Floral Anatomy of the Santalaceae and Some Related Forms

FRANK H. SMITH,
ASSISTANT PROFESSOR OF BOTANY
ELIZABETH C. SMITH

OREGON STATE COLLEGE
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EXPLANATION OF PLATES

The semidiagrammatic illustrations were drawn at various magnifications with the aid of a camera lucida. The magnification used for each figure was determined by the size of the section and the detail to be shown. In general, illustrations of sections of the pedicel and basal portions of a flower are reproduced at greater magnifications than those of the upper portions. Sections of small flowers are reproduced at greater magnifications than those of large ones.

The labels used are listed below together with their meanings.

B	bract or bract trace
B-Se	trace composed of fused bract and sepal traces
C	commissural trace located between sepal positions
D	disk
DC	dorsal carpellary trace
P	petal trace
P-St	trace composed of fused petal and stamen traces
RB	recurrent bundles of the receptacle
RT	residual vascular tissue
S	xylem-like sclerenchyma
Sa	seta or trace to seta of *Myzodendron*
Se	sepal trace or traces
Se-St	trace composed of fused sepal and stamen traces
St	stamen trace
VC	ventral carpellary trace or traces
X	traces that arise from the recurrent bundles and move inward to positions between the dorsal carpellary traces

PREFACE

The nature of the inferior ovary has been under discussion for many years. There are two theories regarding the morphology of the inferior ovary that have been widely accepted by various botanists. According to the first, the appendicular theory, an inferior ovary results from extreme adnation with the sepals, petals, and stamens fused with each other and with the ovary wall. Thus the outer tissues of such an inferior ovary consist of the fused bases of the floral appendages. According to the second, the receptacular theory, an inferior ovary results from invagination of the floral axis so that the ovary itself is embedded in tissues of the receptacle. Thus the outer tissues of such an inferior ovary are axial or receptacular in nature. A third possibility that has been suggested is that an inferior ovary may consist of receptacular tissues in the lower portion and floral tissues above. This situation occurs in the floral cup of several genera of the Rosaceae (Bonne, 1925, 1928 and Jackson, 1934). These are forms with perigynous flowers, however, and the ovary is not inferior. The structure of the apple has also been interpreted in this manner but incorrectly so, as was shown by MacDaniels (1940). The sepals, petals, and stamens of a flower with an inferior ovary appear to be borne on or above the ovary. This would be an actual fact in a receptacular inferior ovary but only apparent for the appendicular type, since in the latter the floral parts originate below the ovary, as in an hypogynous flower, but are so fused with the ovary in their lower portions as to lose their identity.

While the appendicular theory is probably older than the receptacular theory, the latter has been, until recent years, more widely accepted. This was due primarily to the work of Payer (1857) and other developmental morphologists. In general, taxonomists still describe the inferior ovary in terms of the receptacular theory. The work of Eames (1931) and his collaborators has shown rather conclusively that the inferior ovary in the great majority of plant families is the result of adnation and hence is appendicular in nature. Thus the appendicular theory has come to be accepted by most plant anatomists of recent times.

The authors recently described the floral anatomy of *Darbya* in which the inferior ovary is interpreted as receptacular. It was specifically stated, however, that this interpretation applies only to the Santalaceae. Acceptance of the receptacular theory for this family does not deny the existence of the appendicular inferior ovary in other families. In fact, the evidence used to support the receptacular nature of the inferior ovary in the Santalaceae may also be considered as confirming the appendicular nature of the inferior ovary in other forms. This is so because the anatomy of the receptacular inferior ovary is so characteristic and entirely distinct from that of the appendicular type. The floral anatomy of the inferior ovary as it occurs in the higher monocots and in most of the higher dicots, can be adequately interpreted only in terms of cohesion and adnation, while the anatomy of the inferior ovary in the Santalaceae seems impossible of explanation except in terms of invagination of the floral axis. There has been a tendency on the part of some botanists to assume that these two theories are mutually exclusive, and that to accept one is to reject the other. The inferior ovary has undoubtedly appeared independently in different plant lines and there is no reason why all should have the same structure. For example, in the Olacaceae, a few species of which are described in this paper, it seems likely that two and perhaps all of the three possible types of inferior ovary occur in this one family.

Assuming that the receptacular nature of the inferior ovary in *Darbya* has been established, the primary purpose of this publication is to describe the many modifications in structure of the receptacular inferior ovary as it occurs in the Santalaceae. Some additional species in other families of the Santalales were also studied in an attempt to trace the origin of the receptacular inferior ovary in the Santalaceae and to obtain some indication as to relationships within the order.

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FRANK H. SMITH
ELIZABETH C. SMITH

Department of Botany
Oregon State College
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Floral Anatomy of the Santalaceae and Some Related Forms

INTRODUCTION

The Santalales comprise a heterogeneous group that has received much attention from the taxonomist but little from the floral anatomist. Relationships are somewhat obscure and the position of some groups is much in doubt. The taxonomic literature, almost without exception, describes the inferior ovary of the Santalaceae, Grubbiaceae, Myzodendraceae and Loranthaceae as embedded in tissues of the receptacle. This interpretation seems to be based for the most part on popular adherence to the receptacular theory of the nature of the inferior ovary rather than on anatomical evidence. The nature of the inferior ovary in the Santalales has been variously interpreted by the comparatively few floral anatomists who have studied species belonging to this order. Van Tieghem (1869b), from a study of *Thesium* and *Osyris,* and Dowding (1931), from a study of *Comandra* and *Arceuthobium,* concluded that the ovary is appendicular. But Schaeppi and Steindl (1937), from their work on *Osyris,* and Smith and Smith (1942), in their study of *Darbya,* considered the ovary to be receptacular though they did not agree entirely in their interpretations. Rao (1942) made rather minor examinations of floral anatomy in connection with a study of the embryo sacs of *Thesium, Santalum, Osyris* and *Scleropyron.* While no definite statement was made, his descriptions imply acceptance of the appendicular theory. He also stated that from the flower primordia there first develops the perianth followed successively by the androecium, gynoecium, and central placenta.

Investigators have disagreed in their interpretation of the stalk bearing the ovules in various members of the Santalales. This structure has been interpreted as consisting of carpel tissue only (Van Tieghem, 1869b and Smith and Smith, 1942), of axial tissue only (Johnson, 1889 and Rao, 1942), of axial and carpel tissue (Schaeppi and Steindl, 1937) and, on the basis of carpel polymorphism, of a whorl of reduced fertile carpels (Dowding, 1931, and Saunders, 1940).

The floral anatomy of the Santalales, especially of the Santalaceae, shows extreme variation between genera. This is probably to be expected since parasitic forms tend to become more highly diversified than nonparasitic forms. An attempt is made here to explain these variations in terms of the anatomical structure of *Darbya,* which is considered to represent a somewhat primitive condition of floral anatomy in the Santalaceae. In this family there are all gradations between perfect flowers and staminate and pistillate flowers with no trace of organs of the opposite type. In general only perfect or pistillate flowers are considered here since the structure of the inferior ovary is of primary interest.

For most species only herbarium material was studied. This method of investigation has decided disadvantages since it is impossible in most cases to study flowers of different ages. Also there were available only one or a few flowers of some species. While there may be some errors regarding minor details in floral anatomy, the authors believe that the descriptions of the major features are essentially correct. It was also necessary to use somewhat atypical flowers of some species, as for example a 5-merous flower instead of a more typical 4-merous one. The technique for handling herbarium material has been previously described (Smith and Smith, 1942).

To avoid confusion the nomenclature used in Engler and Prantl's "Natürliche Pflanzenfamilien" (1935) has been followed. Taxonomic descriptions are, for the most part, taken from the same source.

SANTALACEAE

The flowers of various species in the Santalaceae may be perfect or imperfect; and polygamous, monoecious and dioecious forms occur. The perianth is simple, consisting of four or five, seldom three, sepals. The stamens are as many as the sepals and are opposite to and usually adherent with them. The ovary is inferior, partly inferior or (in the Anthoboleae) essentially superior, with two to five carpels. The ovary contains a single locule or three to five locules at the base, merging into a single locule above. The ovules, which hang from the tip of a central placental stalk, number one to three, rarely four to five. The Santalaceae occur as trees, shrubs, or herbs and probably all are parasitic or semiparasitic. Usually there are small bracts below the flower which, in some species, have flowers in their axiles. These bracts may be large enough to enclose or partly enclose the flowers. The receptacle surrounds the ovary and is joined with it. In general the ovary occupies only the upper portion of the receptacle. The lower part is usually fleshy. There is a gradual transition between the stem and the fleshy, receptacular portion of the ovary. A disk is usually present but it receives no vascular supply. The lobes of the disk alternate with the sepals.

Pilger, in "Natürlichen Pflanzenfamilien" (1935), divided the family into the following three tribes, the last two of which are rather difficult to separate:

Tribe 1. Anthoboleae. Perianth hypogynous. Ovary superior, 1-loculed with a sessile ovule. Only the base of the ovary is embedded in the receptacle. As the fruit develops the receptacle becomes fleshy and enlarged.

Tribe 2. Osyrideae. Perianth more or less epigynous. The receptacle either does not extend above the ovary or it extends only a short distance above it as a bell-shaped structure, which is more or less covered by the disk.

Tribe 3. Thesieae. Perianth epigynous. Receptacle extends more or less above the ovary, usually in the form of a tube, and is not covered by the disk.

The genera to be discussed here are listed by Pilger in the following order:

- Anthoboleae
    - *Anthobolus*
    - *Exocarpus*
- Osyrideae
    - *Choretrum*
    - *Leptomeria*
    - *Henslowia*
    - *Jodina*
    - *Buckleya*
    - *Omphacomeria*
    - *Darbya*
    - *Pyrularia*
    - *Osyris*
    - *Geocaulon*
- Osyrideae—*Continued*
    - *Comandra*
    - *Nanodea*
    - *Myoschilos*
    - *Acanthosyris*
    - *Santalum*
    - *Colpoon*
    - *Eucarya*
- Thesieae
    - *Osyridocarpus*
    - *Thesidium*
    - *Thesium*
    - *Arjona*
    - *Quinchamalium*

This list includes all of the genera in the family with the exception of five belonging to the Osyrideae. The order of discussion followed in this paper is based on similarities in floral anatomy and is somewhat different from that followed by Pilger.

Darbya umbellulata A. Gray

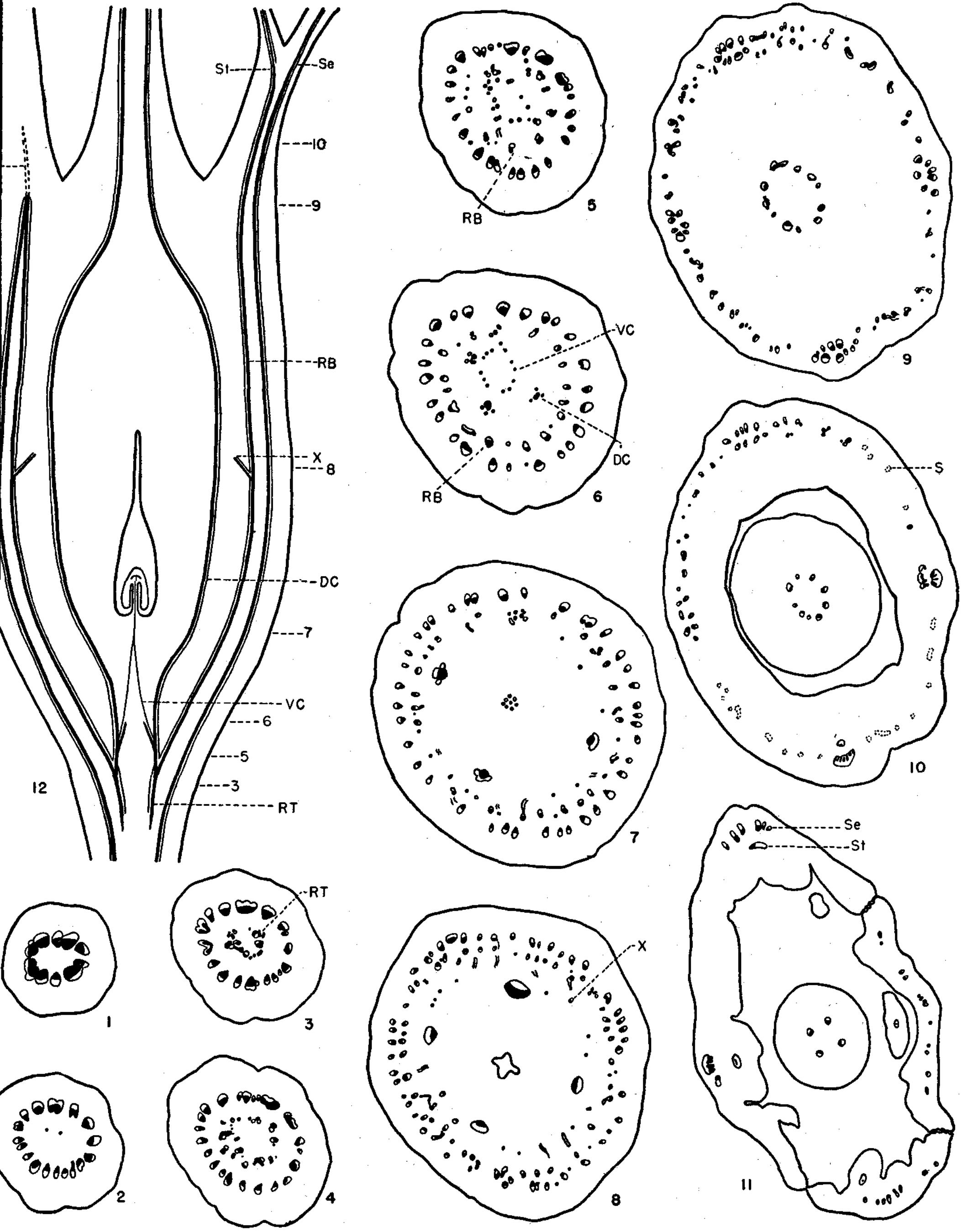
Since *Darbya* apparently represents a somewhat primitive condition in the Santalaceae, the floral anatomy of the pistillate flower is summarized briefly here even though it has previously been described (Smith and Smith, 1942).

The ovary is completely inferior with a single locule and a central placental stalk bearing two or three ovules at the tip. The disk is thin, has four or five lobes alternating with the sepals and is borne on the floral tube. The vascular tissue in the pedicel forms an almost continuous cylinder (Plate I, Figure 1). At the base of the ovary this cylinder begins to separate radially into numerous strands (Figure 2). These strands swing outward and pass up the outer portion of the ovary to approximately the level at which the floral tube is freed from the ovary. The number of traces in this ring of bundles continually increases by radial separation throughout this distance (Figures 2 to 8). A second ring of bundles is present inside the first for the full length of the ovary. These inner traces are inverted with the xylem located outside the phloem (Figures 4 to 8). At approximately the level at which the floral tube is freed from the ovary, the outer ring of normally oriented traces and the inner ring of inverted traces, except those in the positions of the sepals, come together in a series of anastomoses (Figure 9, and left side of Figure 12). This region is the only one in which there are strong connections between the two rings of bundles. Continuing upward from these connections there are a few short strands of xylem-like sclerenchyma (S, Figures 10 and 12). The traces in the two rings have been interpreted as axial or receptacular traces. The traces of the inner ring are considered to be inverted because of invagination of the tip of the floral axis. From this interpretation the outer ring of bundles may be referred to as ascending receptacular traces and the inner ring as recurrent receptacular traces.

Directly opposite the sepals the ascending and recurrent bundles do not connect at the top of the ovary as do the bundles between the sepal positions. Instead they swing closer together to form a large compound amphicribral strand with the individual traces rather loosely arranged (Figure 9). The inner traces opposite each sepal give rise to a single inverted trace (Figure 10) that then swings inward to enter the base of a stamen (Figure 11). The exact point of origin of the stamen trace is difficult to determine (Smith and Smith, 1942). The outer traces continue as large bundles for a short distance after the divergence of the stamen traces. At approximately the level at which the sepal lobes are differentiated, each trace divides radially to form the vascular bundles of the sepal (Figure 11).

Traces to the carpels originate near the ends of the recurrent traces. In cross sections of the base of the ovary the recurrent traces appear as xylem only, or as xylem and phloem in the inverted position (Figure 3). These traces soon form a complete ring, which gives off branches to the inside (Figures 4 and 5). Three or four branches are more strongly developed than the others. These are normal collateral bundles and they swing outward slightly at higher levels while the traces between them move inward (Figure 6). These inner traces, the ventral carpellary traces, move inward and form a compact strand of phloem, which enters the placental stalk (Figures 7 and 12). The larger traces, which are the dorsal carpellary traces, continue to swing outward for awhile and then pass upward through the

PLATE I



Darbya umbellulata

ovary. At approximately the level of the top of the locule branch traces (X, Figures 8 and 12) move inward from the ring of inverted traces and take up positions between the dorsal traces. Thus there is formed at this level a third ring of bundles with the xylem and phloem always normally oriented. This third or innermost ring may be referred to as the dorsal-X ring of bundles. As has been mentioned previously (Smith and Smith, 1942), the nature of the X-traces is in doubt. The dorsal-X traces swing inward at the top of the ovary and form anastomoses with each other just before the style is freed (Figure 9). A varying number of traces continue into the base of the style (Figure 10) but soon they all disappear except the dorsal carpellary traces (Figure 11) each of which extends to the base of a stigma lobe.

It is apparent that the portion of the recurrent bundles below the level of origin of the carpellary traces constitutes vascular tissue of the receptacle that is not used up in the formation of traces to the floral organs. This tissue is designated as residual. Since this is directed downward as a result of invagination, it also follows that the placental stalk must be composed entirely of carpellary tissues.

There are certain cross sections that are considered critical in the interpretation of floral anatomy in other members of the Santalaceae. Figure 3 illustrates a section at or below the base of the ovary, showing the residual tissue located apparently in the pith of the pedicel. Figure 5 shows the origin of the carpellary traces from the recurrent traces. Figure 7, taken just below the locule, shows the ascending receptacular traces, the inverted recurrent traces, the dorsal carpellary traces and, in the center, the strands representing the ventral carpellary traces that enter the placental stalk. Figure 8, taken through the upper portion of the locule, shows the ascending and recurrent traces and a third ring of normally oriented bundles, consisting of the dorsal carpellary traces plus the X-traces. Figure 9, taken near the top of the ovary, shows the sepal-stamen complexes and, between these, the anastomosing of the ascending and recurrent traces. It is in this region that the receptacular traces turn downward as a result of invagination. The extent of the xylem-like sclerenchyma (Figure 12) may indicate that the receptacle actually extends somewhat above this level.

Colpoon compressum Berg.

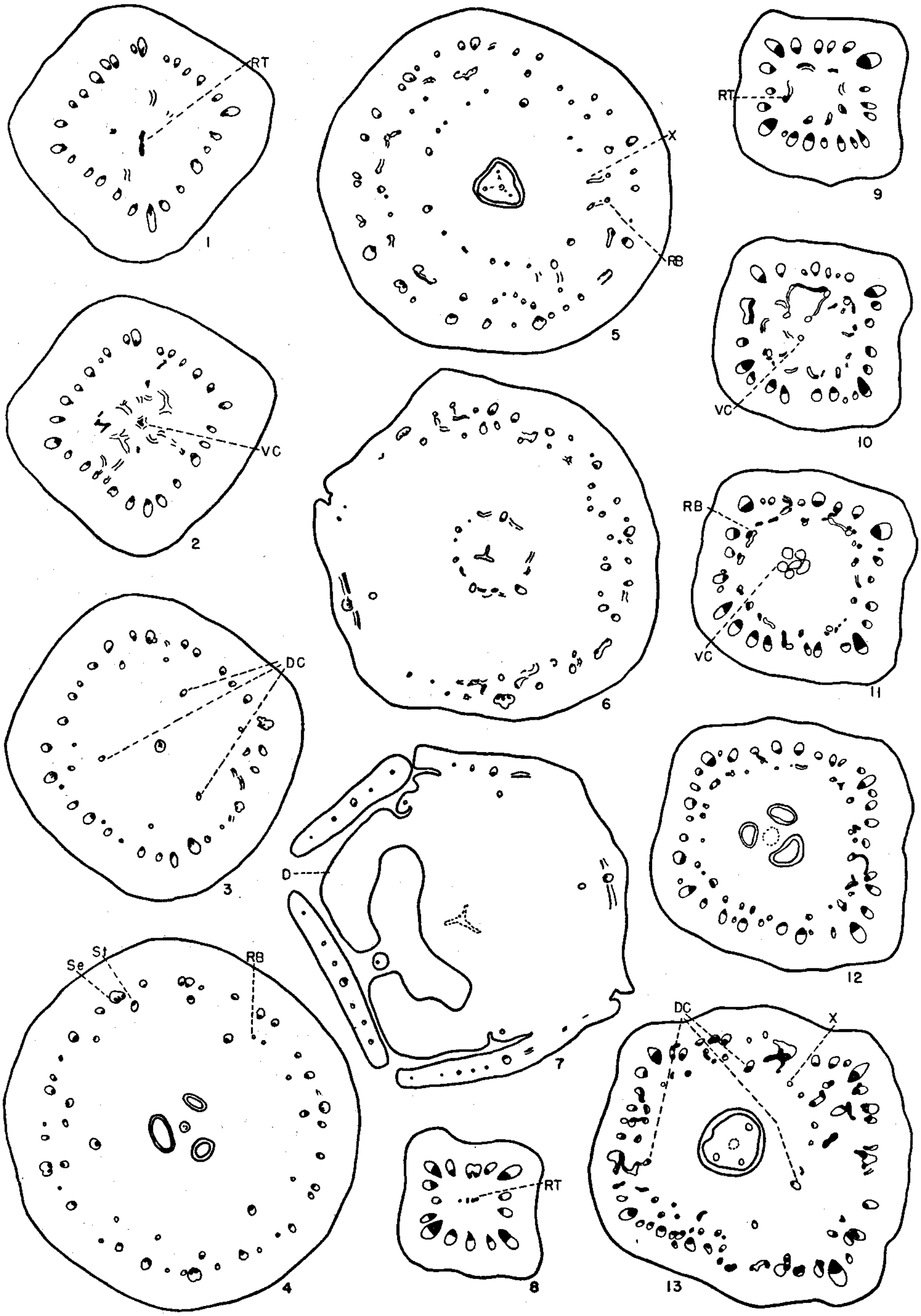
The flowers of *Colpoon* are perfect or pistillate with well developed staminodia. Although they are usually 4-merous, in the material available for this study they are 5-merous. There are three to five ovules suspended from a thick placental stalk. The lobes of the disk alternate with the sepals.

The floral tube is either very short or completely lacking. The four large traces in the pedicel above the bracts separate radially as the pedicel gradually enlarges so that numerous strands are present at the level at which the residual tissue first appears in the pith region (Plate II, Figure 1). Immediately above this level is a more or less saucer-shaped plate of vascular tissue in the center of the pedicel (Figure 2). There may be an occasional weak connection between the inner traces and the ascending receptacular bundles. From the central plate of tissue there are gradually differentiated a weak amphicribral bundle, the ventral carpellary trace, in the center; three stronger collateral bundles, the dorsal carpellary traces, toward the outside; and relatively few inverted recurrent traces between the dorsal carpellary traces and the ascending receptacular bundles. Thus in Figure 3, taken just below the locules, the traces in order from the center toward the outside are the fused ventral traces; the three dorsal carpellary traces; the recurrent traces, which are inverted or represented only by phloem; and the ascending traces.

Colpoon, unlike *Darbya,* has separate locules throughout the length of the ovules (Figure 4). These locules merge into one approximately at the level of attachment of the ovules (Figure 5). As might be expected, the dorsal carpellary traces are located directly opposite the locules. Throughout this distance the number of traces in the ring of recurrent bundles is increased partly by the inward swing of branch traces from the outer ring and their rotation to the inverted position, but principally by the appearance of new traces. In successive sections of the ovary from the base upward, these new traces appear first as phloem only but gradually develop xylem in the inverted position (Figures 4 and 5). The difficulties in determining the extent and origin of the stamen traces are the same here as in *Darbya.* At the base of the locules (Figure 4) the ring of recurrent traces is rather sparse. In the positions of the sepals (Figure 7), however, there is always one strong inverted trace. This may originate either from the plate of tissue in the pedicel as phloem only with the subsequent formation of xylem, as a branch from traces on either side of the sepal trace, or rarely from the sepal trace itself. This single trace inside of each sepal trace eventually leads to a stamen.

Near the top of the locule the X-traces arise from the recurrent bundles and move in to form with the dorsal carpellary traces a third ring of bundles (Figure 5). Thus at this level, as in *Darbya,* there are three concentric rings of bundles, the ascending, the recurrent, and the dorsal-X rings. At the extreme top of the locule the dorsal-X ring of bundles moves in and, after anastomoses are formed (Figure 6), gradually disappears. None of these traces enter the base of the style (Figure 7). At the level of the top of the locule, which is just below the level at which the sepal lobes are freed,

PLATE II



Colpoon compressum (1-7), *Santalum Freycinetianum* (8-13) the ascending and recurrent traces come together in anastomoses (Figure 6). All except those in the positions of the sepals then disappear. The inverted trace opposite each sepal loses its xylem and continues into the stamen as a phloem trace (Figure 7). The sepal trace is much more compact than in *Darbya* and tends to give off lateral traces and to retain a strong dorsal trace instead of separating radially into more or less equal strands as in *Darbya.* The sepals, stamens, and lobes of the disk are freed almost simultaneously.

