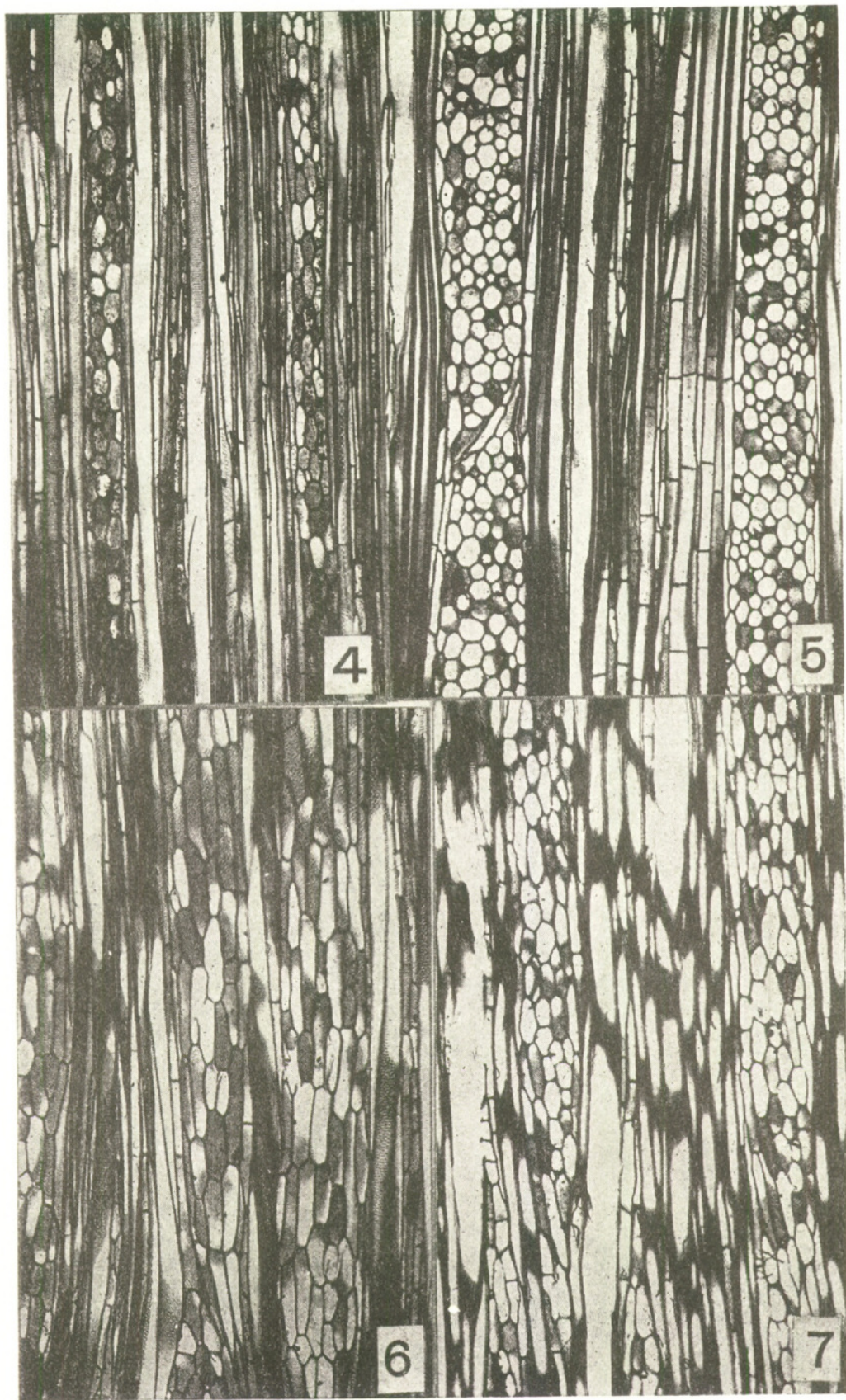
FIG. 4. *Ascarina lanceolata*, tangisection through the earlier formed part of secondary xylem. FIG. 5. Same, through later formed secondary xylem. FIG. 6. *Hedyosmum scabrum*, tangisection through the earlier formed part of secondary xylem. FIG. 7. Same, through later formed part of secondary xylem. All photographs, $\times 60$.