According to Saunders (1933, 1940) the sepals in the flowers of *Colpoon* have commissural marginal veins. No evidence was found to support this statement, though commissural marginal veins do occur in other genera of the family.

Santalum Freycinetianum Gaudich.

The flowers of *Santalum* are perfect and 4- or 5-merous. The ovary is essentially only partly inferior as the floral tube is freed just above the level of ovule attachment. There is but one locule, though there may be slight depressions in its base in which the ovules rest. The placental stalk is extended for some distance beyond the ovules. There is a large floral tube with a well developed disk the lobes of which are freed simultaneously with the sepals and stamens. The style is elongate with two to four short stigma lobes.

Since *Santalum Freycinetianum, S. cuneatum* (Hillebr.) Rock., *S. haleakalae* Hillebr., *S. paniculatum* H. and A. var *angustifolium* Sk. and *S. pyrularium* A. Gray are essentially similar in their floral anatomy, only *S. Freycinetianum* is described in detail.

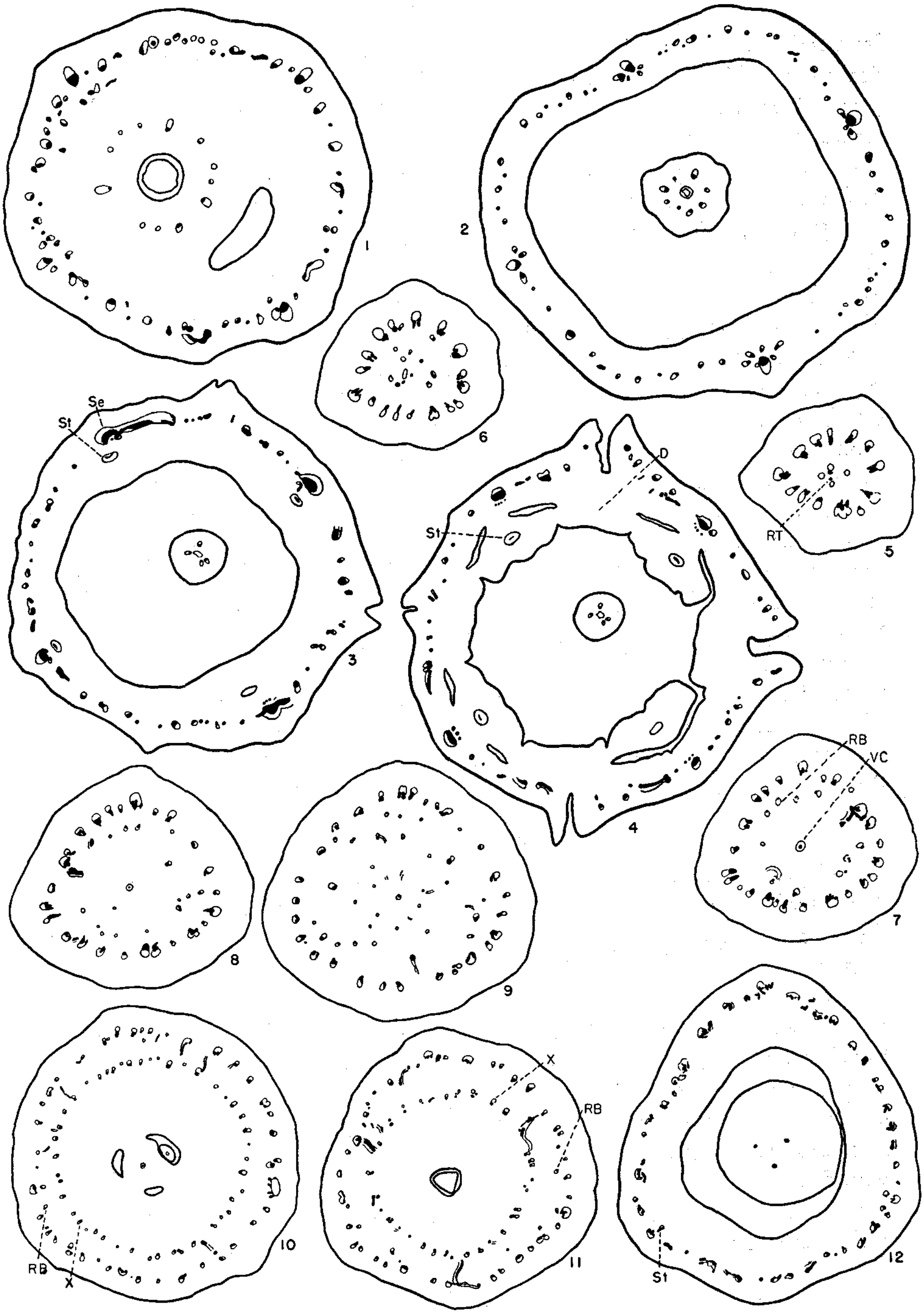
There are four large traces in the base of the pedicel. These divide rapidly so that numerous traces are present in the region in which residual tissue first appears (Plate II, Figure 8). The residual tissue consists at first of xylem only. Later phloem appears and the residual tissue becomes arranged in a definite ring of inverted traces (Figure 9). The traces soon become connected by anastomoses and from these phloem is given off to the inside (Figure 10). The phloem strands come together to form a large strand, the ventral carpellary strand, which remains in the center (Figure 11) and leads to the placental column. The ascending and recurrent traces move outward. Occasionally a small trace connects the two rings of bundles. No dorsal carpellary traces are evident.

The single locule may have partitions at its extreme base. Thus cross sections through this region show apparently three locules, each with a single ovule (Figure 12). The other species studied do not show this condition as frequently as does *S. Freycinetianum.* The number of traces in the ovary wall is increased in the outer ring by branching and in the inner ring principally by the appearance of new traces. At approximately the level of attachment of the ovules to the placental column there are numerous connections between the ascending and recurrent traces (Figure 13). The X-traces originate at the same level and move inward toward the locule. In *Darbya* the X-traces originate some distance below the level at which the ascending and recurrent traces connect with each other. Three or four of the X-traces in *Santalum,* those in the positions of dorsal carpellary traces, are more strongly developed than the others. The X-traces move into the long tapered upper portion of the ovary where their number is gradually reduced to three or four, which are in the positions of dorsals (Plate III, Figures 1 to 3). The absence of dorsal carpellary traces below the level at which the X-traces move in may be interpreted in two ways. It may be due either to their fusion with the recurrent traces through this distance or to their complete disappearance as a result of a gradual reduction in size. In other genera the dorsal carpellary traces may be represented only by weak phloem traces (e. g. *Choretrum*) and in still others the dorsals may appear independently in the ovary wall just below the X-traces (e. g. *Arjona*). Indications are then that the dorsal carpellary traces may actually disappear in the region below the X-traces. They are retained above because the X-traces normally reinforce the dorsals.

As was previously mentioned, the floral tube in *Santalum* is freed only a short distance above the level of attachment of the ovules. This is just above the level at which the X-traces move in. In addition to the sepal-stamen complexes, numerous small traces enter the floral tube. There are some anastomoses between these small traces and many of the traces are inverted. Thus even though most of the ascending and recurrent traces are connected just below the level at which the floral tube is freed, it seems likely that much of the floral tube itself is receptacular. Usually one inverted trace persists inside each sepal trace. In addition the small traces flanking each sepal trace swing around to the inverted position (Figure 2). Thus there are formed at this level loosely arranged amphicribral strands, each representing a sepal-stamen complex. The small inverted traces that originate near each sepal trace may then become incorporated with either the sepal or stamen traces. Eventually there are differentiated from each sepal-stamen complex a single large sepal trace and a single stamen trace, which is usually amphicribral (Figure 3). As the stamen trace moves in, it usually leaves behind a small amount of xylem, which persists for some distance just inside the sepal trace.

Meanwhile some of the small traces between the sepal positions disappear and some additional traces appear that are inverted. These additional

PLATE III



Santalum Freycinetianum (1-4), *Osyris alba* (5-12) inverted traces arise from branches of the sepal traces and are directed downward. The sepal traces give off large branches at almost right angles just before the calyx lobes are freed (Figure 3). From these, small branch traces extend both upward and downward, the latter being inverted. No inverted traces appear above this level (Figure 4). The stamens, calyx lobes, and disk are freed almost simultaneously.

Santalum differs essentially from *Darbya* in only two details. The dorsal carpellary traces present in *Darbya* throughout the length of the ovary are absent in *Santalum* from the base of the ovary to the level at which the X-traces appear. In *Darbya* the sepal traces gradually separate radially to supply the sepals while in *Santalum* the sepal traces give off branches at right angles and from these branches traces extend both upward and downward, the latter being inverted. The distribution of the inverted traces in *Santalum* seems to indicate that here the floral tube is probably receptacular up to approximately the level of branching of the sepal traces.

It is difficult to reconcile the above description with that given by Rao for *S. album* (1942). He described four large strands, which enter the perianth segments after giving off branches to the stamens, and smaller strands between the large ones which supply the carpels. Either two distinct rings of branches do not occur in *S. album* or they were overlooked. Rao did describe two rings of traces in *Scleropyron* but he considered them as outer and inner series of the carpellary strands supplying different layers of the fruit wall. Rao considered that the placental column in *S. album,* as well as in other forms he studied, does not receive any vascular trace from the main floral strands.

Osyris alba L.

Osyris is dioecious or polygamous with staminate, pistillate, and perfect flowers which are 3- or 4-merous. The ovary is inferior with three locules at the base that merge into one above. The style is short and thick with three or four stigma lobes.

There are numerous traces in the pedicel of the pistillate flower at the level at which the residual tissue first appears (Plate III, Figure 5). Additional strands appear in the pith region to form an irregular group of vascular tissue (Figure 6). A few anastomoses may form between the individual strands. There then arise in the center both a single amphicribral bundle representing the ventral carpellary traces and a rather sparse ring of mostly inverted traces, the recurrent bundles of the receptacle (Figure 7). The number of traces in the outer ring of ascending traces is increased by radial separation and in the inner ring by the appearance of additional traces and of an occasional branch from the outer traces. The recurrent traces here are very weak, consisting of phloem only or of phloem with a small amount of xylem. Over a distance of about twenty sections, three stronger traces move inward in the positions of dorsal carpellary traces (Figures 7, 8, and 9). These originate from or frequently near the ascending traces. In this same region, numerous very weak phloem traces move inward from the recurrent traces toward the ventral carpellary strand. These seem to be in the nature of flesh bundles since most of them soon disappear and only a very few actually connect with the ventral strand. Figure 9 is taken from just below the locule.

The dorsal carpellary traces soon branch many times. Numerous branches move inward from the inverted traces and, to a limited extent, from the ascending traces and assume positions between the dorsals. These traces are apparently the X-traces that appear here below the locule instead of above it as in *Darbya.* At the base of the locule (Figure 10), appear first a ring of ascending receptacular traces toward the outside, then a very few inverted recurrent traces inside, and finally a more pronounced ring of normally oriented bundles, the dorsal-X ring, toward the center. At first glance the two rings of traces in Figure 7 appear to be comparable to those in *Santalum* (Plate II, Figure 12) and to those in *Darbya* (Plate I, Figure 7) at the same level. In both *Santalum* and *Darbya,* however, the inner ring consists of inverted traces while in *Osyris* it consists of normally oriented traces. The origin of the X-traces below the locule and the small number of inverted traces present in *Osyris* account for this difference.

Near the top of the locule (Plate III, Figure 11) additional strong traces in the positions of the dorsal carpellary traces move inward from the outer ring. The entire inner ring of traces then moves inward to enter the base of the style and the floral tube is freed from the ovary. Anastomoses are formed between the dorsal-X traces and only the traces in the positions of dorsal carpellaries persist in the style (Figure 12).

There are few inverted traces above the level at which the X-traces appear. In the floral tube numerous anastomoses appear between traces (Figure 12). It is probably at this same level that the ascending receptacular traces become recurrent. An occasional stamen trace may be identified. Unfortunately the material available was very poorly preserved for structure above this level but the vascular structure seems to be similar to that in *Darbya.*

Osyris differs from *Darbya* in the branching of the dorsals and especially in the origin of the X-traces below the level of the base of the locule instead of above the locule. The ring of X-traces is apparently well developed at the expense of the recurrent traces, which are sparsely scattered throughout the length of the ovary.

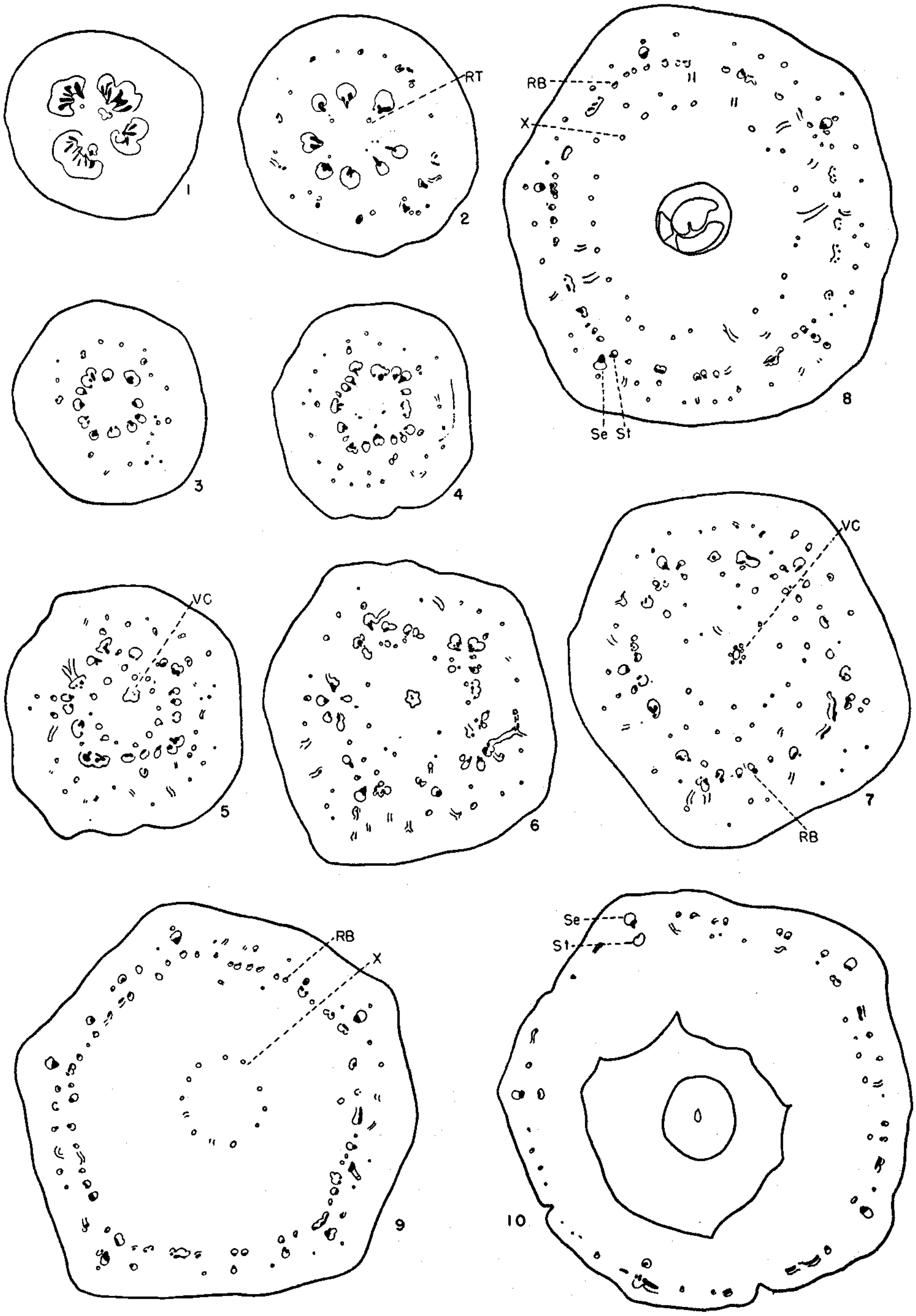
The above description of *Osyris* agrees in general with that given by Van Tieghem (1869b) and by Schaeppi and Steindl (1937). Van Tieghem considered the outer ring of traces as belonging to the calyx and the inner ring as consisting primarily of the three dorsal carpellary traces. He regarded the inferior ovary here as appendicular. He recognized that the inner traces, particularly those in the ventral strand, originate from vascular tissue that appears in the pith region and is thus "vascularly independent" of the main vascular supply. While Schaeppi and Steindl considered the outer traces as belonging to the receptacle, they did not describe invagination and they considered the X-traces as traces of the ovary because they do not appear in the staminate flower. The connections between the outer and inner rings of traces were interpreted as indicating that the carpellary bundles are rather weakly connected below to the main vascular supply.

Acanthosyris falcata Griseb.

The flowers of *Acanthosyris* are 4- or 5-merous and perfect. The ovary has one locule and a much twisted placental stalk bearing three ovules at its tip. The style is somewhat long and the stigma is indistinctly 5-lobed. The floral anatomy of this species is the most complex and difficult of explanation of the entire family.

There are four large traces in the pedicel just above the much reduced bracts (Plate IV, Figure 1). Even at this level there is a tendency toward the amphicribral condition with phloem or a small inverted trace located just inside each of the main bundles. The pedicel enlarges rapidly as the main traces begin to separate in radial planes. The small inner traces branch and tend to merge with the main traces. At the same time a somewhat scattered ring of traces arises independently in the cortical region of the pedicel (Figure 2). These traces may appear as xylem, as phloem or as complete traces more or less inverted. The pedicel then decreases in diameter rather rapidly and the innermost strands merge completely with the main traces (Figure 3). The traces in the cortical region branch. Some of them disappear and most of the rest of them lose their xylem. Five traces tend to remain more strongly developed than the others. These are in the positions of the sepals (Figure 10). The outermost traces, which usually consist of phloem only, continue to branch and occasionally form strands connecting with each other and also with the main traces. The traces in the cortical region then become so rearranged that the five somewhat larger inverted traces in the sepal positions are slightly inside the others (Figure 4). At the same level vascular

PLATE IV



Acanthosyris falcata

tissue arises independently in the pith region. The number of strands in the pith region is increased rapidly by the appearance of new traces and by the inward movement of an occasional branch from the main traces.

The vascular tissue in the pith region is gradually rearranged to form the ventral carpellary strand and a ring of phloem or inverted traces, which are located just inside the main vascular bundles (Figure 5). The main traces continue to divide by radial separation. Throughout this region many more anastomoses are formed between the various rings of traces than in any of the other forms studied. The main traces are then gradually rearranged into five groups opposite the sepal positions and just inside the five larger traces in the cortical region (Figure 6). This rearrangement results from a partial rotation of some of the traces between the sepal positions. The inverted traces of the inner ring (just inside each of the five groups) become somewhat more strongly developed. Thus there are formed five very loosely arranged amphicribral strands in the sepal positions. Continuous anastomosing and shifting of traces occur over a distance of about thirty sections. As in *Osyris* additional weak phloem strands are given off toward the ventral carpellary strand. Though these usually disappear they may occasionally connect with the ventral strand. As a result of the extensive anastomosing and shifting of traces the arrangement illustrated in Figure 7 emerges. There is a rather sparse outer ring, which consists mostly of weak phloem traces and a few weak collateral traces. Inside of this ring is a ring of strongly developed inverted traces, and further toward the inside are scattered phloem strands leading toward the ventral carpellary strand in the center. The section illustrated in Figure 7, taken just below the locule, is comparable with Figure 9 (Plate III) of *Osyris*. It is to be noted that at this level in *Osyris* the outer ring of normally oriented traces is well developed while the inner ring of recurrent inverted traces is sparse, with the traces rather weakly developed. This situation is just the reverse of that in *Acanthosyris*.

Many of the scattered phloem traces in the central region below the locule disappear but the outermost of these persist. At about the level of the base of the locule additional phloem strands are given off to the inside from the ring of inverted traces. This shifting continues throughout the height of the locule, resulting in a definite third ring of traces toward the inside of the ovary wall (Plate IV, Figure 8). Thus near the top of the locule there is an outer ring of phloem traces and weak collateral bundles with a second ring of strongly developed inverted traces and a third ring toward the center consisting only of weak phloem traces. The five strong collateral bundles in the sepal positions are crowded between the first and second rings. The five small inverted traces of the outer ring, one just outside each of the strong collateral bundles, are the five inverted traces shown in Figure 4. These are continuous through the flower to the top of the ovary.

The inner ring of phloem traces moves in to enter the base of the style (Figure 9) and can therefore be regarded as the dorsal-X ring. All of these traces disappear, however, before the style is freed. At the same time there are an increasing number of connections between the inverted traces and the outer traces, the connections usually being through xylem only. There are thus formed in the outer ring normally oriented collateral bundles that become increasingly pronounced. By the time the calyx tube is freed, all the xylem of the inner traces has been "transferred" to the outer traces (right side of Figure 10). The large trace in each sepal position moves out and combines with the small trace just outside it to form the sepal trace. The inverted trace just inside each of these becomes the stamen trace. The bundles of the outer and inner rings, except for the sepal and stamen bundles, come together in the base of the floral tube, form anastomoses and gradually disappear just before the sepal traces branch to supply the sepals. The sepals, stamens and disk are freed almost simultaneously.

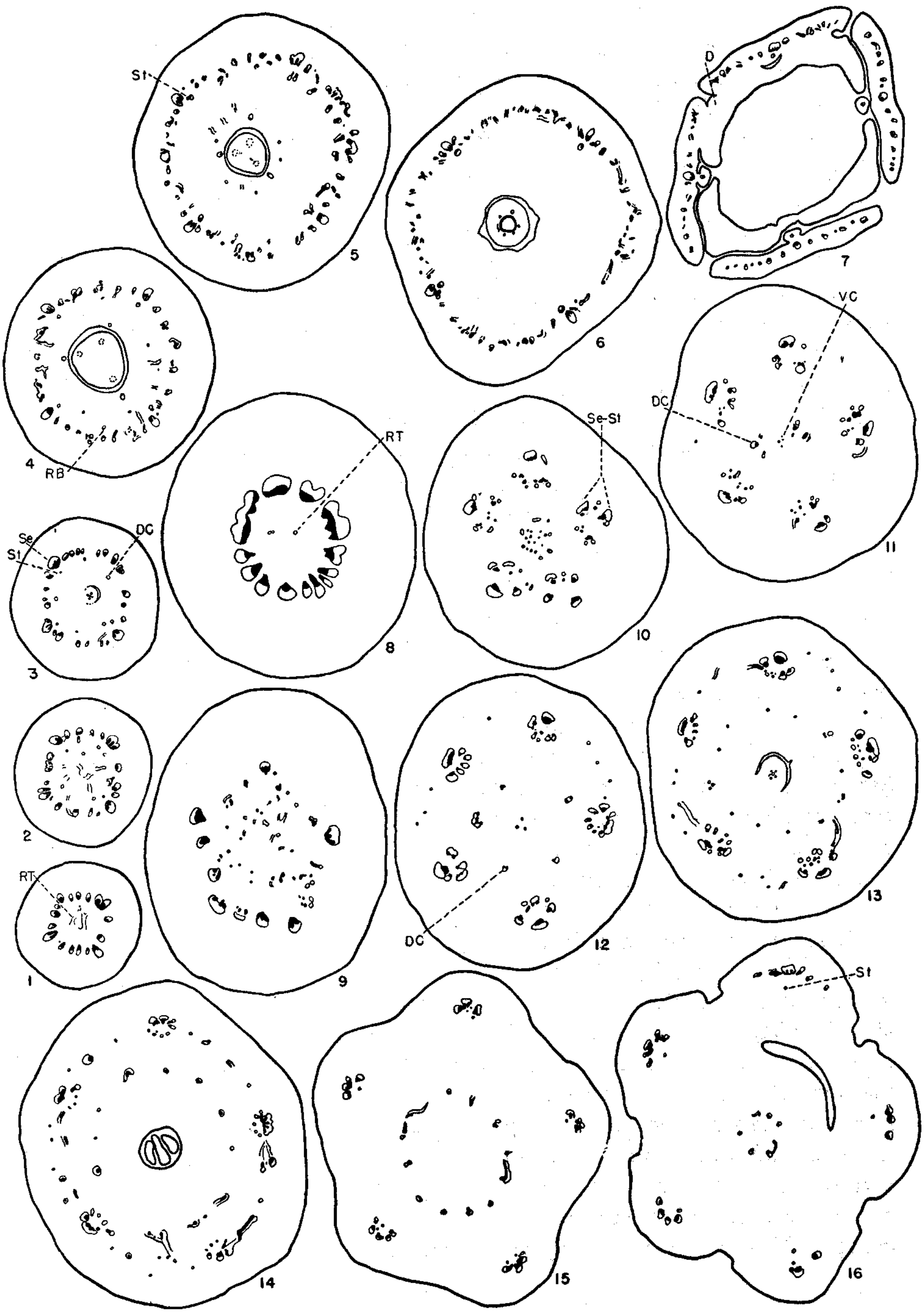
A comparison of Figure 8 with Figure 5 (Plate II) of *Colpoon* or with Figure 8 (Plate I) of *Darbya* helps to explain what may have happened in *Acanthosyris* to give this anomalous anatomical structure. In both *Colpoon* and *Darbya* there are three rings of well developed traces at the level indicated, the ascending traces, the recurrent traces, and the dorsal-X traces. At this level in *Acanthosyris,* both the ascending and the X-traces are represented only by weak phloem traces while the inverted recurrent traces are strongly developed. Much anastomosing and shifting of traces also occur throughout the lower portion of the ovary, always so that the more strongly developed traces are located deep inside the ovary wall. These facts considered together make the following interpretation seem the most likely. In *Acanthosyris,* as in *Osyris,* the X-traces apparently originate below the locule, in the former perhaps even lower than in the latter. Thus the "nodes" or levels of origin of the X-traces are very close to the ventral carpellary traces. In following the strongly developed traces from the base to the top of the ovary, their location gradually shifts to the outside. At the base of the ovary the most strongly developed traces are those normally oriented traces that lie deep in the tissues of the ovary inside approximately two rings of weaker traces (Plate IV, Figures 4 and 5). Above this the shift is outward to mostly inverted traces with a definite ring of weaker traces both inside and outside (Figure 8), and at the top of the ovary to the outermost ring of normally oriented traces (Figure 9 and right side of Figure 10). In both *Darbya* and *Colpoon* the main path of water conduction from the pedicel, as indicated by the distribution of xylem, is up through the ascending traces and down through the recurrent traces to the inner parts of the flower. For some unknown reason the main path of conduction, as indicated by xylem development, seems to have shifted in *Acanthosyris* so that it cuts across to the innermost traces at the base of the ovary, moves out to the inverted traces, and finally out to the outermost ring of ascending traces. While this interpretation may seem illogical from a physiological point of view, the confusion caused by the crowding of the "nodes" where the ventrals and X-traces originate may make this shift possible. This interpretation is supported also by the fact that in the basal portion of the ovary, where the greatest change must occur, there are many more anastomoses and connections between rings of traces than in any other form studied.

Eucarya acuminata (R. Br.) Sprague and Summerhayes

The flowers of *Eucarya* are perfect and 4-merous. The ovary is partly or completely inferior with a single locule and a placental stalk bearing two or three ovules. The stalk extends up into the short style much as in *Santalum.* There are as many stigma lobes as there are ovules.

Eucarya presents a much simpler and more direct modification of the receptacular inferior ovary than *Acanthosyris.* There are four large traces in the pedicel that divide radially to form numerous strands at the level at which the residual tissue first appears (Plate V, Figure 1). A short distance above this level a loose plate of vascular tissue appears in the pith region (Figure 2). The plate consists chiefly of phloem. Xylem, when it is present, appears in the traces adjacent to the main vascular bundles and in the inverted position. A strand of phloem continues upward from the plate to enter the placental stalk (Figure 3). The remaining traces in the pith region move outward and upward. Some of them connect to the main traces, others disappear and a few persist just inside the main bundles. Three of these persistent strands are dorsal carpellary traces. They move in near the locule, one opposite each ovule, and persist as weak phloem traces (Figure 4). In addition to these a single weak strand (Figure 3), which later becomes a stamen trace, appears just inside each of the four larger traces of the outer ring of bundles. One instance was found in which a single strand divided to form both a dorsal and a stamen trace. There are very few traces present at the level of the base of the locule to represent recurrent traces. A few additional traces appear at higher levels and an occasional trace swings

PLATE V



Eucarya acuminata (1-7), *Pyrularia pubera* (8-16) inward from the main bundles. The X-traces originate near the top of the locule as weak phloem strands from the recurrent traces. They then move in between the dorsal carpellary traces, which become stronger at this level (Figures 4 and 5). A variable number of traces enter the base of the style. All of these disappear except three, which extend nearly to the base of the stigma lobes.

After the X-traces move in, there is a rapid increase in the number and strength of the recurrent bundles (Figure 5). The ascending and recurrent traces merge in a series of anastomoses in the base of the floral tube just above the level at which the style is freed (Figure 6). The sepal traces begin to branch at about this level. The anastomoses of the ascending and recurrent traces become reduced to xylem-like sclerenchyma, which merge with the branches of the sepal traces as in *Santalum*. No inverted traces appear above the level at which these branch traces arise (Figure 7).

Eucarya differs from *Santalum* in the presence of weak dorsal carpellary traces and in the weak development of the lower portions of the recurrent traces. This tendency of the recurrent traces to become reduced is still more apparent in other forms.

Pyrularia pubera Michx.

In *Pyrularia* the flowers are 5-merous and are either perfect or imperfect by partial reduction. The ovary is completely inferior with a single locule and a coiled placental stalk.

The pedicel grades imperceptibly into the ovary. The residual tissue first appears some distance up in the flower (Plate V, Figure 8). For a considerable distance there is a very gradual increase in the amount of residual tissue. There are about 125 sections between Figures 8 and 9. Through this same distance five large traces persist in the sepal positions. The bundles between the sepal positions break up rapidly into smaller traces. Some of these swing inward and form anastomoses with the residual tissue in the pith region (Figure 9). Others swing around to a partly inverted position just inside each of the five main traces. These changes are completed at the slightly higher level shown in Figure 10. A loosely arranged group of xylem and phloem strands remains in the pith region. From these arise both the ventral and dorsal carpellary traces. Outside of the central vascular group are five very loosely arranged amphicribral strands. The large outer trace in each group comes directly from the pedicel and the smaller half-inverted traces flanking these originate, as already described, by the rotation of the small traces between the sepal positions. The innermost traces of each group, which are inverted, apparently represent the recurrent traces, since most of them originate from the scattered strands shown in the pith region in Figure 9. Thus the loosely arranged amphicribral strands originate here in approximately the same manner as in *Darbya* and *Santalum.* In *Pyrularia,* however, they originate low in the ovary and all traces between them disappear. While there is some branching from these groups throughout the length of the ovary, the branches seem to be mostly in the nature of flesh bundles.

From the central group of vascular strands shown in Figure 10, five traces move outward (Figure 11). Two of these become much more strongly developed than the others (Figure 12). These five traces are the dorsal carpellary traces. The ventral traces, represented by a variable number of xylem and phloem strands, remain in the center and continue up into the placental column. The dorsal carpellary traces branch to form a ring of more than five traces at the level of the base of the locule (Figure 13). The amphicribral strands give off a few traces to the inside at various levels throughout the height of the locule and the traces of the inner ring become gradually stronger. These branch traces probably represent the X-traces that arise at various levels instead of simultaneously at one level as in forms previously described. Toward the top of the locule (Figure 14) an inner ring of well developed bundles is formed which moves inward (Figure 15) toward the base of the style. This is the dorsal-X ring of traces. A variable number of traces from the ring enter the style (Figure 16). Only two persist and these are in the positions of the two stronger dorsal carpellary traces shown in Figure 12.

The flesh bundles between the main traces become stronger toward the top of the locule (Figures 13 and 14) and then gradually disappear. The amphicribral strands become more compactly arranged (Figure 15). Most of the inner traces of each group disappear by fusing with adjacent traces, but at least one weak phloem trace persists as a stamen trace. The main sepal trace then divides radially, as in *Darbya,* as the floral tube is freed (Figure 16). The sepals, stamens, and disk are freed almost simultaneously.

Comandra pallida A. DC.

The flowers of *Comandra* are perfect and 4- or 5-merous. The ovary is completely inferior with a single locule and a much twisted placental stalk bearing two or three ovules at the top. *Comandra pallida, C. umbellata* (L.) Nutt., *C. Richardsiana* Fernald, and *C. californica* Eastw. were studied, but only *C. pallida* is described in detail.

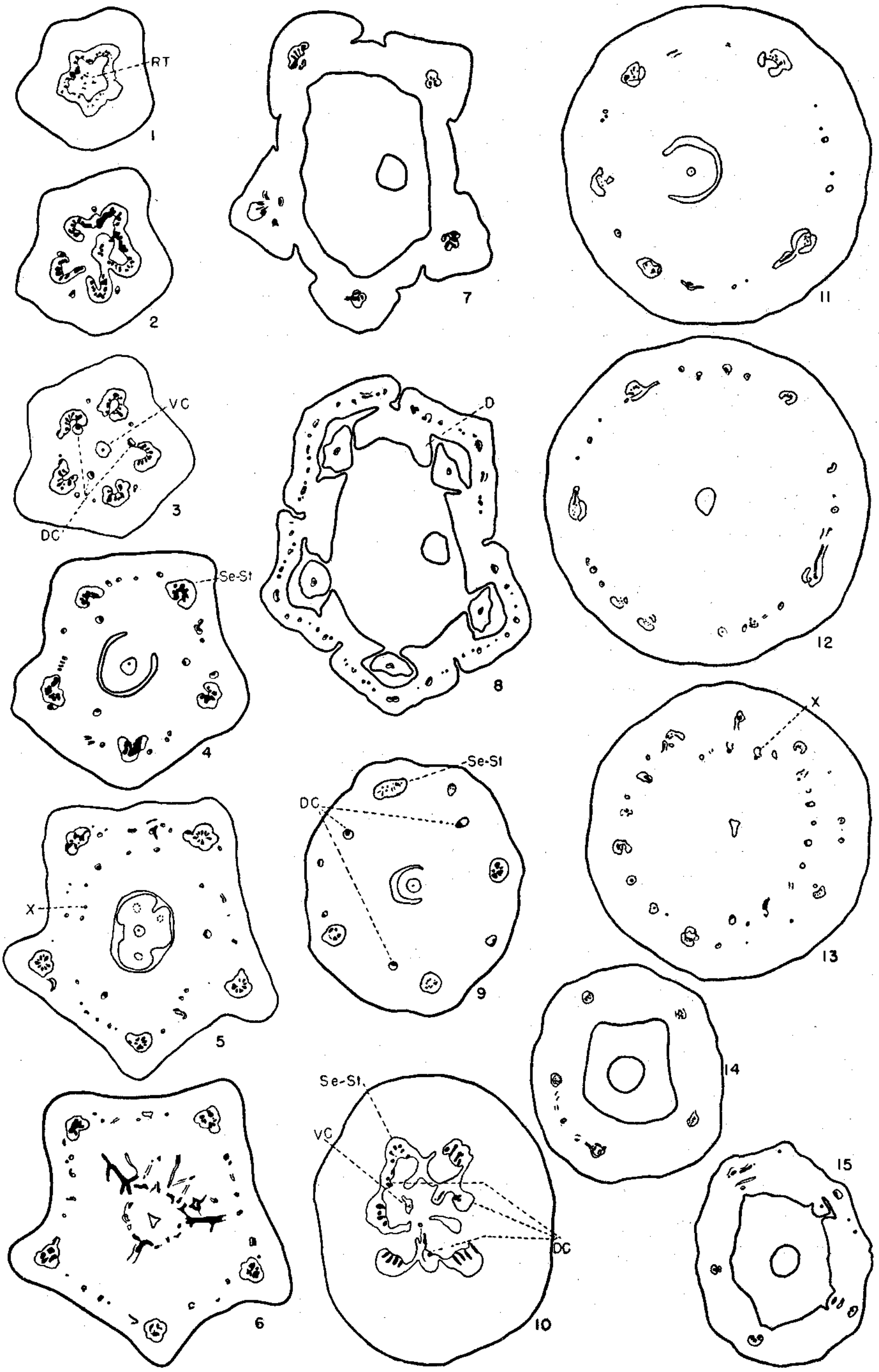
There is a continuous vascular cylinder in the pedicel above the bracts. The residual tissue appears as scattered xylem strands in the pith region at approximately the level at which the sepal-stamen traces begin to move out (Plate VI, Figure 1). These strands become connected to the outer traces by vascular tissue that moves in from between the main lobes of the stele (Figure 2). This situation is very similar to that in *Pyrularia* (Plate V, Figure 9) in which the residual tissue is connected to the smaller traces between the sepal positions. The ventral carpellary traces are represented by a single amphicribral strand (Plate VI, Figures 2 and 3) formed by the grouping of the xylem traces in the center in a single strand and the inward movement of phloem through gaps in the stele. Occasional small traces move laterally from the lobes of the stele and usually become inverted.

The main traces become partly or completely amphicribral as they move out to enter the ovary wall (Figure 3). The method of formation is similar to that in *Pyrularia* (Plate V, Figures 9 and 10), the xylem strands at the margins tending to swing around toward the inside and phloem moving in behind them. The resultant amphicribral bundles are more compact throughout than in *Pyrularia.* As these large traces move out, three, or more rarely four, normally oriented traces are left behind as the dorsal carpellary traces. These originate either from the margins of the main traces before they close to become amphicribral (Plate VI, Figure 3) or from the connecting tissue between the ventral strand and the traces between the lobes of the stele. The dorsals may at first be partly or completely inverted since they frequently originate from the margins of the main traces after these have swung partly around. The dorsals immediately become rearranged, however, and are normally oriented at the level of the base of the locule (Figure 4).

Additional small traces are given off from the main traces throughout the length of the ovary. These are usually inverted and frequently directed downward. Toward the top of the locule, weak traces move in between the dorsal carpellary traces (Figure 5). These are the X-traces and they originate mostly from the small traces between the sepal positions. Their mode of origin offers additional evidence that the small inverted traces between the sepal positions represent largely the recurrent traces. Just before the style is freed, the traces of the dorsal-X ring move in abruptly (Figure 6) and form numerous anastomoses below the base of the style. Only three traces from this ring, those in the positions of the dorsals, persist as weak traces and extend for a short distance into the base of the style.

Near the top of the locule the main traces, which are combined sepal-stamen traces, become distinctly amphicribral (Figure 5). The small bundles remaining between the main traces after the X-traces are given off form anastomoses with each other (Figure 6) and rapidly disappear as the floral tube is freed from the ovary. At the level at which the stamen traces sepa-

PLATE VI



Comandra pallida (1-8), *C. Richardsiana* (9), *Geocaulon lividum* (10-15) rate from the sepal traces (Figure 7) all of the smaller traces have disappeared. The sepal traces immediately branch repeatedly to supply the sepals (Figures 7 and 8). As in *Santalum* there may be a few inverted traces directed downward from the first branches of the sepal traces. The stamens are usually freed before the disk.

In *C. Richardsiana* the residual tissue extends over a much greater distance than in *C. pallida.* The main traces, however, become arranged as amphicribral bundles within a shorter distance. There are fewer inverted branch traces given off laterally from the main bundles but these are much larger (Figure 9) than in *C. pallida.* The dorsal carpellary traces are farther from the locule and more inverted traces are directed downward from the branches of the sepal traces. *Comandra californica* is very similar to *C. Richardsiana. Comandra umbellata* differs from *C. pallida* principally in that the dorsal carpellary traces are smaller and farther from the locule, the main traces are not so distinctly amphicribral, and more inverted traces are directed downward from the branches of the sepal traces.

Dowding (1931) described but did not illustrate the floral anatomy of *C. pallida* and *C. umbellata.* His description, however, differs greatly from that given here. He interpreted the anatomy of the flower in terms of the appendicular theory and the theory of carpel polymorphism. According to his description the perianth tube is traversed by five main vascular bundles that run to the sepals and superimposed stamens. Though this much is in agreement, no support was found for his statement that five strands branch off from the main vascular bundles to supply the carpels and that five alternate strands supply the placental column. Neither could evidence be found that the gynoecium is composed of two alternate whorls of carpels differentiated into an outer sterile and an inner fertile whorl.

Geocaulon lividum (Richardson) Fernald

In *Geocaulon* the central flowers in each cyme are usually pistillate and the outer flowers staminate. All are 5-merous. The ovary is inferior with a single locule and a placental stalk that is less twisted than that in *Comandra.* Although *Geocaulon* was formerly considered to be *Comandra,* its separation from the latter genus is in accord with differences in floral anatomy, although close affinity is also indicated.

There is a continuous vascular cylinder in the pedicel as in *Comandra.* The residual tissue appears in much the same manner but extends for only a very short distance. Anastomoses are formed between the residual tissue and the margins of the main traces as the latter move out to enter the ovary wall (Plate VI, Figure 10). A single amphicribral strand continues upward into the placental column. Three traces arise from the anastomoses or from the margins of the main traces. These probably represent the dorsal carpellary traces. Their subsequent behavior, however, is quite different from that of the dorsal carpellary traces in *Comandra*. They move out into the ovary wall as far as the five principal traces and begin to branch immediately. Thus at the level of the base of the locule (Figure 11) there are three groups of small traces derived from the three dorsals. These are not inverted as are most of the small traces at the corresponding level in *Comandra* (Figure 4). A few additional traces, however, are inverted or amphicribral. These arise from the main traces, as in *Comandra*. The margins of the main traces swing inward gradually to produce the amphicribral condition. There is only a small amount of xylem in each trace, as one might expect considering the fleshy nature of the fruit.

Numerous traces are given off from the main traces beginning at approximately the base of the locule. These are usually amphicribral or inverted. Since the normally oriented traces derived from the dorsals gradually disappear, all of the small bundles present near the top of the locule (Figure 12) are branches from the principal traces. The X-traces then move in toward the base of the style (Figure 13). These originate mostly from the small traces just as in *Comandra* but occasionally also from the large traces. There are no indications of dorsal carpellary traces at this level and all traces in this ring disappear before the style is freed.

The small traces left between the sepal positions after the X-traces are given off disappear in the base of the floral tube. A few short, inverted traces, directed downward, are given off at this level (Figure 14). The stamen traces, leading to staminodia, then separate tangentially from the sepal-stamen bundles. The sepal traces branch immediately afterward (Figure 15). The staminodia are freed usually slightly before the disk and sepals.

Nanodea muscosa Gaertn. f.

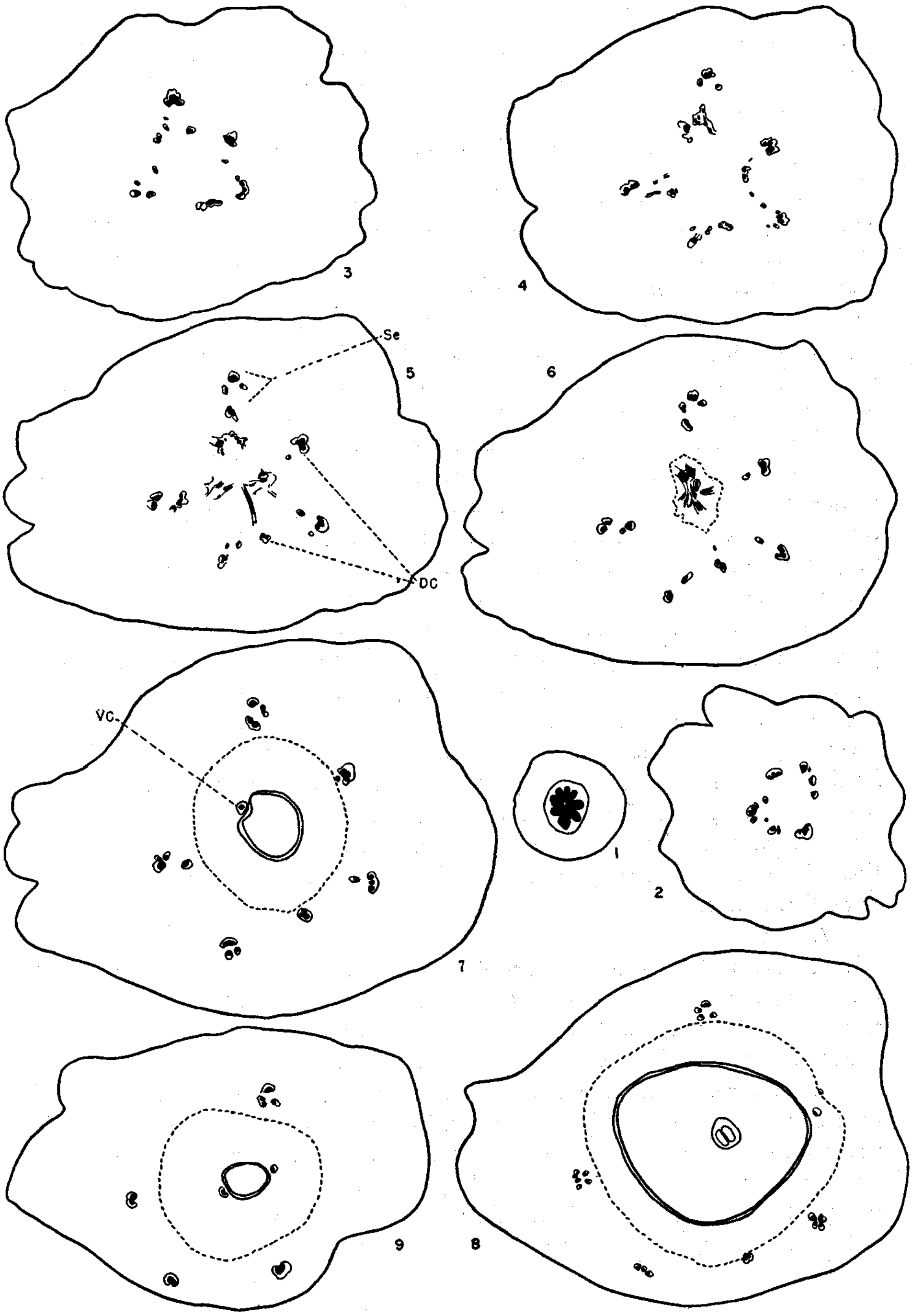
The flowers of *Nanodea* are 4-merous and either perfect, or pistillate with aborted stamens. The ovary is inferior with a single locule and a short central placenta bearing at its tip two ovules, only one of which matures. The style is short and has a stigma that is indistinctly two-lobed. The only available material of this species was of young fruits and these were in rather poor condition.

In the pedicel above the bracts the vascular cylinder is continuous and encloses a very small pith (Plate VII, Figure 1). The cylinder then separates radially (Figure 2) into traces that gradually move out into the enlarged base of the flower. Smaller traces continue to separate from the margins of the larger ones. The first of these smaller traces remain near the center of the ovary (Figure 3) while those produced later swing around to become partly or completely inverted, thus forming a loosely arranged amphicribral strand in each sepal position (Figures 4 and 5). At this level two of the traces either do not become amphicribral, or accompanied each by a single small inverted trace become partly so (Figure 5). One of the traces arises directly from the stele of the pedicel, the other from the margin of one of the larger traces. These two traces are apparently the dorsal carpellary traces since they continue directly into the style. The innermost traces become connected by anastomoses (Figure 5) and move in (Figure 6) to enter the placental stalk.

While at first glance the floral structure of *Nanodea* may appear quite different from that of *Comandra* and *Geocaulon,* a careful comparison reveals many similarities. The principal difference lies in the development of residual tissue. Fruits of *Nanodea* that were studied showed no indication of residual tissue. Residual tissue is well developed in *Comandra* but only slightly developed in *Geocaulon.* In *Comandra* as the residual tissue and the ventral strand form anastomoses with the margins of the sepal-stamen traces, the latter move out to enter the base of the ovary (Plate VI, Figure 2). The same is true but less obvious in *Geocaulon* (Plate VI, Figure 10). In *Nanodea,* however, the first traces given off from the margins of the sepal-stamen bundles form anastomoses, which give rise to the ventral carpellary strand (Plate VII, Figures 3 to 6). Thus it appears that in *Nanodea* both the residual tissue and the ventral strand below these anastomoses have disappeared, thus establishing a more direct vascular connection between the axis and the placental stalk. Of course it should be kept in mind that the anatomy of the young fruits of *Nanodea* is compared with that of the flowers of *Comandra* and *Geocaulon.*

The behavior of the dorsal carpellary traces in *Nanodea* differs only slightly from that in *Comandra.* The two traces move out into the ovary wall almost as far as the sepal-stamen bundles. They are appreciably closer, however, to the stony endocarp layer (indicated by a dotted line) just above the base of the locule (Figure 7). The placental trace here is at one side of the seed. No small branch traces are given off from the main bundles and no X-traces appear at the top of the ovary. Instead, the dorsals move inward through the sclerenchyma of the endocarp (Figure 8) and assume positions on opposite sides of the locule (Figure 9) near the top of the ovary. Here they are lost in the sclerenchyma tissue and apparently do not enter the base of the style. The sepal-stamen traces tend to become collateral as the inverted traces swing back and around and fuse with the main trace of each

PLATE VII



Nanodea muscosa

group. The material available apparently consisted of fruit from pistillate rather than from perfect flowers, since it showed only occasional traces leading to staminodia.