PLATE III

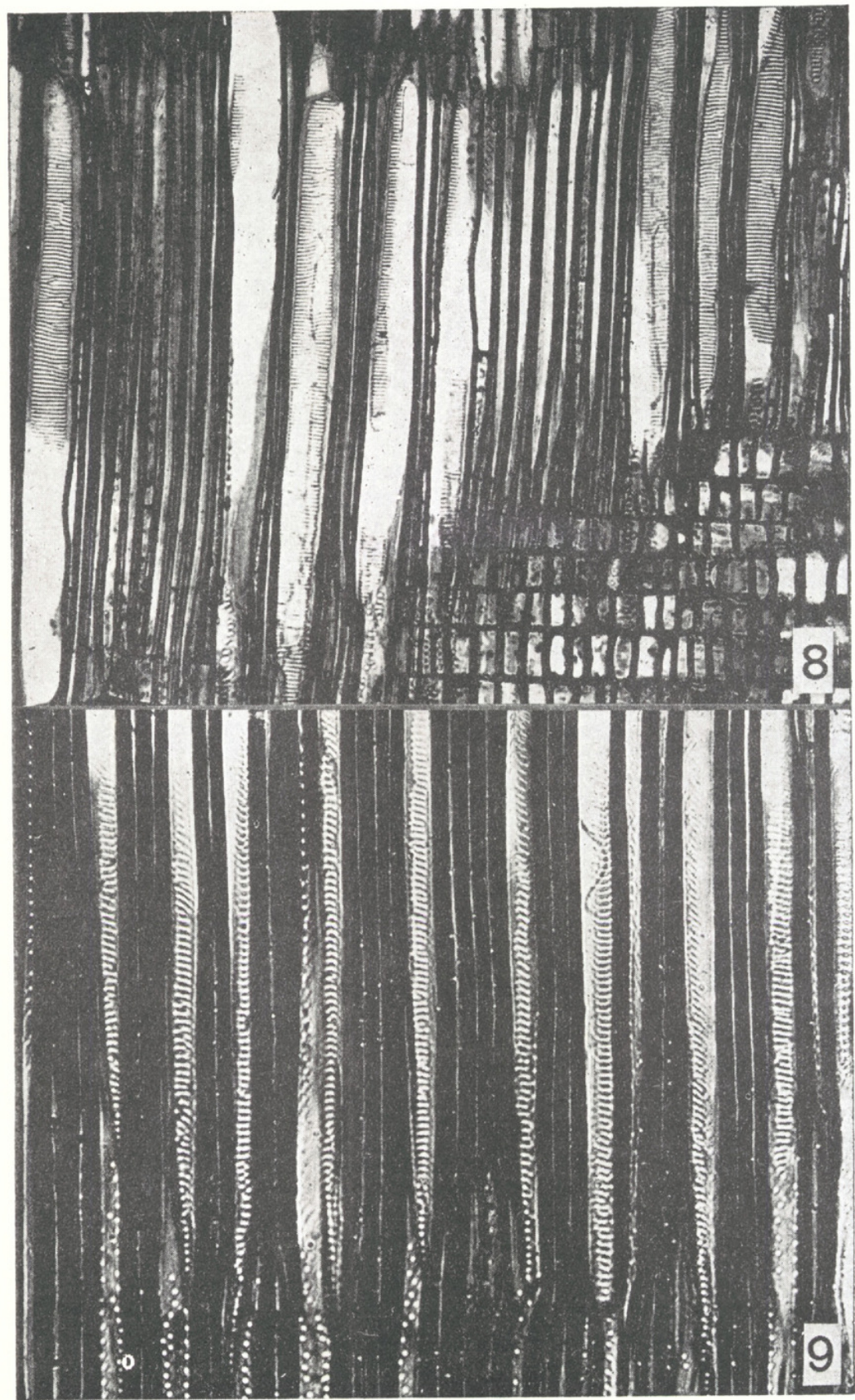
FIG. 8. Radial-longisection through mature secondary xylem of *Hedyosmum nutans*, $\times 60$. FIG. 9. Radial-tangisection through mature secondary xylem of *Chloranthus officinalis*, $\times 75$.



SWAMY, MORPHOLOGY OF THE CHLORANTHACEAE



SWAMY, MORPHOLOGY OF THE CHLORANTHACEAE



SWAMY, MORPHOLOGY OF THE CHLORANTHACEAE



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