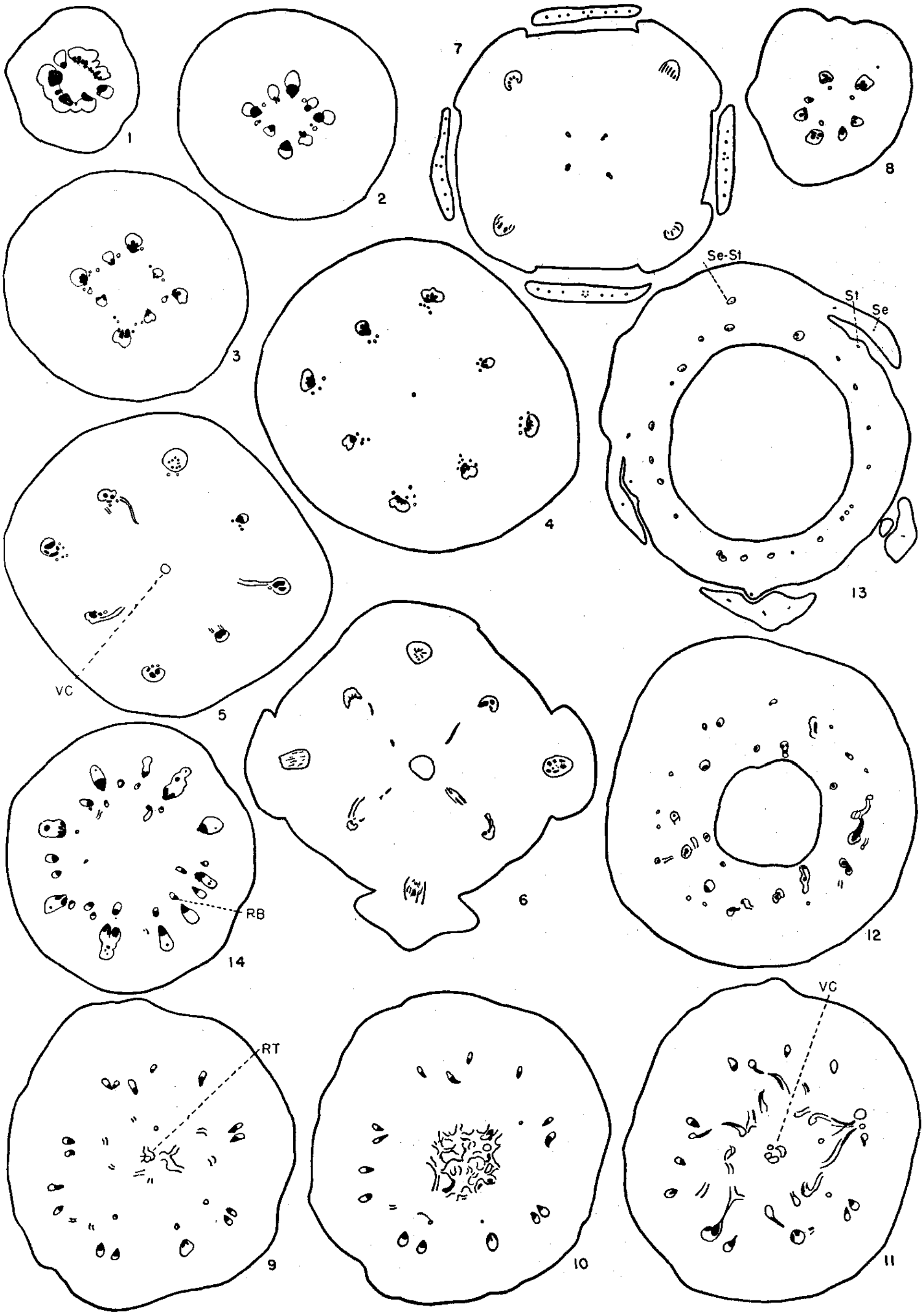
Buckleya distichophylla (Nutt.) Torrey

Buckleya is dioecious with 4-merous flowers. The ovary is inferior with a single small locule and a short thick placental column bearing three or four minute ovules. The style is short with a 4-lobed stigma. Unlike the other members of the Santalaceae, *Buckleya* has two alternate whorls of sepal-like structures instead of only one. The extra whorl has been interpreted in various ways, probably most commonly as bracts or bracteoles (Engler and Prantl, 1935), but for lack of any definite indication of their nature they will be referred to here simply as the outer and inner whorl of floral parts.

The vascular cylinder is practically continuous in the pedicel above the bracts (Plate VIII, Figure 1). The pedicel enlarges very gradually to merge with the ovary. The vascular cylinder separates into eight main traces, alternate ones being somewhat larger (Figure 2). The larger traces supply the outer whorl of floral parts and the smaller traces supply the inner whorl. There are a few additional strands, usually consisting of phloem only, which originate from the sides of the eight principal traces. These phloem traces, together with additional branch phloem traces originating at higher levels, swing around inside the larger traces (Figure 3). Xylem is present only occasionally in these small traces but when it occurs it is in the inverted position. This xylem soon disappears so that there remain at higher levels only scattered strands of phloem inside each of the main traces (Figure 4). Except for the lack of xylem in the inner traces, all eight strands resemble the amphicribral strands of *Comandra* and *Nanodea.* The derivation of the inner traces from the margins of the principal bundles is similar in all three forms.

A weak strand of phloem appears in the center of the pith region some distance below the locule (Figure 4). Near the base of the locule phloem traces are given off from the eight principal strands, either from the main trace of each group or from the small phloem strands inside (Figure 5). These traces extend inward for some distance but apparently do not connect with the central strand of phloem. The four larger traces in the ovary wall gradually become distinctly amphicribral (Figure 6) and move out into the outer whorl of floral parts. The four alternating traces give off toward the locule rather strong traces that should probably be considered as X-traces in the positions of the dorsal carpellary traces. All four of these enter the style. The traces supplying the second whorl of floral parts become more

PLATE VIII



Buckleya distichophylla (1-7), *Exocarpus Gaudichaudii* (8-13), *E. cupressiformis* (14) nearly collateral after the departure of the X-traces (Figure 7). The second whorl of floral parts is then freed and the ovary tapers rapidly to form the style.

All eight of the principal strands thus behave alike except at the top of the ovary. Since the branch traces leading inward at the top of the ovary arise only from the traces supplying the second whorl of floral parts it might be assumed that the second whorl is composed of sepals and the first whorl of bracts. The staminate flower is of no assistance in identifying the extra whorl in the pistillate flower. The staminate flower is supplied by four traces in the pedicel, each of which moves out into the base of a sepal, where it divides to form the sepal and stamen traces.

Exocarpus Gaudichaudii A. DC.

The staminate flowers of *Exocarpus* have reduced pistils. The pistillate flowers have rather weakly developed staminodia. The ovary in the pistillate flower is either apparently superior or partly surrounded by the receptacle, and has a single locule with one more or less sessile ovule. As the fruit develops, the axis below the ovary becomes enlarged and fleshy. Only well developed fruits were available for study. *Exocarpus Gaudichaudii, E. cupressiformis* Labill. and *E. aphyllus* R. Br. were all studied but only the first will be described in detail. Since the seed was poorly preserved, it is omitted from drawings of sections made through the locule. So also is the extent of the sclerenchymatous endocarp.

There are four or five traces in the lower portion of the pedicel. Some of these divide radially at the base of the enlarged portion of the axis. Small phloem strands appear independently just inside some of the main traces (Plate VIII, Figure 8). Occasionally a few of the main traces tend to become amphicribral but this condition is only temporary. If the main traces are followed over a considerable distance some will be found that divide once, some twice, and some not at all (Figure 9). At the same time the number of phloem traces inside the main traces is increased by the appearance of new strands and by the formation of a few weak branch traces that swing inward from the larger bundles. These inner traces may develop a small amount of xylem in any position. In *E. cupressiformis* the inner traces are well developed and definitely inverted (Figure 14) and thus may be considered as recurrent traces, or as residual traces below the level at which the ventral carpellary strand originates.

Anastomoses appear in the pith region in *E. Gaudichaudii* (Figure 9) that connect with the recurrent traces to form a large flat plate of vascular tissue in the center (Figure 10). The ventral carpellary strand continues upward from this plate toward the placental knob and the remaining vascular tissue moves outward to connect with some of the outer traces (Figure 11). A comparison with Figure 13 shows that these connections are mostly with traces between the sepal positions. Figure 11 illustrates a section taken just below the locule. The region above this is characterized by much branching and anastomosing of traces (Figure 12). In this same region the ascending and recurrent traces come together, the dorsal-X ring of traces is given off and the sepal-stamen traces are differentiated, all of which probably contribute to the confused branching and anastomosing. While the sepal-stamen traces are extremely small (Figure 13), the traces that continue in the ovary wall are well developed. There are no inverted traces above the level at which the small sepals are freed. Each staminodium receives a weak trace from one of the sepal-stamen bundles. The traces in the ovary wall gradually disappear and only a few enter the base of the style.

It appears from the above description that the enlarged receptacle here is definitely invaginated. Also, since the ventral carpellary strand originates approximately halfway down in the enlarged axis, the ovary is not as completely superior as it appears to be.

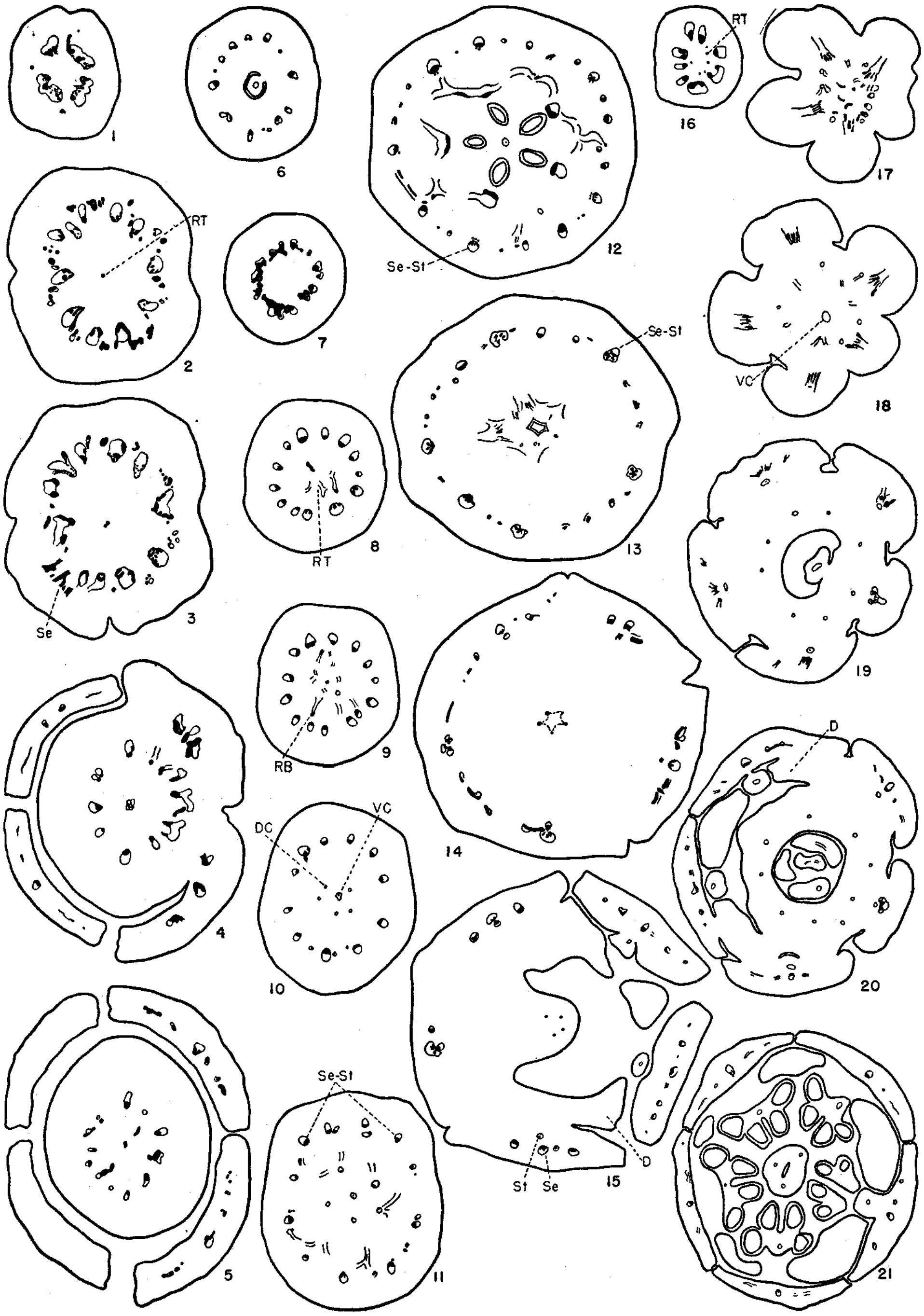
One characteristic of this genus particularly difficult to explain is the presence in *E. cupressiformis* of small xylem strands, or complete vascular bundles, within the phloem of the larger bundles (Figure 14). These strands swing out into the phloem at the base of the enlarged portion of the axis, continue to a level just below that at which the sepals are freed, and then swing back to the xylem. The only condition approaching this appears in *Acanthosyris* where several bundles are arranged close together in the same radius in each sepal position (Plate IV, Figure 8). The two outer traces of each group merge at a higher level to form a single trace to each sepal.

Anthobolus leptomerioides F. Müll.

Anthobolus is dioecious and has flowers that are 3- or 4-merous. There are no evidences of staminodia in the pistillate flowers. The ovary is apparently superior on a fleshy axis just as in *Exocarpus*. There is a single small locule with one sessile ovule.

The stele in the pedicel may be divided into a variable number of strands. Extending outward from the margins of these are short traces consisting of xylem only and ending in xylem-like sclerenchyma (Plate IX, Figure 1). The main traces divide radially in the lower portion of the enlarged axis and produce additional xylem-like sclerenchyma from the xylem (Figure 2). Residual tissue appears here in the center of the pith region as one or more xylem strands. At higher levels some anastomoses are formed

PLATE IX



Anthobolus leptomerioides (1-7), *Henslowia frutescens* (8-15), *Jodina rhombifolia* (16-21) between the main traces, and the sepal traces begin to move out (Figures 3 and 4). Either one large trace or three smaller traces enter each sepal. There are no indications of stamen traces or of staminodia. Following the departure of the sepal traces the remaining traces form a ring of simple collateral bundles. At some distance below the locule a few weak xylem traces may extend inward toward the ventral carpellary strand (Figure 5) but they apparently do not become connected with it. The locule is high in the ovary (Figure 6). Just above the locule the traces in the ovary wall form anastomoses with each other (Figure 7) and then all traces rapidly disappear.

Henslowia frutescens Benth.

The flowers of *Henslowia* are usually imperfect. The staminate flowers have a fleshy receptacle. The pistillate flowers have aborted stamens, are usually 5-merous and have an inferior ovary. In the material available there are five locules that merge into one at the top with a single ovule suspended in each locule. The style is short with a 5-lobed stigma. In contrast with most of the forms previously described, the floral parts are freed at the top of the ovary and there is no indication of a floral tube.

In the base of the flower, at the level at which the residual tissue first appears independently in the pith region, the number of traces is somewhat variable, usually twelve or thirteen (Plate IX, Figure 8). The amount of xylem in the residual tissue is small. One strand moves into the center, and phloem or weak inverted traces extend upward and outward to connect with the margins of the main traces (Figure 9), forming a saucer-shaped group of vascular tissue across the pith region. One weak amphicribral trace, which is the ventral carpellary strand, and five dorsal carpellary traces of phloem only arise in the center from this group of vascular tissue (Figure 10). The number of principal traces is meanwhile reduced somewhat by the fusion of some of the traces and the gradual disappearance of others. Above this level for a considerable distance small traces are given off from the margins of the main traces. Some of these branch traces move laterally, some swing around almost to the inverted position and numerous others move in to connect with the dorsal carpellary traces (Figure 11). Some of the latter branch traces may extend upward for a considerable distance before they connect with the dorsals. As more and more connections are formed with the dorsals the latter become more strongly developed. At the base of the locules the dorsal traces are very large and have well developed xylem and phloem (Figure 12). The main traces become essentially amphicribral either by the inward rotation of the marginal strands or by the formation of additional phloem strands that may appear independently just inside some of the main traces. At higher levels the locules gradually merge into one. The sepal-stamen traces can be identified as definite amphicribral traces (Figure 13) located opposite the carpels. The last traces to move in toward the dorsals arise between the sepal positions and apparently receive the small strands located inside these traces. Thus only the sepal-stamen traces remain amphicribral while the traces between them become once more collateral. The inner traces then form anastomoses and move in toward the base of the style. Just before the style is freed all but five of these traces disappear. These five weak traces in the positions of the dorsals (Figure 14) enter the base of the style (Figure 15) and continue upward almost to the 5-lobed stigma.

Meanwhile the outer traces located between the sepal positions form anastomoses, some of which are inverted (Figure 13 and left side of Figure 14) and gradually disappear. Each main amphicribral strand then divides to form a stamen and a sepal trace (Figure 14). At higher levels the stamen traces move in to enter the rudimentary stamens (Figure 15) and each of the sepal traces forms two branch traces each of which soon divides again. The sepals, stamens, and disk are freed almost simultaneously.

The receptacular nature of the inferior ovary of *Henslowia* is not as apparent as that of *Darbya* and closely related forms. A comparison with some of the species already described reveals that despite the presence of a larger number of carpels the vascular anatomy here represents an advanced system derived from the *Darbya* type. The distinct inner ring of inverted recurrent traces has almost disappeared even though the more primitive number of carpels has been retained. The following characteristics are evidences of an advanced vascular system: First, the appearance of residual tissue in the pith region before any connections are formed with the main traces (Figure 8); second, the origin of branch traces from the margins of the main traces and their inward rotation to form amphicribral sepal-stamen traces (Figures 11, 12, and 13), a behavior comparable to that in *Comandra* and closely related forms; third, the anastomosing of the small traces, some of which are inverted, between the sepal positions and their subsequent disappearance (Figures 13 and 14), a behavior characteristic of most of the forms already described; and, fourth, the nature of the stamen traces, which are at first inverted, later amphicribral, a behavior likewise characteristic of the forms previously described. Thus it seems that the ascending and recurrent traces in *Henslowia* have become reduced to form more nearly a single ring of collateral bundles. The reduction is comparable to that in the series from *Colpoon* to *Pyrularia* and it apparently occurred early in the phylogenetic development of this and the following genera of the Santalaceae. It becomes even more complete in the forms yet to be described.

Jodina rhombifolia Hook. and Arn.

The flowers of *Jodina* are perfect and 5-merous. The ovary is only partly inferior in the young flower but it becomes completely inferior in the older flower. There is a single locule with a twisted placental stalk, which bears three ovules at its tip. The style is thick with a stigma that is indistinctly 3-lobed. The fruit is drupe-like with a fleshy exocarp divided into five easily detachable segments.

A variable number of traces occur in the pedicel. Residual tissue appears below the ovary as scattered protoxylem strands in the pith region (Plate IX, Figure 16). At the base of the flower, five of the main strands begin to move out into the segments of the ovary (Figure 17). Anastomoses are formed that connect the remaining traces with each other and also with the residual tissue. Just above this level the five large strands, the sepal-stamen traces, move out rather abruptly (Figure 18). From the anastomoses of the traces between the sepal positions there persists a ring of phloem traces that continues upward into the ovary wall (Figure 19). A single strand of phloem from the traces in the pith region continues upward to enter the placental column.

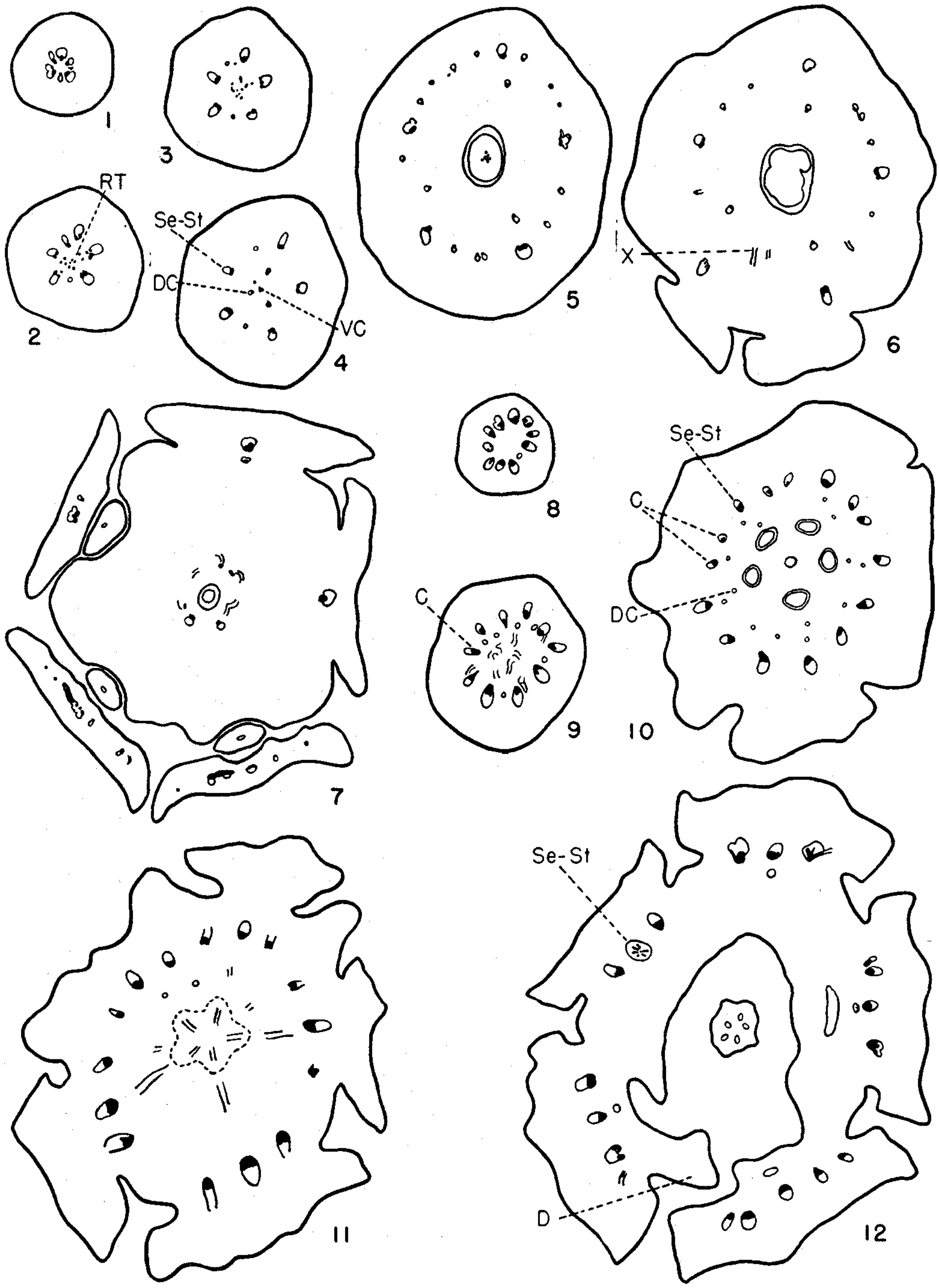
The sepal-stamen bundles gradually become amphicribral by the rotation of the marginal strands to a partly or completely inverted position. At approximately the level of the base of the locule (Figure 19) the stamen traces separate from the sepal-stamen bundles. The sepal traces then branch immediately to supply the sepals (Figure 20). The sepals, stamens, and disk are freed at a level that is a little more than halfway up the ovary. The ring of phloem traces between the outer traces and the locule (Figure 19) continues in the ovary, but in the base of the style the number of traces in the ring is reduced to three (Figure 21) which are in the positions of dorsal carpellary traces. This ring of traces must be considered as the dorsal-X ring of traces that originates here below the locule.

Myoschilos oblongus Ruiz and Pav.

The flowers of *Myoschilos* are perfect and 5-merous. The ovary is inferior with a single locule and a short thick placental column bearing at its tip three to five ovules. The style is short with a 2- to 5-lobed stigma.

The number of traces in the pedicel is variable, usually five to seven (Plate X, Figure 1). Some of these traces become reduced in size, just as in *Henslowia,* while others branch. The residual tissue appears as scattered xylem strands in the pith region (Figure 2). Five strong bundles, the sepal-stamen bundles, move outward, leaving near the residual tissue a few addi-

PLATE X



Myoschilos oblongus (1-7), *Choretrum glomeratum* (8-12) tional xylem strands that originate from the margins of the traces. This behavior is similar to that at a comparable level in *Jodina* (Plate IX, Figure 17). The traces between the sepal positions become reduced to phloem strands (Plate X, Figures 3 and 4). The residual tissue together with the traces from the margins of the principal traces forms a compact group of strands in the center (Figure 3). These strands form a few anastomoses and then separate to form a ventral carpellary strand and three dorsal carpellary traces (Figure 4).

Xylem appears in the small phloem strands in the outer ring of traces. Additional small traces may be formed from branches from these strands and from the sepal-stamen bundles. Thus at the level of the base of the locule (Figure 5) numerous small traces are interspersed between the five sepal-stamen bundles and the three dorsal carpellary traces lie just inside them. Near the top of the locule the small traces between the sepal-stamen bundles form a few anastomoses and then they all move in between the dorsals (Figure 6) to form the dorsal-X ring of traces. Anastomoses are formed in this ring below the base of the style (Figure 7). Only three traces in the ring, those in the positions of the dorsals, enter the base of the style and these soon disappear.

The sepal-stamen traces begin to move out at the level of the top of the locule (Figure 6). They never become amphicribral as they do in forms previously described. The stamen traces separate tangentially from the sepal-stamen bundles (Figure 7) and the sepal traces branch immediately to supply the sepals. Occasionally there may be a small branch directed downward in the base of the sepals. Sepals and stamens are freed before the disk.

Choretrum glomeratum R. Br.

Choretrum, Leptomeria, Thesium, Thesidium and *Omphacomeria* are grouped together in a single series because in all these forms there are twice as many traces in the pedicel as there are floral parts. Alternate traces become the sepal-stamen traces and each of the remaining traces branches to supply a lateral trace to the sepals on either side of it. These lateral traces have been termed commissural marginal traces by Saunders (1933, 1940) who considered that their presence indicates that each sepal actually consists of one sepal plus half of the neighboring petal on either side. Thus sepals with commissural marginal veins show petaloid coloring while those with only a single trace, and therefore individual sepals, are green. There seem to be many exceptions, however, to this generalization in the Santalaceae.

The flowers of *Choretrum* are perfect and 5-merous. The ovary is inferior with five locules at the base, which merge into one above. There is a thick central placental column bearing five ovules. The style is short and thick with a 5-lobed stigma. *Choretrum glomeratum, C. Candollei* F. Müll. and *C. spicatum* F. Müll. were studied but only *C. glomeratum* is described in detail.

There are ten main traces in the pedicel (Plate X, Figure 8) and in addition an occasional phloem strand. As these traces move out to enter the base of the ovary most of them give off weak phloem traces to the inside (Figure 9). At the same time phloem appears independently in the pith region and connects upward and outward to these inner (phloem) traces. In *C. Candollei* the traces connecting with the phloem traces occasionally show xylem in the inverted position. As the principal traces continue to move outward, the phloem traces are left behind. From these and from the plate of phloem tissue in the center, the following traces arise: the ventral carpellary strand, which later enters the placental column (Figure 10); the dorsal carpellary traces of phloem only, one opposite each locule; and a ring of phloem bundles, probably representing the recurrent traces, located between the dorsals and the main traces. In both *C. spicatum* and *C. Candollei* this ring occasionally shows xylem in the inverted position. Dorsal carpellary traces are lacking in both these forms.

At or slightly below the base of the locules alternate strands in the outer ring of bundles divide so that fifteen large traces are present (Figure 10). Each of the five sepals receives three of these traces (Figure 11), a sepal-stamen trace that comes directly from the pedicel and two lateral traces, each resulting from the division of the alternate trace; i.e., the commissural trace on either side of the sepal-stamen bundle. At this level the phloem in the placental column separates into five strands supplying the ovules. The locules merge into one just below the level of ovule attachment. The dorsal carpellary traces and the recurrent traces move in toward the locule. It is probably more correct to consider the latter traces as X-traces, and that the recurrent traces are used up in the production of the X-traces. Weak anastomoses are formed between the dorsal-X traces. All these traces soon disappear except for five phloem strands in the positions of the dorsals, which enter the base of the style (Figure 12) and extend about halfway to the 5-lobed stigma. A short floral tube is freed from the style. The sepal-stamen traces soon become amphicribral and the stamen traces then separate as phloem only or as weak inverted traces. The lateral sepal traces divide to form most of the traces in the sepals. The filaments are short and almost completely fused with the sepals.

Leptomeria pauciflora R. Br.

The flowers of *Leptomeria* are perfect and 5-merous. As in *Choretrum* the ovary is inferior with five locules at the base that merge into one above. The style is small with a 5-lobed stigma. *Leptomeria pauciflora, L. acida* R. Br. and *L. Cunninghamii* Miq. were studied but only *L. pauciflora* is described in detail.

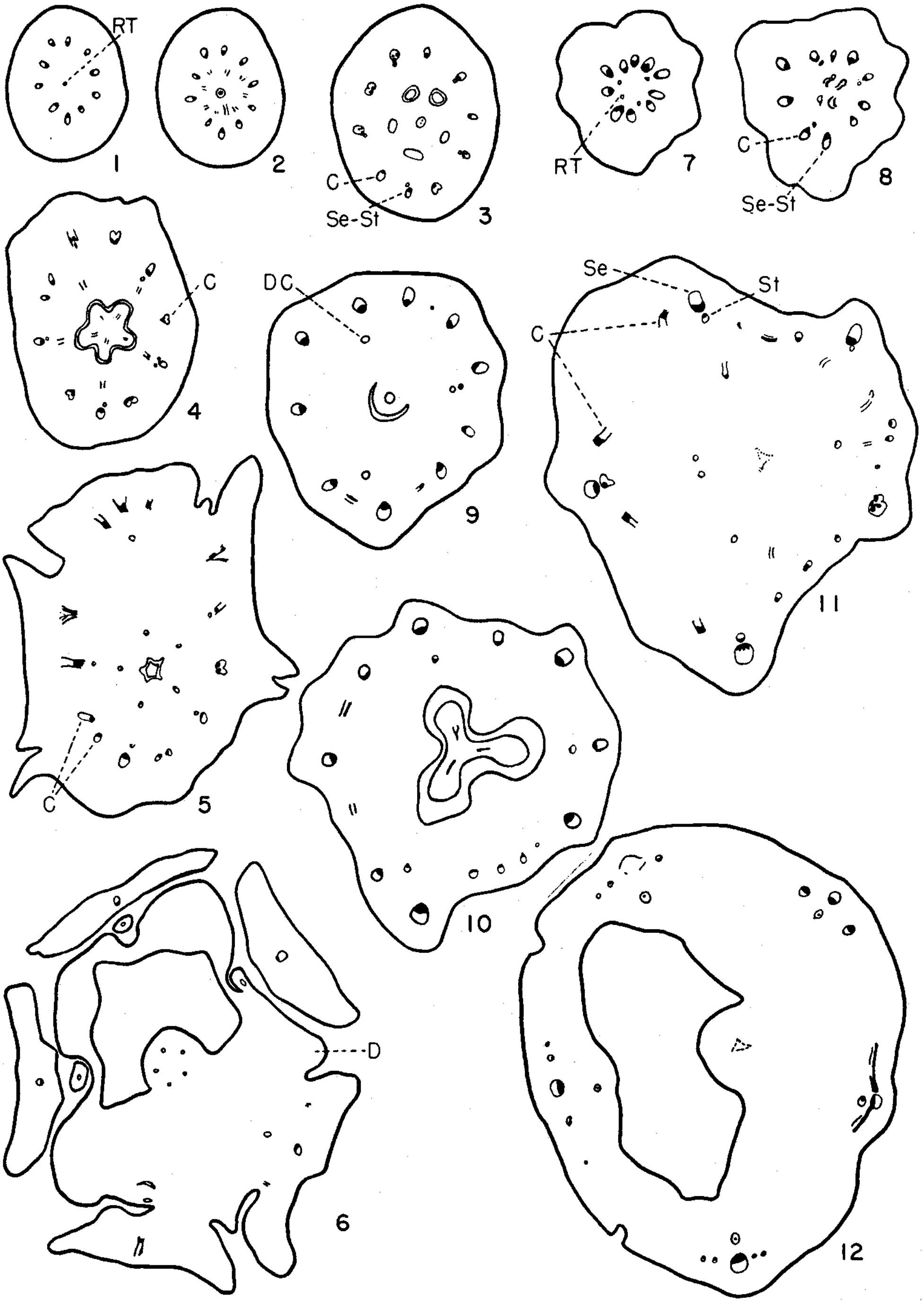
As in *Choretrum* there are ten traces in the pedicel (Plate XI, Figure 1). Some distance below the ovary a single xylem strand representing the residual tissue appears in the center of the pith region. A short distance above, phloem appears around the xylem strand to form an amphicribral bundle (Figure 2). At the same level phloem strands move outward toward the main traces. These phloem strands either connect with the phloem of the principal traces or they take up positions just inside the main traces where they continue for a short distance and then disappear. The amphicribral trace in the center continues upward into the placental column.

Since the commissural traces that form the lateral traces of adjacent sepals begin to branch at a higher level than in *Choretrum,* only the ten principal traces are present at the base of the locules (Figure 3). A single phloem strand appears just inside each of the sepal-stamen traces, which are located opposite the locules. These phloem strands either appear independently in these positions or originate as branches from the phloem of the main traces. They probably represent only the recurrent traces, although there is the possibility that the recurrent traces and the dorsal carpellary traces are fused. At the level of ovule attachment weak traces are given off from these phloem strands and move in toward the locule (Figure 4), leaving one or two strands of phloem inside each dorsal sepal bundle. Xylem in the normal position appears temporarily in the inner traces (Figure 5) before they enter the base of the style. Xylem may also appear in the inverted position in the small traces inside the dorsal sepal bundles.

The traces alternating with the sepal-stamen strands branch at the level of the top of the locule (Figures 4 and 5) increasing the number of principal traces to fifteen. The phloem trace inside each of the larger bundles now swings inward to enter the stamen (Figure 6). The lateral sepal traces disappear at the base of the sepals in a group of xylem-like sclerenchyma. The dorsal sepal traces may or may not branch in the sepals.

Leptomeria Cunninghamii and *L. acida* are essentially the same as *L. pauciflora* except that the residual tissue does not extend as far down in the pedicel.

PLATE XI



Leptomeria pauciflora (1-6), *Thesium Schumannianum* (7-12)

Thesium Schumannianum Schlecht.

The flowers of *Thesium* are perfect and 4- or 5-merous. The ovary is inferior with a single locule and a slender and somewhat twisted placental column bearing two or three ovules. The style is short with a stigma that is indistinctly 3-lobed.

In the 5-merous flower there are ten traces in the pedicel at the level at which the residual tissue first appears (Plate XI, Figure 7). The residual tissue consists of a few scattered strands of phloem and only an occasional xylem cell in the inverted position. The residual tissue appears in the pith region either independently or as branches from some of the main traces. A few anastomoses are formed between the residual traces (Figure 8) and they then move in to form a single phloem strand that enters the placental column (Figure 9). At the same time the principal traces begin to move outward into the ovary wall, leaving behind three dorsal carpellary traces (Figures 8 and 9). The dorsal traces may originate either independently or as branches from the sepal-stamen or the commissural traces, usually the latter. Occasional branch traces are given off laterally from the main traces.

The dorsal carpellary traces become stronger near the top of the locule. The traces between the sepal-stamen bundles branch one or more times (Figure 10) and from these branches weak traces arise that move in between the dorsal carpellary traces (Figure 11). The traces of the dorsal-X ring then move in toward the base of the style but disappear completely before the style is freed. The sepal-stamen bundles usually become amphicribral. Sometimes, however, a single inverted trace is formed inside by the inward rotation of a strand from the margin (Figure 11). Each of the traces between the sepal positions then swings over near the adjacent sepal-stamen strand (left side of Figure 11) where it persists for some time as an inverted trace. It is difficult to explain why these traces are inverted when those in *Choretrum* and *Leptomeria,* which apparently have the same origin, are normally oriented. Just before the floral tube is freed these inverted traces connect with the sepal traces (right side of Figure 12). Above this level there arise several small, normally oriented traces that continue into the sepal (left side of Figure 12). The inverted stamen traces become amphicribral but may be reduced to phloem only as they enter the stamens.

This description agrees in general with that of *T. linophyllum* given by Van Tieghem (1869b) though it differs in that here the carpellary traces are not completely independent of the main traces.

Thesidium fragile Sonder.

The flowers of *Thesidium* are imperfect and 4-merous. The pistillate flower has an inferior ovary with a single locule and an erect or twisted placental column bearing two or three ovules. The style is short with a stigma that is indistinctly 2- or 3-lobed. There are no stamen traces or staminodia in the pistillate flower.

Just above the level at which the traces to the bracts are given off, the three or four strands present in the pedicel divide radially to form eight traces that enter the base of the flower (Plate XII, Figure 1). One or more of these traces may consist of phloem only. The xylem eventually disappears from all but the four dorsal sepal traces. The behavior of the commissural traces is quite variable. The commissural trace shown at 7 o'clock in Figure 2 behaves as a dorsal carpellary trace and enters the base of the style. The one at 9 o'clock divides to form two traces, probably the marginal traces of adjacent sepals, which disappear before the sepals are freed. The one at 12 o'clock divides to form the two marginal traces and another dorsal carpellary trace. The one at 4 o'clock divides only once to form a dorsal carpellary trace and a phloem trace, which soon disappears. The commissural traces and the dorsal carpellary traces associated with them are very much reduced in this species. The ventral carpellary strand appears independently in the pith region (Figure 2) and continues into the placental stalk. There are no connections between this strand and any of the other traces.

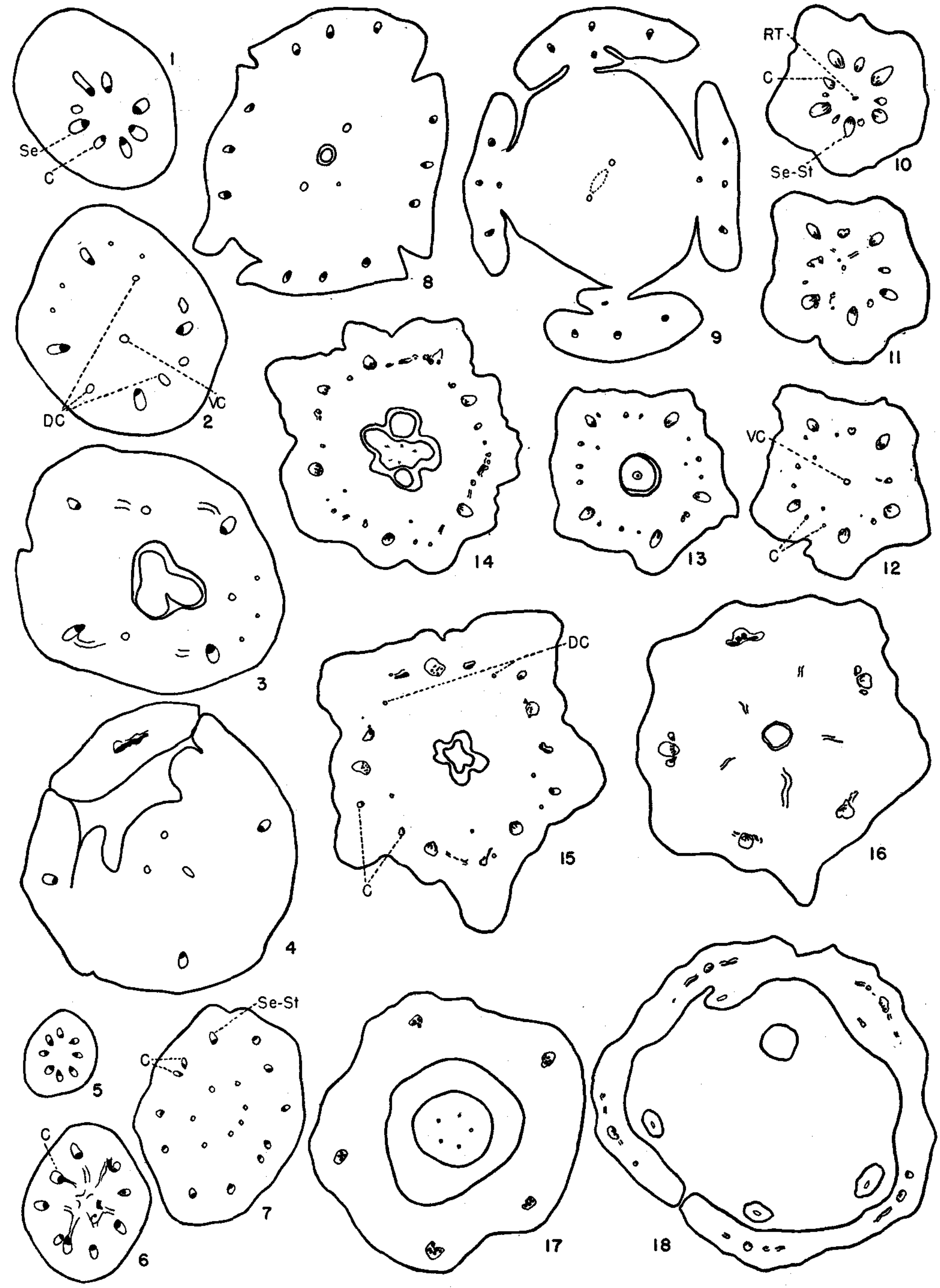
At the top of the locule (Figure 3) the dorsal traces move inward and a few weak traces are given off from the sepal bundles. These branch traces either connect with the dorsals or move laterally and soon disappear. The dorsal carpellary traces continue into the base of the style (Figure 4) where they also disappear. The sepal traces may or may not branch as the sepals are freed.

Omphacomeria acerba (R. Br.) A. DC.

Omphacomeria is monoecious or polygamous with 4-merous flowers. The ovary is practically inferior with a single locule. The style is short and thick with a 2-lobed stigma.

Since the flowers are 4- instead of 5-merous the pedicel contains eight traces (Plate XII, Figure 5) instead of ten as in *Choretrum, Leptomeria* and *Thesium*. The residual tissue appears in the pith region and connects immediately with the main traces (Figure 6). A ring of phloem traces arises from these anastomoses (Figure 7). The number of traces in the ring gradually is reduced to two (Figures 8 and 9), which enter the base of the style. Probably the number of carpels has likewise been reduced to two.

Plate XII



Thesidium fragile (1-4), *Omphacomeria acerba* (5-9), *Osyridocarpus natalensis* (10-18)

There is no indication of a ventral carpellary strand. Alternate traces in the ring of principal bundles branch low in the ovary (Figure 6), forming the twelve traces that are present in the ovary wall (Figure 7). As in *Choretrum* these continue directly into the sepals (Figures 8 and 9). The stamen traces arise from the sepal-stamen bundles as inverted or amphicribral traces.

Osyridocarpus natalensis A. DC.

The flowers of *Osyridocarpus* are perfect and 5-merous. The ovary is inferior with a single locule and a slender twisted placental column bearing two or three ovules. The style is long with a stigma that is capitate or indistinctly 2- or 3-lobed.

At the level at which the residual tissue first appears, there are ten traces in the pedicel (Plate XII, Figure 10). The five traces in the sepal positions are considerably larger than the others. Occasionally an additional small trace may appear. The residual tissue consists at first of a few strands of xylem, which soon disappear and are replaced by phloem (Figure 11). A few weak phloem traces connect to the traces, especially the smaller traces, of the outer ring at this level. The single strand of phloem tissue in the center continues upward into the placental column (Figures 12 and 13). At the level at which the phloem traces in the pith region connect to the outer traces the bundles between the sepal positions begin to branch (Figure 11). Some of these branch traces connect with the residual tissue as just described. Other traces continue upward in the outer part of the ovary (Figures 11 to 13).

There are five very weak traces representing the dorsal carpellary traces. These are not continuous throughout the ovary but may appear and disappear at various levels. Just above the point of ovule attachment (Figure 15) all five traces are present. A comparison of Figures 14 and 15 shows that these traces are opposite the points of ovule attachment. Near the top of the ovary the dorsals move inward (Figure 16) and enter the base of the style (Figure 17). The dorsal carpellary traces are alternate with the sepals instead of opposite them as in *Choretrum, Leptomeria* and *Henslowia.*

Near the top of the ovary the smaller traces in the outer ring form anastomoses with each other (Figure 14) and occasionally with one or more of the dorsal carpellary traces. Above this level two traces continue upward from each group of anastomoses between the sepal-stamen bundles (Figure 15). These two traces are derived indirectly from the single trace in the region between the sepals just as in *Choretrum* and *Leptomeria* though here the situation is complicated by anastomoses near the top of the ovary. Each of these traces then moves to the nearest sepal-stamen trace and fuses with it completely (Figure 16). The floral tube is freed just above this level. The sepal-stamen bundles then become amphicribral by the rotation of the marginal traces to the inverted position (Figure 17). The stamen traces separate a short distance below the level at which the stamens are freed while the sepal traces branch laterally to supply the sepals (Figure 18).

From the behavior of the commissural traces here it seems possible that *Osyridocarpus* may form a connecting link between *Choretrum, Leptomeria* and *Thesium* on the one hand and *Arjona* and *Quinchamalium* on the other.

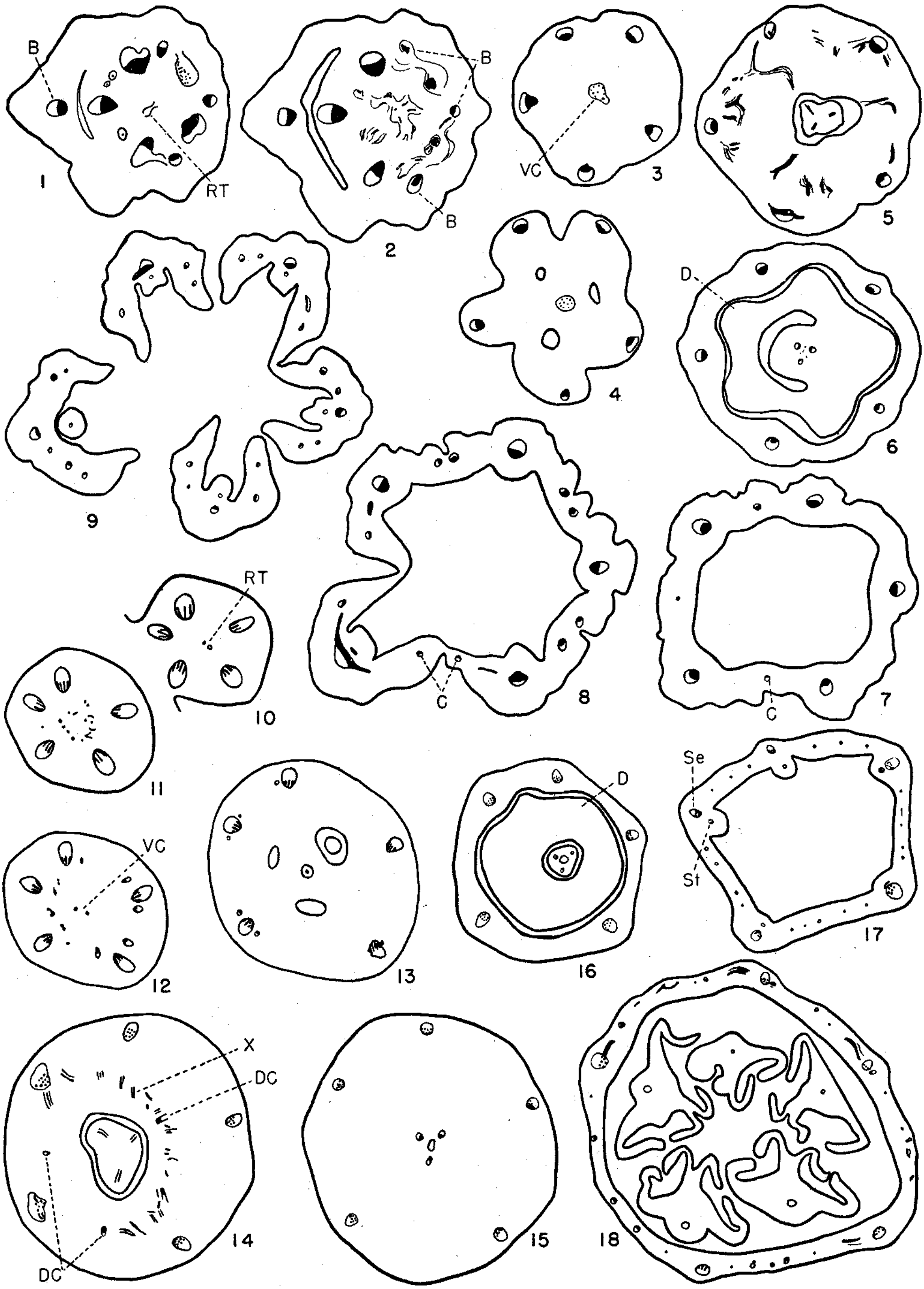
Quinchamalium majus Brongn.

The flowers of *Quinchamalium* are perfect and 5-merous. The flower is surrounded at the base by a tubular structure formed by the union of floral bracts. The floral tube is very much elongate, small and cylindrical with the stamens adnate to the base of the sepals. The ovary is inferior with three locules below, which merge into one above the level of ovule attachment. There is a short placental column bearing three ovules at the tip. The style is filiform and extends approximately to the middle of the floral tube. The stigma is capitate.

The residual tissue appears in the pith region before the tubular bract is entirely freed (Plate XIII, Figure 1). One trace to the bract moves out well below the others and the bract is freed on that side first. As the remaining three traces of the bract move out, anastomoses (consisting mostly of phloem) are formed between most of the traces present at this level (Figure 2). The residual tissue connects upward and outward to these anastomoses. As the bract is freed, the phloem between the main traces disappears (Figure 3). The ventral carpellary strand, consisting of phloem and scattered xylem cells, continues upward into the placental column. The three locules appear immediately above this level (Figure 4). There is no change in vascular structure from here up to the level of ovule attachment. At this level (Figure 5) numerous anastomoses are formed between the sepal-stamen traces. Branch traces move in toward the locule in the positions of dorsal carpellary traces and then continue upward to enter the base of the style (Figure 6). Weaker traces move inward at the same time as those in the positions of the dorsal carpellary traces but extend for only a short distance. The anastomoses then disappear and the floral tube and circular disk are freed in close succession.

Approximately in the middle of the floral tube single traces appear independently between the sepal-stamen bundles (Figure 7). These gradually

Plate XIII



Quinchamalium majus (1-9), *Arjona tuberosa* (10-18) enlarge as they extend toward the top of the tube. Just before the calyx lobes are formed, each of these traces divides into two branches that enter adjacent sepals (Figure 8). Thus the lateral traces of adjacent sepals here are derived from a single commissural trace as in *Choretrum* and *Leptomeria.* Here, however, the commissural traces appear independently about halfway up the floral tube. Thus they have lost direct connection with the main vascular system. The sepal-stamen bundles do not become amphicribral. As the stamen traces are given off from the sepal-stamen bundles, the lateral traces connect with the dorsal sepal traces. Both the lateral and dorsal sepal traces branch to supply the sepals (Figure 9).

Arjona tuberosa Cav.

The flowers of *Arjona* are perfect and are usually 5-merous. The ovary is inferior with three locules below, which merge into one above and a short thick placenta bearing three ovules. The style is filiform with a stigma that is capitate or indistinctly 3-lobed. Since *Arjona pusilla* Hook. f. and *A. longifolia* Phil. differ only slightly from *A. tuberosa,* only the last mentioned species is described in detail.

Above the level at which the bracts are given off there are five traces in the pedicel. The residual tissue appears in the pith region just as the last bract is freed (Plate XIII, Figure 10). In the center appear additional strands that lead upward and outward toward the sepal-stamen bundles (Figure 11). At least one xylem strand remains in the center, develops phloem to form an amphicribral strand and enters the placental column (Figures 12 and 13). The traces that move outward assume positions on either side of the sepal-stamen bundles (Figure 12), and then continue upward beside them for varying distances before fusion occurs. In *A. longifolia,* however, these traces are immediately incorporated into the sepal-stamen bundles.

Near the top of the locule weak traces appear independently in the ovary in the positions of dorsal carpellary traces (left side of Figure 14). Immediately above, anastomoses are given off from the main traces and move inward with the dorsals (right side of Figure 14) to form the dorsal-X ring of traces. Before the style is freed, all traces in this ring disappear except the three dorsal traces (Figure 15), which enter the style (Figure 16) and extend to the lobes of the stigma. In *A. pusilla* the dorsal carpellary traces do not appear below the level at which anastomoses are formed.

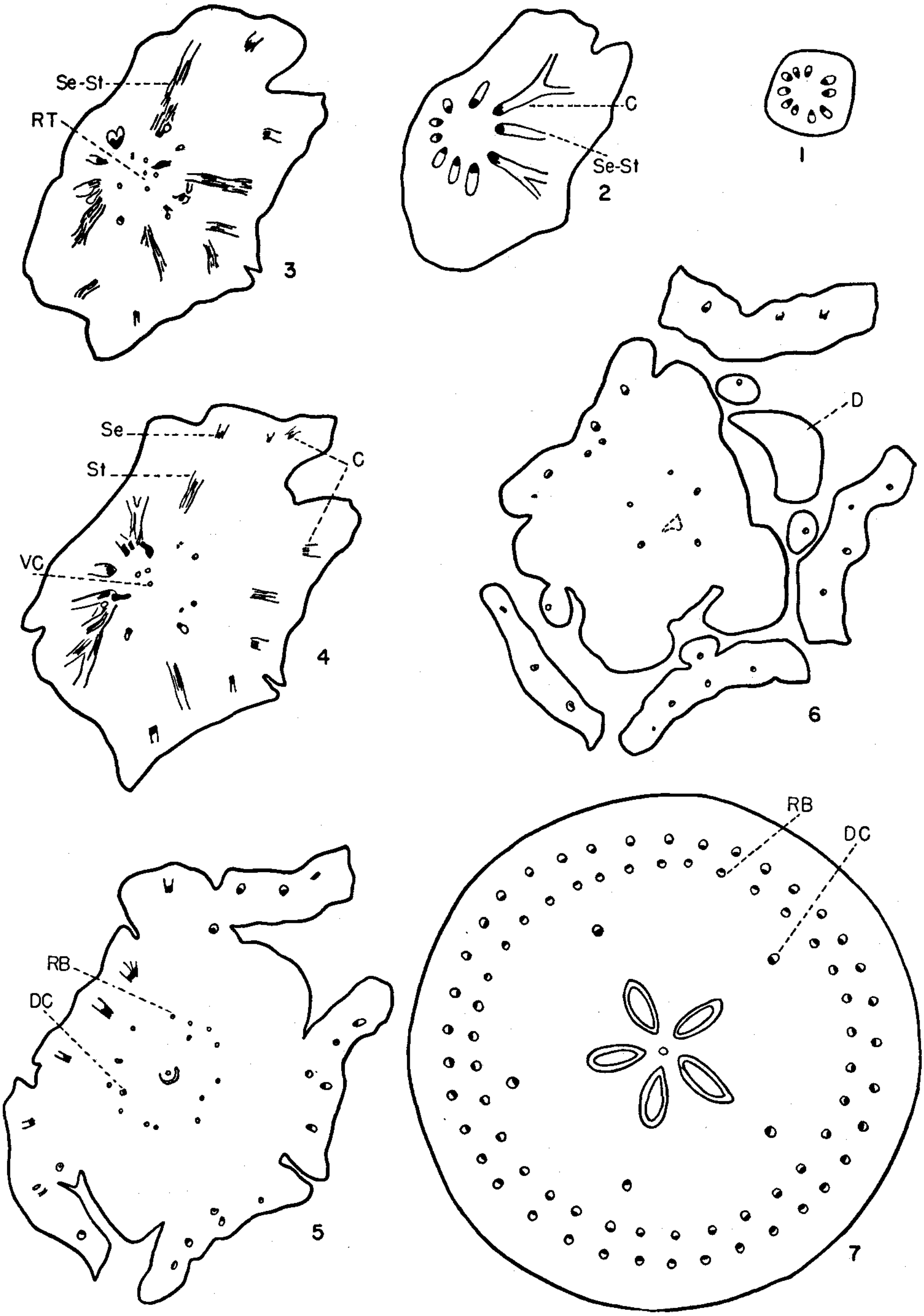
Here, as in *Quinchamalium,* there is a ring-shaped disk. The floral tube contains only the five principal traces for approximately two-thirds of its length. The stamen traces originate as separate phloem traces inside each main bundle. Just above the level at which the stamen traces originate, numerous small traces appear independently between the large ones (Figure 17). These gradually increase in size. Just before the sepals are formed and above the level at which the stamens are freed all the traces in the floral tube are connected by anastomoses (Figure 18). Above this level a variable number of traces enter the sepals.

THE STAMINATE FLOWER

The staminate flowers of only a few species with imperfect flowers were available. The staminate flowers of *Osyris* and *Henslowia* closely resemble those of *Darbya* in their floral anatomy. The floral anatomy of *Darbya* has already been described (Smith and Smith, 1942). Residual tissue is more often present in *Osyris* than in the other two species. The staminate flowers of *Pyrularia* contain a rather large but nonfunctional ovary with ovules and, as might be expected, differ less from the pistillate flowers than do those of other species. In the staminate flowers of *Pyrularia* there are fewer traces, the amphicribral strands are not so well developed and the traces in the ovary are reduced in size and number. The staminate flowers of *Buckleya* are the most reduced of those studied. There are only four strands in the pedicel and each of these moves out into a sepal as a sepal-stamen trace. Each trace then separates at the base of a sepal to supply a sepal and a stamen.

The anatomy of the staminate flowers of *Exocarpus sandwicensis* Baill. resembles that of the perfect flowers of *Choretrum* and *Leptomeria* and not at all that of other staminate flowers studied. This species of *Exocarpus* was the only one in which staminate material was available. Of the ten traces present in the pedicel just below the flower (Plate XIV, Figure 1), five move out into the flower directly to form the dorsal sepal-stamen traces. The alternate, or commissural, traces branch to form lateral traces of adjacent sepals (Figure 2). Since the laterals may subsequently also branch, more than three traces may enter a single sepal (Figures 4 and 5). Residual tissue appears in the pith region as the sepal traces move out (Figure 3). This connects upward and outward to anastomoses between the principal traces. The ventral carpellary strand continues upward from the residual tissue to enter a reduced placental stalk (Figures 4 and 5). From the anastomoses between the principal bundles traces continue upward into the rudimentary ovary wall (Figures 4 and 5). The stamen traces separate from the sepal-stamen bundles just before the sepals are freed. At the level of the small locule the following traces are present in the reduced ovary: an outer ring of weak traces of phloem only, or occasionally also of xylem in the inverted position, and three or occasionally five weak dorsal carpellary

PLATE XIV



Exocarpus sandwicensis (1-6), hypothetical primitive santalaceous species (7) traces inside (Figure 5). The only essential difference between Figure 5 and Figure 10 (Plate X) of *Choretrum* is in the number of locules. There are five locules in *Choretrum* but only one in *Exocarpus.* The sepals, stamens, and disk are freed somewhat irregularly (Plate XIV, Figure 6). All traces in the ovary disappear except the dorsal carpellary traces, which enter the base of the style. Figure 6 closely resembles Figure 12 (Plate X) of *Choretrum* and Figure 6 (Plate XI) of *Leptomeria.*

Calyptosepalum sumatranum S. Moore

It has been suggested that *Calyptosepalum* may possibly belong to the Santalaceae but its position here is doubtful. Only male flowers are known. There are four sepals arranged in pairs with the outer pair larger and enclosing the inner pair. The stamens are opposite the sepals. Traces are given off first to the two outer sepals and then to the two inner sepals. The remaining traces form a complete ring of bundles in the center. Four of the bundles move out to form stamen traces opposite the sepals. Three others form weak dorsal carpellary traces that enter a rudimentary ovary with no locule. In addition to the structure described thus far there are several cortical traces, some of which are inverted, which arise independently in the lower portion of the flower and connect with the main traces in the upper portion. On the basis of floral anatomy there seems to be no reason for placing *Calyptosepalum* in the Santalaceae. Though it seems to bear some slight resemblance to the Olacaceae, its relation to this family seems almost as doubtful.

DISCUSSION

The inferior ovary of the Santalaceae is extremely varied in its anatomical structure. Every species studied shows the characteristics that indicate a receptacular inferior ovary in either the primitive or some derived condition. The three most important characteristics of a receptacular inferior ovary are: first, the presence of recurrent inverted traces; second, the presence of residual tissue that is directed downward into the pith region; and third, the origin of the carpellary bundles from the recurrent inverted traces. In the species that are more primitive in the family, these characteristics are more evident than in the advanced species. Since they can be recognized to some extent in all species studied, the inferior ovary throughout the family may be considered as receptacular. In all species the placental column is interpreted as consisting entirely of carpellary tissue, since the residual tissue of the floral axis is directed downward. The number of carpels varies from five to two, with three the most common number. Saunders (1940) concluded, on the basis of carpel polymorphism, that the ovary in *Colpoon* consists of alternate whorls of sterile and fertile carpels (G 5 + 5 or G 4 + 4). She designated the ovary of *Osyris* as G 4 + 4 and of *Thesium* as G 3 + 3. No evidence was found to support this interpretation of the ovary of the Santalaceae.

Van Tieghem (1869b) considered that the carpels in the flowers of *Thesium* and *Osyris* have a vascular system independent of that of the sepals. Schaeppi and Steindl (1937) and Rao (1942) agreed with this interpretation. The carpellary traces show definite connections with the main vascular supply in the more primitive species, such as in *Darbya.* These traces arise from the recurrent inverted traces in the base of the flower. Since, in the more advanced forms, the recurrent traces become more and more reduced, it is to be expected that the carpellary traces may show a tendency to lose their connections with the main vascular supply or that new connections may be established. That the latter occurs more frequently has been shown in many of the species described. Connections always appear except in species where the recurrent traces have practically disappeared by gradual reduction in size. In only a few species, such as in *Thesidium* and *Omphacomeria,* is the ventral carpellary strand completely free from connections to the other traces.

As might be expected, because of the parasitic nature of the family, a large number of variations in the anatomy of the inferior ovary occur in the Santalaceae. Variations in one characteristic may occur quite independently of variations in other characteristics in the same species. The ovary of *Colpoon,* for instance, has retained three locules and three well developed dorsal carpellary traces, but the recurrent traces are less clearly defined than in *Darbya,* in which the ovary has been reduced to one locule. *Santalum* has a single locule in the ovary and rather strong recurrent traces but shows no evidence of dorsal carpellary traces below the level at which the X-traces appear. Thus the presence or absence of dorsal carpellary traces in different genera is not dependent on the advanced or primitive condition of the rest of the flower.

There are indications that in the Santalaceae the dorsal carpellary traces in some species actually disappear. That is to say, they fail to differentiate rather than that they are not evident because of fusion with other traces. In *Santalum,* for example, the recurrent traces are variable in size but the traces opposite the points of ovule attachment are not more strongly developed as might be expected if the dorsals were fused with them. Also, if dorsals were present there should be in the inner ring some indication of collateral traces in the positions of dorsal carpellary traces. Instead, all of the traces in this ring are inverted. The dorsal traces are evident above the level at which the X-traces appear, however, because in most instances the X-traces seem to reinforce or strengthen the dorsals. Because of this, the dorsals are not so likely to disappear above these rather strong connections as they are below. In various forms, such as in *Osyris* and *Arjona,* the dorsals are strongly developed above the level of the X-traces and weakly developed or lacking below. No dorsal traces are evident at the level of the locules in *Arjona.* Before the X-traces move in, however, the dorsal traces appear independently in the proper positions and are strongly developed above the anastomoses with the X-traces. Also, in *Osyridocarpus* the dorsals may appear and disappear at irregular intervals in the same flower.

On the other hand, the recurrent traces may be lacking as distinct traces either because of failure to differentiate or because they are incorporated with the ascending traces. In genera closely related to *Colpoon, Darbya* and *Santalum,* it is evident that the distinct rings of ascending and recurrent traces have been gradually replaced by large amphicribral strands. Many of the traces located between the sepal positions form anastomoses low in the ovary and disappear. Other traces swing inward and rotate to the inverted position to form the inner portions of the amphicribral strands. The amphicribral strands undoubtedly contain more than just the dorsal sepal and stamen traces. In the genera related to *Henslowia* and *Choretrum,* on the other hand, the recurrent traces are early reduced in size until, within the series, they gradually disappear. It is interesting to note in *Thesidium* and *Omphacomeria,* which are advanced forms in this series, the complete independence of the ventral carpellary strand from the main vascular supply. The loss of the recurrent traces in these forms apparently resulted in the removal of any connection between the ventral strand and the main traces.

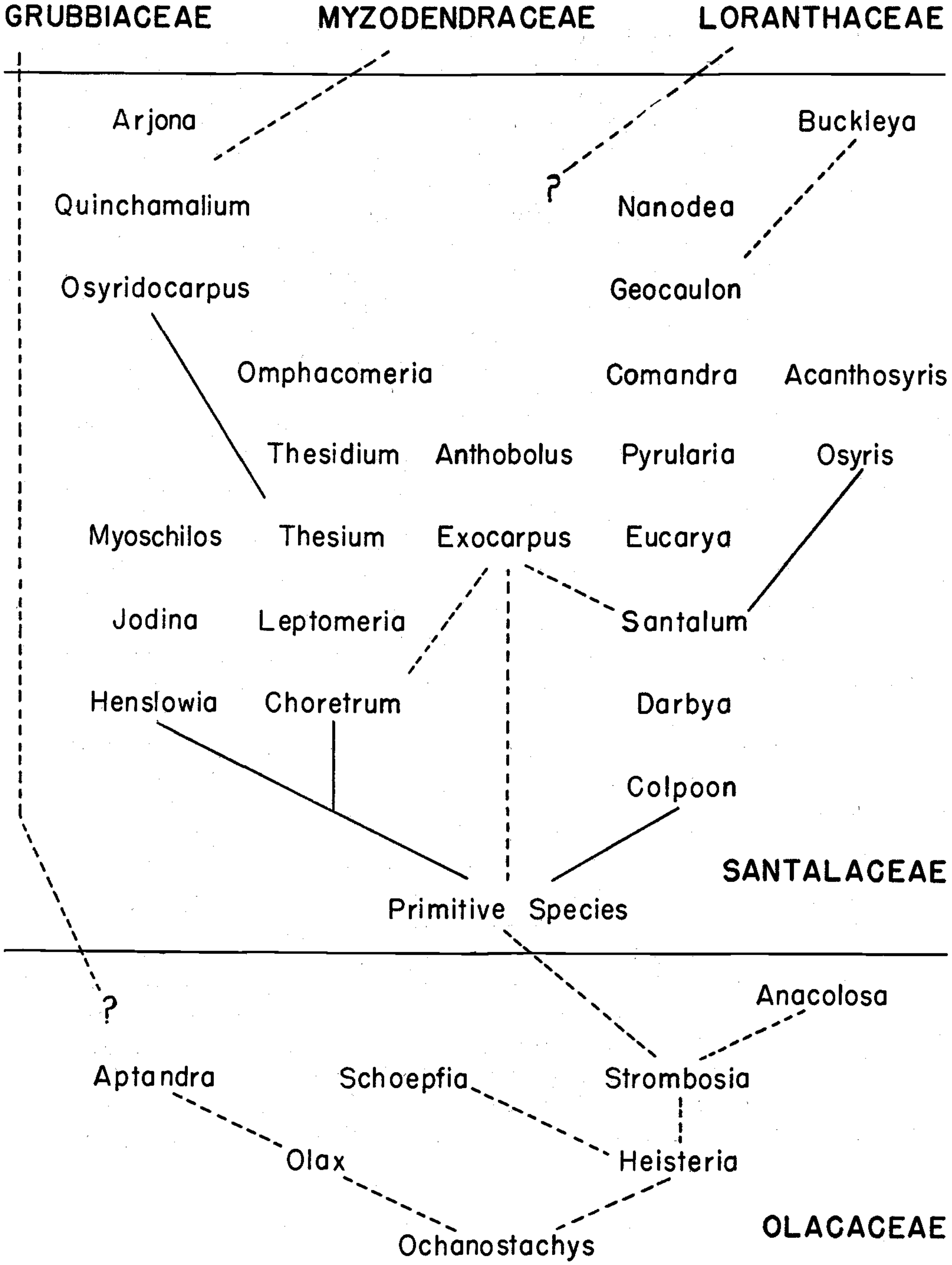
On the basis of the floral anatomy of the genera studied it appears likely that the primitive santalaceous flower was probably 5-merous with a partly or completely inferior ovary that had five more or less separate locules and a well developed vascular structure of the type described for *Darbya.* A cross section of this hypothetical flower, taken at the level of the locules, would appear as in Figure 7, Plate XIV.

From this primitive type two main lines seem to have been developed within the family (Plate XV). In one line there was an early reduction in the number of carpels and locules but a retention of the well developed rings of ascending and recurrent traces. *Colpoon, Darbya* and *Santalum* represent the more primitive members of this group. *Eucarya* shows definite indications of relationship to *Darbya* and *Santalum* but the recurrent traces show a considerable reduction in both size and number. Characteristic of the anatomy of the remaining members of this group is the formation of the more or less loosely arranged amphicribral strands representing sepal-stamen bundles. In *Colpoon* (Plate II, Figure 6) and *Darbya* (Plate I, Figure 9) these amphicribral strands are formed near the top of the ovary or in the base of the floral tube by the persistence of a varying number of both ascending and recurrent traces in the sepal positions. The traces between the sepal positions form anastomoses and disappear. In *Santalum* the loosely arranged amphicribral strands originate in the base of the floral tube partly by the persistence of ascending and recurrent traces and partly by the rotation to the inverted position of the small traces on either side of the sepal traces (Plate III, Figures 1 and 2). In *Pyrularia* both of these tendencies are expressed in the base of the ovary. The traces between the sepal positions form anastomoses and disappear and small traces on both sides of the sepal traces swing inward and rotate to the inverted position (Plate V, Figures 9 and 10). Thus a large, loosely arranged amphicribral strand appears in each sepal position throughout the length of the ovary. The traces or their anastomoses between the sepal positions show a stronger tendency to form connections with the residual tissue or the ventral carpellary strand than do the traces in the sepal positions. This is a possible indication that the recurrent traces between the sepal positions are the traces that originally gave rise to the ventral carpellary traces.

In *Comandra* and *Geocaulon* more compactly arranged amphicribral strands are formed in the ovary wall. There is a continuous stele in the pedicel in these genera, which separates to form five large strands in each sepal position. Few traces appear between the sepal positions. The large strands become amphicribral as they move out from the stele because the marginal portions swing inward and rotate to the inverted position (Plate VI, Figures 2, 3, and 10). The origin of the amphicribral strands in *Nanodea* is similar, though in this genus the traces become amphicribral much more gradually. The number of carpels here is reduced to two. *Nanodea* probably is the most advanced form in this series.

Osyris and *Acanthosyris* appear to represent a side branch from the main line of development in this group. They should probably be considered as derivatives from the line at the level of *Darbya* or *Santalum.* In *Osyris* the X-traces appear low in the ovary, are well developed and have established connections with the ascending traces. The recurrent traces are much reduced in size and number above the level of origin of the X-traces. Thus the main path of conduction to the carpels, as indicated by the development

PLATE XV



Suggested relationships within the Santalales as indicated by floral anatomy. The more uncertain relationships are indicated by broken lines.

of xylem, has been shifted inward low in the flower. The X-traces apparently originate at a lower level in *Acanthosyris* than in *Osyris* so that the carpellary traces and X-traces originate at approximately the same level. This results in a much confused system of vascular tissue in the base of the flower. The development of the xylem at successive levels seems to indicate that the path of conduction is shifted to the innermost traces low in the ovary and passes outward first to the recurrent traces and finally to the ascending traces. This may explain why the more strongly developed traces are at first normally oriented in the inner layer of the ovary wall, then inverted in an intermediate position and finally normally oriented in the outer layer of the ovary wall.

Although *Buckleya* resembles *Comandra* and *Nanodea* in the nature of the main traces, there seems to be insufficient evidence definitely to associate it with these forms. That *Buckleya* is considerably advanced is indicated by the structure of both the staminate and pistillate flowers. There is no definite indication as to the nature of the extra whorl of floral parts in the pistillate flowers of this genus.

The second line of development in the Santalaceae with regard to floral anatomy seems to have been an early reduction of the recurrent and carpellary traces with the retention of the five carpels of the primitive santalaceous flower. There then followed a further reduction in the inner traces and in the number of carpels. The inferior ovary in this group thus differs markedly from that in the first group in that inverted recurrent traces are represented by much reduced strands or are entirely lacking. The receptacular nature of the inferior ovary in this group is indicated by the presence in the pith region of residual tissue that connects upward and outward to the main traces, by the presence of occasional inverted traces (e.g., in *Henslowia*), and usually by the rotation to the inverted position of the marginal strands of the sepal-stamen bundles to form amphicribral bundles in the same manner as in *Santalum, Pyrularia* and other members of the first group.

Within this second group there seem to be two subdivisions. In one, all traces between the sepal-stamen traces disappear near the top of the ovary just as in the first line of development described. Each sepal then receives only a single strand, the sepal-stamen trace, which first divides tangentially to form the stamen trace and then radially to supply the sepal. The three genera in this subdivision are *Henslowia, Jodina* and *Myoschilos*. They are characterized by a reduction from five carpels to three and also by a reduction in the number of traces representing the recurrent bundles. In the second subdivision of this group, each sepal receives three traces, a dorsal sepal-stamen trace and two lateral sepal traces. The pedicel contains twice as many traces as there are floral parts in each whorl. Alternate traces then become dorsal sepal-stamen traces and the remaining traces, which are commissural, branch to produce lateral traces of adjacent sepals. The genera in this subdivision are *Choretrum, Leptomeria, Thesium, Thesidium* and *Omphacomeria.* Within this subdivision there is a reduction in the number of carpels from five to two and a marked reduction in the number of recurrent and carpellary traces.

Osyridocarpus, Quinchamalium and *Arjona* seem to have been derived from this group, which has commissural marginal traces. In *Osyridocarpus* there are twice as many traces in the pedicel as there are floral parts in each whorl. The commissural traces, which alternate with the sepal-stamen bundles, do not continue directly through to the sepals but instead form a series of anastomoses. At higher levels in the ovary, however, the anastomoses form the lateral traces so that each sepal receives one dorsal and two lateral traces just as in *Choretrum* and related genera. Each lateral sepal trace fuses for a time with its adjacent dorsal sepal-stamen bundle but separates in the base of the sepal. In *Quinchamalium* each sepal receives three traces, but the lateral traces are derived from traces that appear independently halfway up the floral tube. It can probably be assumed that here the commissural traces have lost their connections below with the main vascular supply. *Arjona* resembles *Quinchamalium* in practically all respects except in the absence of lateral sepal traces, and hence is included with it.

Anthobolus and *Exocarpus* have been considered previously as rather primitive members of the Santalaceae because of their superior or nearly superior ovaries. As has already been pointed out in describing the structure of these forms, the ovary is not as nearly superior as it appears since the ventral carpellary strands arise deep in the fleshy receptacle that bears the ovary. The lack of a clearly defined ring of inverted recurrent traces, except for a short distance in *Exocarpus cupressiformis,* the single locule and the lack of dorsal carpellary traces all indicate a rather advanced condition and are suggestive of *Santalum,* which at times has a practically superior ovary. On the other hand, the structure of the staminate flowers of *Exocarpus* resembles that of the perfect flowers of *Choretrum* and *Leptomeria.* There is also the possibility that *Anthobolus* and *Exocarpus* were derived directly from the primitive santalaceous species and may thus be related to the two main series only in having a common origin. While the origin of *Anthobolus* and *Exocarpus* may be in doubt, it seems entirely unlikely that these genera represent primitive forms in the Santalaceae.

The relationships indicated by floral anatomy in the Santalaceae are given in Plate XV. This chart should not be interpreted as phylogenetic in the usual sense of the term. The arrangement of genera is based almost entirely on floral anatomy of perfect or pistillate flowers. Taxonomic features generally have not been considered. The primary function of the chart is to show the relation of variations in structure of the receptacular inferior ovary. Since floral anatomy is very important in determining phylogeny, however, it is to be expected that the arrangement of the genera given approaches rather closely a phylogenetic arrangement.

The division of the Santalaceae into three tribes is supported by the floral anatomy of the genera studied. The Anthoboleae are distinctly separated from the Osyrideae and the Thesieae. It is difficult to separate the two latter tribes on purely taxonomic considerations since this involves the use of characteristics more or less present in both tribes. The results obtained in this study indicate that *Choretrum, Leptomeria, Omphacomeria, Henslowia, Jodina* and *Myoschilos* are more closely related to members of the Thesieae than they are to those of the Osyrideae. Relationship is particularly evident between *Choretrum* and *Leptomeria* on the one hand and *Thesium* and *Thesidium* on the other. Numerous changes in the relative positions of the genera within the Thesieae and Osyrideae are suggested by their floral anatomy. Probably the most important of these is the placing of *Colpoon* and *Santalum* in the position of more primitive forms and of *Buckleya* in an advanced position.

OLACACEAE

Olacaceae is considered by most taxonomists as the most primitive family of the Santalales. Sleumer, in "Natürlichen Pflanzenfamilien" (1935) lists twenty-three genera that are arranged in three subfamilies and further subdivided into six tribes. Since the authors are interested in the Olacaceae primarily because of their possible relationship to the Santalaceae as indicated by floral anatomy, taxonomic groupings within the family are not discussed. It may be mentioned, however, that the seven species studied represent all but one of the six tribes.

Most of the flowers in this family are perfect with both sepals and petals present. The ovary is superior or inferior with two to five locules below, which merge into one above. There are two to five ovules suspended from the central placental column.

Ochanostachys amentacea Mast.

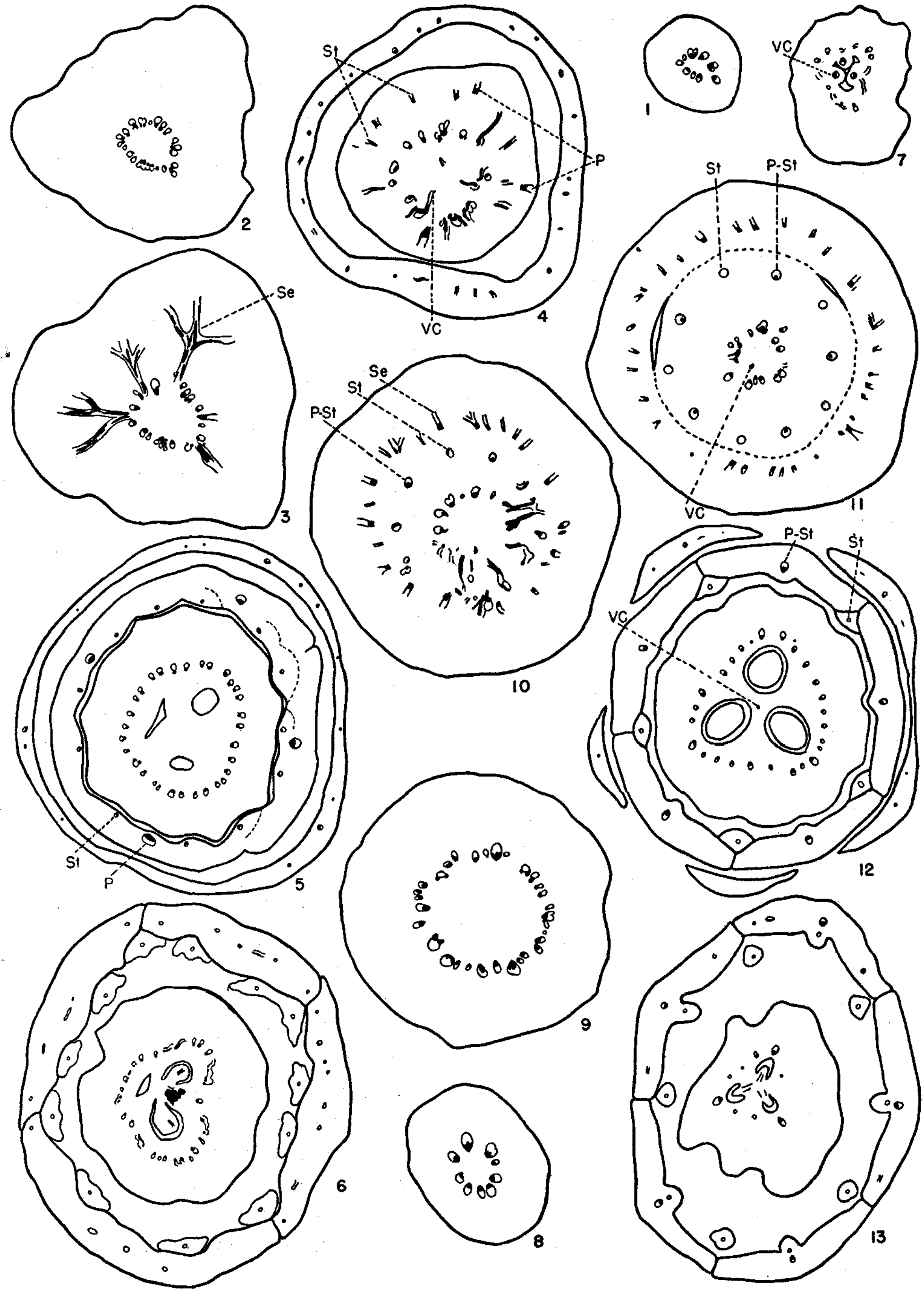
In *Ochanostachys* the calyx is small and cup-shaped. The twelve to fifteen stamens are so arranged that two are opposite each of the four or five petals and one is in each position alternating with the petals. The ovary is superior with three locules below, which merge into one above the level of ovule attachment. The style is short and thick with a 3-lobed stigma.

In the pedicel there are usually eight or nine traces (Plate XVI, Figure 1), which divide radially to form numerous traces in the base of the flower (Figure 2). Four large traces, and occasionally additional smaller ones, move out to supply the calyx tube (Figure 3). Each large trace immediately branches to form three traces, which then divide to form numerous traces in the calyx tube (Figure 4). The calyx tube is freed immediately above the level at which these traces originate. Four petal traces then move out followed by the twelve stamen traces. The section illustrated in Figure 4 is cut at a slight angle across the flower with the lower side of the figure at a lower level. In the small amount of material available, no evidence was obtained to indicate that the stamens are borne in more than one whorl. As the stamen traces move out, three weak traces move in. The latter undoubtedly represent ventral carpellary traces. They soon disappear, however, and do not enter the placental column. The remaining traces enter the ovary wall. The corolla tube with its adnate stamens is freed just below the level of the base of the locules (Figure 5). The traces remaining after the departure of the stamen and ventral carpellary traces divide to form a ring of numerous small bundles that continue upward in the ovary wall. The stamens, arranged so that usually two are opposite each petal and four are alternate with the petals, are then freed from the corolla tube (Figure 6). Vascular tissue appears in the partitions near the top of the locules and then connects to the ovules. The strands continue upward in the ovary wall and, as the locules merge, become connected above the top of the locule. Extending upward from these connections are three inverted traces that alternate with the locules (Figure 7). These are the ventral carpellary traces that by a somewhat devious route are continued above the central placenta to the base of the style. Meanwhile the traces in the outer ovary wall move in and form anastomoses with each other near the level of ovule attachment (Figure 6). Some of the traces disappear and at the base of the style the remainder form anastomoses with the inverted traces (Figure 7). The three inverted traces then disappear and three traces that are normally oriented and in the positions of dorsal carpellary traces continue up the style almost to the 3-lobed stigma.

Heisteria nitida Engl.

The calyx of *Heisteria* is small in the flower but it enlarges considerably as the fruit matures. There are usually five petals and ten stamens. Five of the stamens are epipetalous and shorter than the five that alternate with the

PLATE XVI



Ochanostachys amentacea (1-7), *Heisteria nitida* (8-13) petals. If, as rarely occurs, there are only five stamens, then these alternate with the petals. The ovary is superior with three locules and a placental column bearing three ovules.

In the pedicel there are eight or nine traces (Plate XVI, Figure 8), which divide radially to form numerous traces in the base of the flower (Figure 9). These traces move inward rapidly and at the same time give off two successive whorls of traces (Figure 10). The outer whorl moves outward rapidly and enters the calyx tube, which is freed immediately (Figure 11). Although originally xylem is present in all of the traces of the second whorl (Figure 10), it is soon lost from alternate traces (Figure 11). The traces retaining xylem are petal-stamen traces, while the phloem traces alternating with these are the traces of the stamens that alternate with the petals. All of the central traces enter the ovary. A few xylem strands move in slightly beyond the others (Figure 11). These possibly represent ventral carpellary traces that are more reduced than those in *Ochanostachys.* They disappear very shortly but reappear as a single strand at the base of the locules (Figure 12). Meanwhile both the corolla tube and the filaments of those stamens that alternate with the petals have been freed. At this level three of the traces in the ovary wall, those opposite the locules, become somewhat more strongly developed than the others. They continue to enlarge while the others become smaller and gradually disappear (Figure 13). Only the three traces in the positions of dorsals continue into the style. The ventral carpellary strand divides at the top of the placental column to supply the ovules and then disappears. The stamen traces separate from the petal-stamen traces at approximately the base of the style.

Anacolosa luzoniensis Merr.

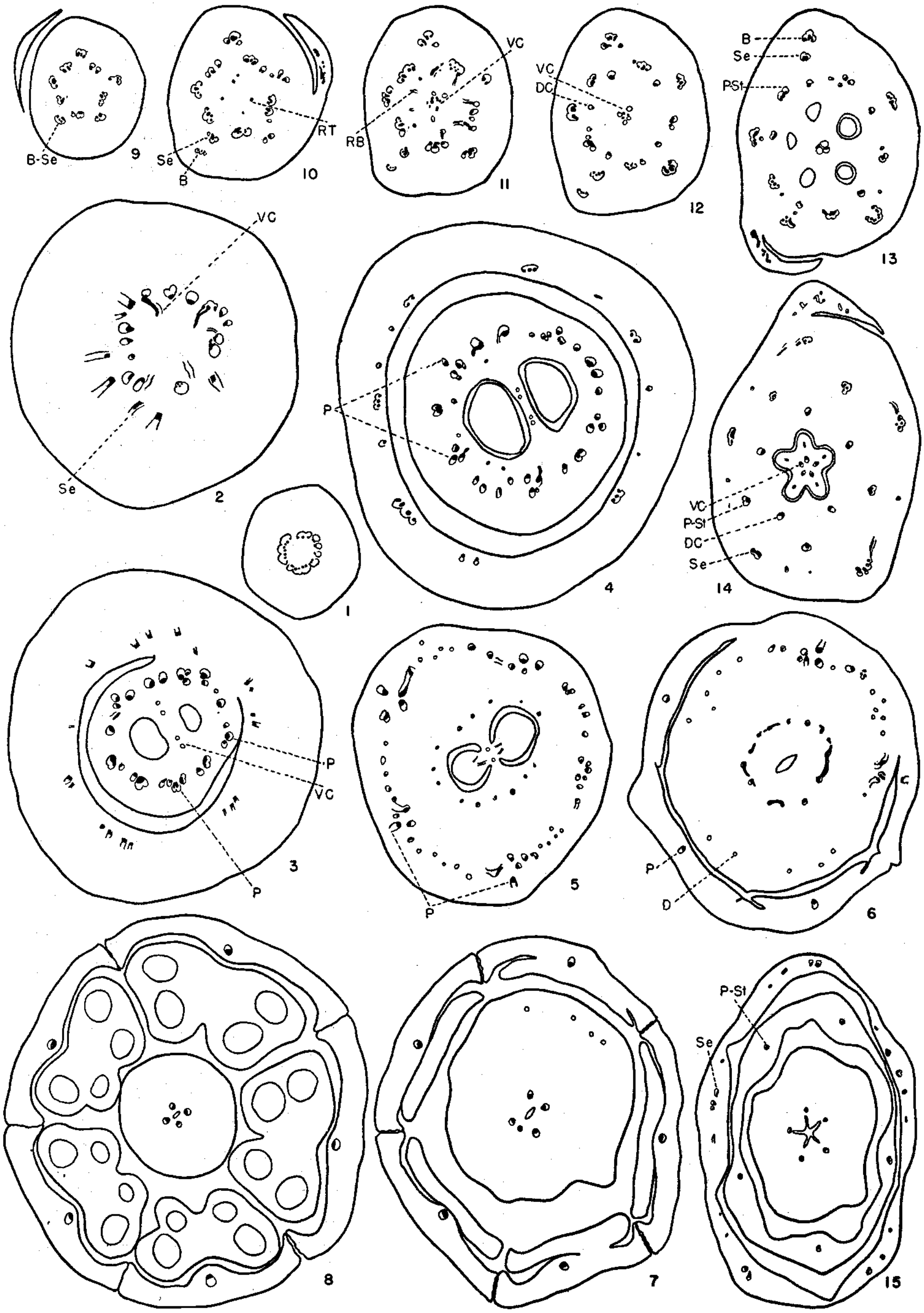
The material that was available of *Anacolosa* differs somewhat from that described in Engler and Prantl (1935). There are five petals and five stamens instead of six of each. The stamens are epipetalous with much flattened filaments. The calyx tube is small and cup-shaped. There are two locules, which merge into one at the top, and two ovules, which are suspended from the placental column. The flower is peculiar in that the calyx is freed below the ovary while the corolla tube, with its adnate anthers, is fused with the ovary almost to the top. There is a fleshy disk adnate to the ovary.

There is an almost continuous cylinder in the pedicel (Plate XVII, Figure 1), which soon separates into fairly numerous individual strands. At the base of the flower a variable number of traces move out and enter the calyx tube, which is immediately freed (Figures 2 and 3). As the first of the traces to the calyx tube move out, several strands of xylem or phloem or both extend into the pith region (Figure 2) and almost disappear. The two locules appear immediately above (Figure 3). Two pairs of phloem strands are arranged in a single row along the partition or placental column. These phloem strands either originate independently near the main traces or they originate from the inwardly directed strands shown in Figure 2. The traces of each of these pairs fuse near the top of the placental column (Figure 5) and both of the traces thus formed supply both ovules.

At the level of the base of the locules the petal traces begin to move out and the traces on either side of each petal trace begin to swing around to the inverted position. These traces are easily distinguishable at approximately the middle of the ovary (Figure 4). At this level small traces are given off to the inside, move in near the locules (Figure 5) and form anastomoses with each other above the level of ovule attachment (Figure 6). These traces originate in the same manner and follow the same paths as the X-traces in the Santalaceae. The number of traces in this inner ring is then gradually reduced to four, which enter the style (Figure 8). Perhaps this is an indication that there are four carpels but only two locules in this species. After these traces are given off to the inside, the outer traces between the petal positions soon lose their xylem (Figure 5). In each petal position at this level there is a loose amphicribral strand of the type seen in the Santalaceae. The outermost trace from each strand moves out to enter the corolla tube (Figure 6), which is freed immediately. The remaining traces of each group, as well as the phloem strands that have persisted between the petal positions, enter the fleshy disk, which is adnate to the ovary. The inverted and partly inverted traces branch laterally in the disk. Both these and the phloem traces between the petal positions then gradually disappear. The stamens are freed opposite each petal (Figure 7) but no stamen traces are distinguishable at any level in the flower.

The nature of the inferior ovary here is somewhat in doubt. Since the exact origin of the ventral carpellary traces is difficult to determine, this type of evidence cannot be considered. The loosely arranged amphicribral strands and the behavior of the stylar traces, however, would seem to indicate a receptacular inferior ovary as in the Santalaceae. If the inferior ovary here is receptacular, then it seems likely that the so-called calyx is actually a whorl of bracts. The gradual disappearance of the traces between the amphicribral strands is also typical of the Santalaceae. In *Anacolosa,* however, these traces disappear in the disk after the corolla tube has been freed instead of at the base of the calyx tube as in the Santalaceae. Before their disappearance in the disk the inner traces of each amphicribral group form anastomoses. It seems most likely that the inferior ovary here is receptacular

PLATE XVII



Anacolosa luzoniensis (1-8), *Strombosia philippinensis* (9-15) in nature and that the disk is fleshy receptacle tissue that has grown up between the corolla and the ovary. The complete absence of traces in the stamens may be interpreted in two ways. Either the stamen traces are so completely fused with the petal traces that they do not separate, or they fail to move out from the receptacle. In the Santalaceae the innermost inverted trace of each amphicribral strand goes to the stamen, while in *Anacolosa* this trace remains in the receptacle.

Strombosia philippinensis (Baill.) Rolfe

The genus *Strombosia* is divided into two sections. In one there is a superior ovary, in the other a more or less inferior ovary. *Strombosia philippinensis* belongs to the latter section. The ovary is almost completely inferior with five locules that merge into one above the attachment of the ovules. The style is short with a 5-lobed stigma. There are five stamens, which are opposite the petals and adnate to the corolla tube.

Small bracts are present in 2/5 phyllotaxy from the pedicel to the top of the ovary (Plate XVII, Figures 9, 10, 13, and 14). The bracts are approximately in the positions of the sepals and a single trace supplies a bract and a sepal. Each of these bract-sepal traces moves out a short distance from the stele (Figure 9) and then divides tangentially. One half remains while the other half moves out and continues up the ovary some distance before entering the bract (Figures 10 to 13). Since the floral traces otherwise appear independently of the bracts, the latter will usually not be referred to in describing the remainder of the floral structure.

The sepal-bract traces move out from the stele relatively low in the pedicel (Figure 9). The pedicel increases very gradually in size to the level at which the next bract appears (Figure 10). This distance is approximately one-third of that between the levels shown in Figure 9 and Figure 15. Vascular tissue appears in the pith region at the level of Figure 10. As in the Santalaceae, this represents residual tissue that is directed downward as a result of invagination of the tip of the floral axis. Anastomoses connect this residual tissue and give rise to xylem and phloem strands, which represent the ventral carpellary traces (Figure 11), and also to inverted recurrent traces, which connect upward and outward to the vascular tissue on either side of the gaps left by the bract-sepal traces. The traces that connect with the inverted traces then swing out into the gaps to form the dorsal carpellary traces opposite the sepals (Figure 12). The remaining traces in the stele constitute the petal-stamen traces.

At the level of the base of the locules, both the ventral carpellary strand and the petal-stamen traces become more compactly arranged (Figure 13).

An occasional inverted trace may be formed inside either the sepal or petal-stamen traces by the rotation of a small branch trace to the inverted position. Usually these either disappear or move back into the parent trace, which then becomes temporarily amphicribral (Figure 14). The sepal and petal-stamen traces move outward. The sepal traces begin to branch before the calyx tube is freed. The ventral carpellary strand separates into five strong, inverted traces that supply the ovules. The locules merge into one at the top. First the calyx tube is freed (Figure 15) and immediately after the corolla tube is also freed. The five dorsal carpellary traces extend up the style almost to the 5-lobed stigma. The stamens are freed from the corolla tube at a higher level.

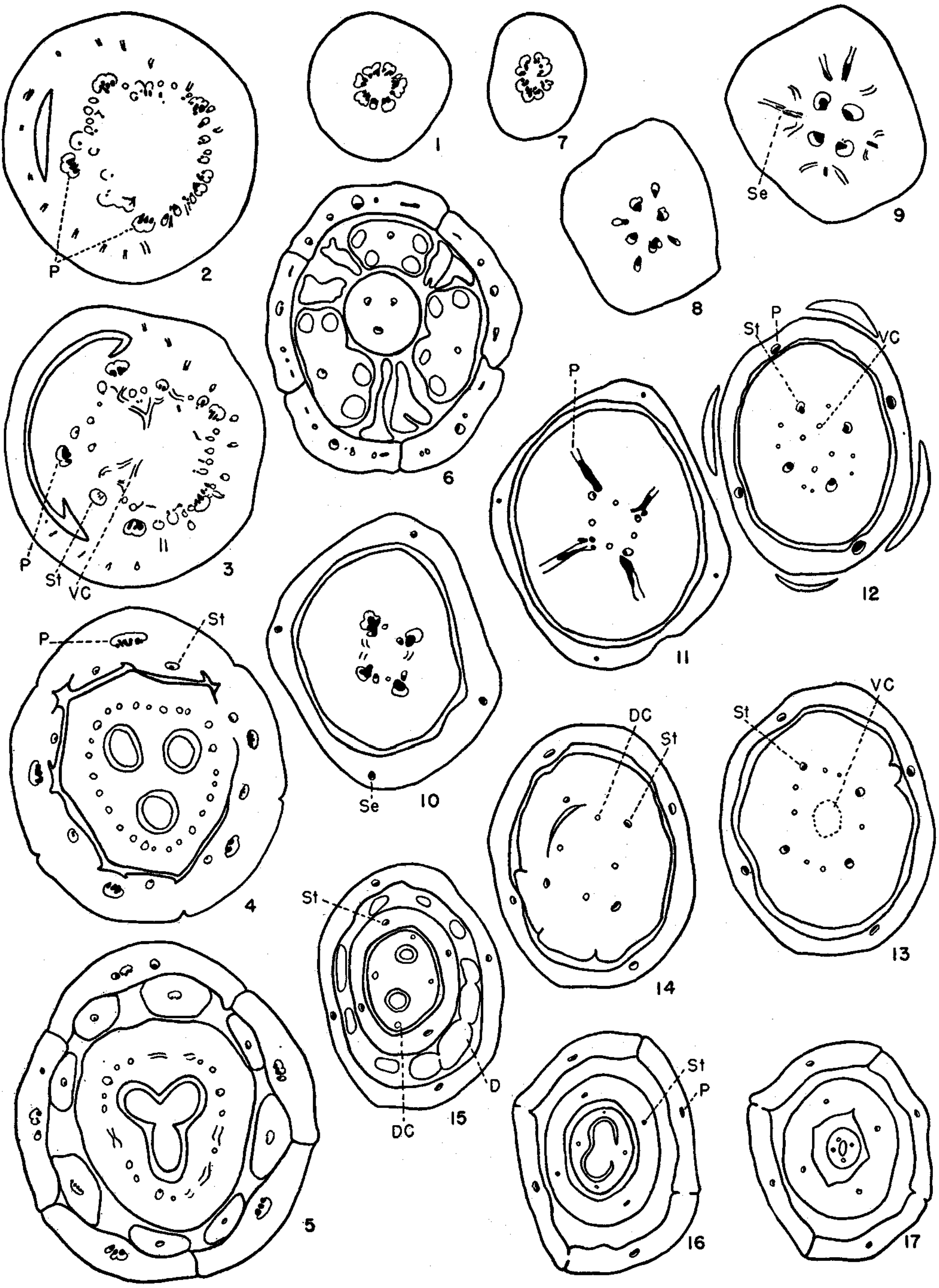
The inferior ovary in *S. philippinensis* seems to have resulted partly from invagination of the floral axis and partly from adnation. Invagination has not progressed very far in this case. The distribution of the residual tissue and of the recurrent traces seems to indicate that the lower portion of the ovary, up to approximately the level of the base of the locules, is receptacular while the portion above this level is appendicular. The petal and stamen traces are fused throughout the ovary while the bract-sepal traces are fused for varying distances, depending on the level at which the individual bract is freed.

Olax imbricata Roxb.

In *Olax* the calyx is a small cup-shaped structure that enlarges as the fruit matures. There are five or six petals and, in this species, three fertile stamens and five staminodia. The ovary is superior with three locules below, which merge into one above and with a central placental column that bears three ovules.

There is an almost continuous vascular cylinder in the pedicel (Plate XVIII, Figure 1). As the pedicel enlarges an indefinite number of small traces move out into the calyx tube, which is then freed immediately (Figure 2). Just above this, five large traces, the petal traces, move outward (Figures 2 and 3) and the smaller traces between them form anastomoses. From these anastomoses, traces move both inward and outward (Figure 3) and some traces continue almost directly upward into the flower. The traces that move inward are the ventral carpellary traces and these immediately disappear. The traces that move slightly outward are the stamen traces, while those that continue upward enter the ovary wall. The calyx does not extend as far as the base of the locules (Figure 4). The corolla tube with its adnate stamens is freed at this level. There is no fusion of petal and stamen traces. Within the ovary wall the traces opposite the locules are more strongly developed than the others. The three locules merge into one at the

PLATE XVIII



Olax imbricata (1-6), *Aptandra Spruceana* (7-17) level of ovule attachment (Figure 5). Anastomoses are formed between the traces in the ovary wall and then all but those in the positions of dorsal carpellary traces disappear. The dorsals continue in the style (Figure 6) almost to the 3-lobed stigma. The stamens and staminodia are freed at approximately the same level as the corolla lobes.

Aptandra Spruceana Miers

The flowers of *Aptandra* are 4-merous. The stamens are united in a tube and are located opposite the petals. The stamen tube is separated from the corolla tube by thick, scale-like glands that are adnate to the stamen tube at its base. The ovary is superior with two locules below, which merge into one above and with a central placental column that bears two ovules. The style is slender with a thickened club-shaped stigma.

In the upper portion of the pedicel there is an almost continuous cylinder (Plate XVIII, Figure 7) which soon separates into eight strands (Figure 8). The smaller traces then move out and each branches immediately into three traces (Figure 9). The lateral traces disappear as the calyx tube is freed (Figure 10). At this same level the four traces remaining in the center give off branches from both sides and the strong petal traces move outward (Figure 11) into the corolla tube, which is then freed immediately. Four strong traces remain in the petal positions and alternate with four phloem traces. The latter divide once or twice and four traces then move inward (Figure 12). The inner traces merge into a mass of phloem-like tissue in the center, the ventral carpellary strand (Figure 13), which then disappears below the level of the locules. The four strongly developed traces opposite the petal traces are the stamen traces. The phloem traces between these are reduced to four (Figure 14), which enter the ovary wall. The stamen traces move out slightly and almost at the same time the mass of tissue inside the corolla tube is differentiated into a fleshy disk that is lobed at the top, a stamen tube, and the 2-loculed ovary (Figure 15). It seems very probable that the glandular disk between the stamen tube and the corolla tube represents reduced stamens. The two locules merge into one near the top of the ovary (Figure 16). The four traces in the ovary wall enter the style (Figure 17) and extend almost to the stigma. In this species, as in *Anacolosa,* there are possibly four carpels but only two locules. The stamens are united by their anthers as well as by their filaments.

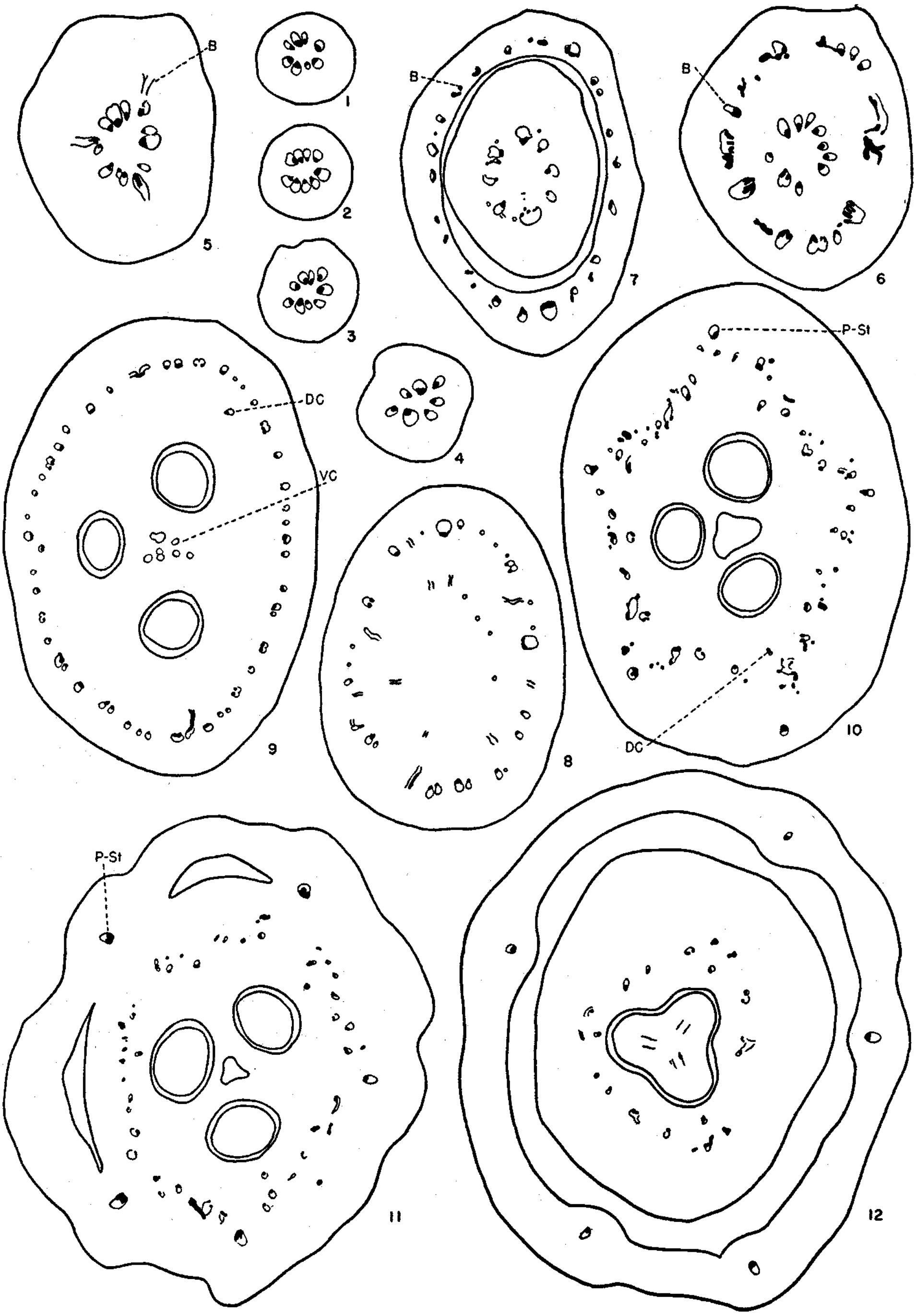
Schoepfia californica Brandeg.

According to the accepted description of the flowers of *Schoepfia,* the calyx, while not distinguishable is, if present, perhaps united with the receptacle. Subtending bracts are united to form a cup-shaped involucre below the ovary. Five petals are united into a corolla tube bearing five stamens opposite the petals. The ovary in this species is inferior with three locules below, which merge into one above the level of attachment of the ovules. The three ovules are borne on the tip of the central placental column.

Throughout the pedicel, gradual changes occur in the number and arrangement of traces. In the material studied there are eight traces low in the pedicel (Plate XIX, Figure 1). One of these divides and the nine traces thus formed become arranged on opposite sides, leaving two gap-like bands of parenchyma in the stele (Figure 2). Some of the traces then swing over into the gaps (Figure 3). In the upper portion of the pedicel some of the traces fuse, reducing the number to seven (Figure 4). The number of traces is increased again by radial separation and a variable number, usually three or four, move out from the stele (Figure 5). These traces then branch many times and enlarge considerably to form an outer ring of well developed traces (Figure 6). The involucre, which is freed immediately above, receives all of these traces (Figure 7). Meanwhile the traces in the central region divide radially to form additional traces, some of which consist of phloem only. This radial separation of traces continues throughout the length of the ovary. Some distance below the locules phloem traces are given off to the inside (Figure 8). These originate mostly from the smaller traces, especially from those consisting of phloem only. They move inward to form an almost continuous ring of phloem tissue, which later forms several large strands of phloem in the base of the placental column (Figure 9). These strands, representing the ventral carpellary traces, later merge into a single large phloem strand.

Just at the level of the base of the locules, three traces in the positions of dorsal carpellary traces move inward from the traces in the ovary wall (Figure 9). These traces appear to arise at slightly different levels in the flower. The petal-stamen traces gradually enlarge to form quite well developed traces near the top of the ovary. They move out slightly while the traces between them form numerous anastomoses and move inward (Figure 10). As the corolla tube is freed (Figure 11) the traces in the ovary wall begin to disappear. Anastomoses continue to be formed between these traces but apparently none are formed with the dorsal carpellary traces. Only a few of these traces persist at the level of ovule attachment (Figure 12) and soon all disappear except the three dorsals, which continue in the style almost to the 3-lobed stigma. The stamens are freed a little more than halfway up the corolla tube.

PLATE XIX



Schoepfia californica

DISCUSSION

The presence in this family of two and possibly all three of the possible types of inferior ovary is of especial interest. The three possible types, as have been previously discussed, are the appendicular, the receptacular, and a combination in which the inferior ovary is receptacular below and appendicular above. The inferior ovary of *Schoepfia californica* appears clearly to be appendicular. The floral traces originate in the manner of a typical appendicular ovary and there are no inverted or amphicribral traces to indicate that invagination has occurred. The inferior ovary of *Strombosia philippinensis* appears just as clearly to be receptacular below the base of the locules and appendicular above. The receptacular nature of the base of the ovary is indicated by the presence of downwardly directed residual tissue and of inverted recurrent traces that connect the residual tissue with bundles of the stele at a level near the base of the locules. The vascular anatomy of the flower above this level is that of an appendicular inferior ovary. The floral parts are fused but the traces to the various parts, except the petal-stamen traces, are separate. The inferior ovary of this species is complicated by the adherence of bracts, fused to both the receptacular and appendicular portions of the ovary.

If the authors' interpretation of the anatomy of *Anacolosa luzoniensis* is correct, then the receptacular inferior ovary also is present in this family. It seems difficult to explain the amphicribral strands and the traces to the disk on any other basis. On the other hand, if the cup-shaped structure beneath the flower is the calyx, as it has been considered, it must be concluded that elongation and invagination of the axis have occurred above the level at which the calyx is freed. On the basis of information available at present, this does not seem plausible. *Anacolosa* resembles *Schoepfia* in that in both there is present the cup-shaped structure at the base of the ovary and also a single whorl of floral organs borne at the top of the ovary. In both forms the whorl at the top of the ovary is interpreted as corolla, while the cup-shaped structure in *Anacolosa* is interpreted as calyx and that in *Schoepfia* as involucre. The interpretation of the inferior ovary in *Anacolosa* would be simplified if it could be shown that the cup-shaped structure is an involucre instead of a calyx. Much additional work should be done on the floral anatomy of this family and also on the relation of bracts and floral parts.

The relatively few species of Olacaceae studied offer insufficient evidence to justify any conclusions regarding relationships within the family. There are some definite similarities, however, between some genera that have heretofore not been considered as closely related. *Ochanostachys* and *Olax* show the most marked similarity. The species of these genera studied differ essentially in their floral anatomy only in the continuation of the ventral carpellary strands in *Ochanostachys*. Additional relationships in the Olacaceae are suggested by the arrangement of genera in Plate XV. This arrangement is admittedly based on insufficient evidence. The only justification for offering it here is that it seems possible that the Grubbiaceae and the Santalaceae were derived from divergent branches of the Olacaceae. The inferior ovary in the Santalaceae is receptacular while that in the Grubbiaceae is apparently appendicular as will be subsequently discussed.

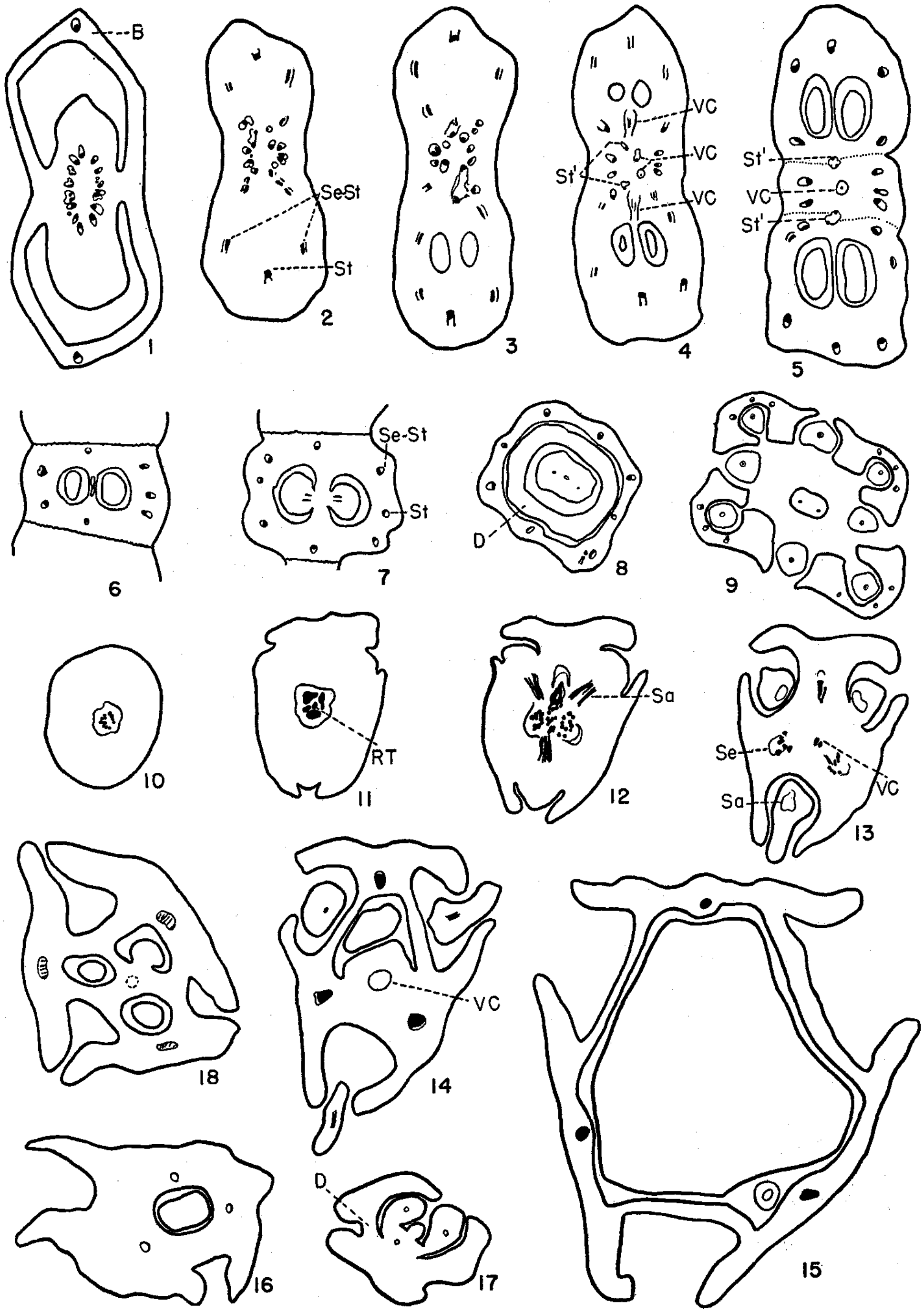
GRUBBIACEAE

The flowers of the Grubbiaceae are perfect with a simple perianth. There are four sepals and eight stamens. Four of the stamens are alternate with the sepals and four are opposite the sepals and slightly attached to them at the base. The disk consists of a narrow ring between the calyx tube and the base of the style. The ovary is inferior with two locules merging to one above the point of ovule attachment and a central placental column bearing two ovules. The style is small with a 2-lobed stigma. The flowers of the species studied are borne in groups of three with the ovaries united. There is considered to be only one genus, *Grubbia,* though this is sometimes subdivided.

Grubbia rosmarinifolia Berg.

Each group of flowers is partly enclosed by two lateral bracts, each of which receives a single trace (Plate XX, Figure 1). After the traces to the bracts have moved out and before the resultant gaps are closed, traces begin moving out to the outer flowers. The first three traces to each lateral flower are two sepal-stamen traces and one stamen trace between them (Figure 2). Then two additional traces move out to supply each of the lateral flowers. These then branch either immediately (Figures 2 and 5) or at higher levels, each to form a stamen and a sepal-stamen trace. The traces remaining in the center swing around to close the gaps. A few of them divide at this time (Figure 3). The ventral carpellary traces to the lateral flowers arise only slightly below those of the central flower but their origin is not clear. The central flower receives two traces from opposite sides of the stele (Figure 4), which then fuse to form a single amphicribral trace (Figure 5), which enters the placental column. The approximate limits of the flowers are indicated by dotted lines in this figure. Each of the traces labeled St′ in Figure 4 divides immediately to form two strands of xylem with a common mass of phloem (Figure 5). At higher levels these separate to supply

PLATE XX



Grubbia rosmarinifolia (1-9), *Myzodendron punctulatum* (10-18) stamens in separate flowers. In this region the vascular supplies to the three flowers may be easily identified. The upper flower has five large traces, the two lower of which each subsequently divide to form a stamen and a sepal-stamen trace. Half of the upper St′ trace, moreover, supplies a stamen in this flower. The central flower also has five large traces of which the upper left one later divides. This flower receives a half of each of the St′ traces. The lower flower has seven traces and receives half of the lower St′ trace. Thus each flower is eventually supplied by eight traces in the ovary wall, four sepal-stamen traces and, alternating with these, four stamen traces (Figure 7). The ventral carpellary strand is flattened in the partition between the locules (Figure 6) and is used up in supplying the ovules (Figure 7). Above the point of attachment of the ovules the locules merge into a single cavity extending for some distance up the style. The calyx tube, to which all the filaments are fused, is freed almost simultaneously with the disk (Figure 8). The stamens that alternate with the sepals are freed from the tube first, followed by the stamens opposite the sepals. In each sepal the sepal trace branches to form three (Figure 9). At the base of the style two traces appear in the positions of dorsal carpellary traces. There is no evident connection between these and any of the other floral traces.

The inferior ovary seems to be entirely appendicular in nature since there are indications neither of residual tissue directed downward in the pith region nor of inverted recurrent traces.

MYZODENDRACEAE

The species in the Myzodendraceae are dioecious with usually 3-merous flowers. The pistillate flower has an inferior ovary. In the young pistillate flower there are three locules below and three ovules suspended from a central placental column. Only one ovule develops and this enlarges to fill the entire cavity. The placental stalk is crowded to one side of the locule. In the ovary wall there are three longitudinal furrows, each of which contains a seta, which becomes long in the fruit. These setae have been considered as homologous with stamens. *Myzodendron* is the only genus in this family.

Myzodendron punctulatum Banks and Sol.

The pedicel of *Myzodendron* has a very slender stele with a small pith (Plate XX, Figure 10). While interpretation is difficult because of the small stele and irregular distribution of the xylem, it seems likely that xylem appears independently in the pith region (Figure 11) at the base of the ovary. Traces are given off first to the setae (Figure 12) and then just above this to the ovary wall in the sepal positions (Figure 13). Since the traces to the setae are given off first, it seems rather improbable that these structures are staminodia. After the departure of the traces to the ovary wall there is a small amount of xylem left in the pith region. This gradually disappears and is replaced by phloem-like tissue (Figure 14), which continues into the placental column. In an older flower, such as the one described here, a single seed is present and the placental stalk is crowded over to one side of the locule (Figure 15). In the younger flower, however, one ovule is suspended in each of three locules (Figure 18). The locules merge into one above the level of ovule attachment. The three traces in the ovary wall do not enter the sepals. This was recognized by Johnson (1889). Instead, the traces swing inward at the top of the ovary as the sepals are freed (Figure 16) and enter the style, which almost immediately branches into three stigmas (Figure 17). A small ring-shaped disk is present between the sepals and the style.

The extreme reduction in *Myzodendron* makes it difficult of interpretation. Unfortunately only limited material was available. The probable occurrence of residual tissue in the pith region below the ventral carpellary strand seems to indicate invagination of the axis. Hence the inferior ovary is probably receptacular.

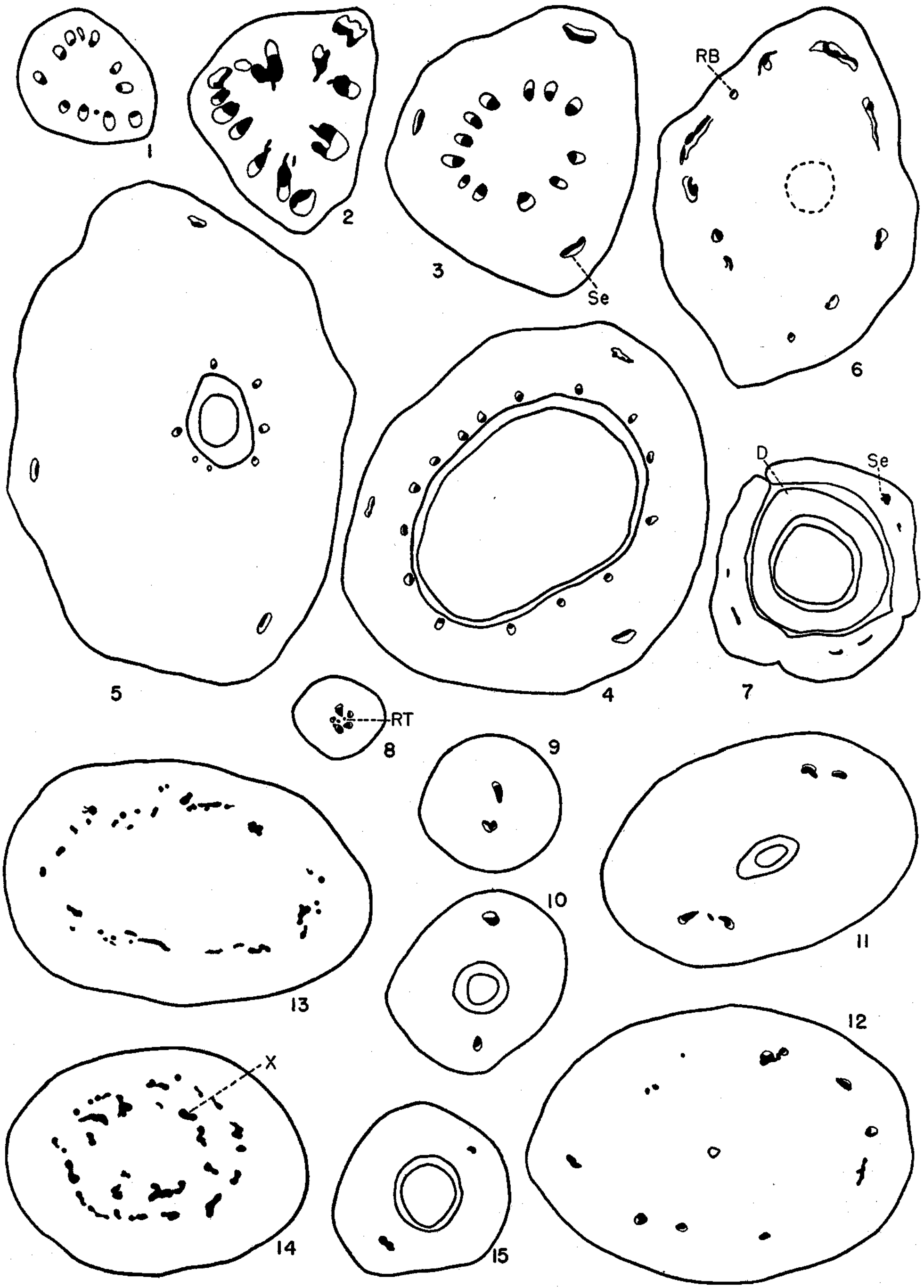
LORANTHACEAE

In the species of the Loranthaceae that were studied, the pistillate flowers are characterized by an inferior ovary with a single locule. There is little or no differentiation between the ovule and the placenta. There are two or three sepals and sometimes a circular disk. There are no indications of either stamens or staminodia.

Phoradendron villosum Nutt.

The material studied of *Phoradendron* consisted of young fruits containing well developed seed. There are ten to twelve traces in the pedicel (Plate XXI, Figure 1). At the base of the ovary three large sepal traces move outward at slightly different levels (Figure 2). The remaining traces, some of which divide radially, become rearranged into a somewhat irregular ring of bundles just below the level of the base of the locule (Figure 3). There are no traces connecting these strands with the placental knob. As this ring of bundles moves into the ovary wall there is some increase in number of traces by radial separation and the bundles become smaller in size (Figure

Plate XXI



Phoradendron villosum (1-7), *Arceuthobium americanum* (8-15)

4). As the locule closes, these traces move inward toward the base of the style and their number is gradually reduced by the disappearance of traces (Figure 5). All of these traces disappear above the locule. Meanwhile at approximately the level of the top of the locule, additional traces appear independently in the outer portion of the ovary. Most of these traces are inverted and directed downward (Figure 6). They connect to the sepal traces at higher levels and then disappear rather rapidly. Few traces persist to enter the sepals (Figure 7). The sepals, disk, and style are freed almost simultaneously.

Arceuthobium americanum Nutt.

In the flowers of *Arceuthobium* there are four or five traces in the pedicel just below the ovary. There are apparently a few strands of residual tissue in the pith region (Plate XXI, Figure 8). The vascular tissue gradually separates into two traces (Figure 9), which enter the ovary wall on opposite sides of the locule (Figure 10). There is no trace leading to the placental knob. Near the top of the locule each of the traces branches once (Figure 11). At slightly higher levels additional traces appear independently in the ovary wall (Figure 12). Most of these traces consist only of xylem and gradually the phloem disappears from all traces. Toward the top of the ovary the traces are all connected by a series of anastomoses (Figure 13), which are formed over a considerable distance. Gradually more and more of the anastomoses lead inward until finally two distinct rings of xylem traces can be recognized (Figure 14). The inner ring, possibly representing the X-traces, is directed toward the base of the style but all of the traces disappear before the style is freed. The traces of the outer ring disappear more gradually and usually only two persist at the level at which the short calyx tube is freed (Figure 15).

There is no indication in the floral anatomy of the number of carpels in either *Arceuthobium* or *Phoradendron*. Van Tieghem (1869a) described two carpels in *Viscum album*. Dowding (1931), on the basis of morphological development, concluded that the ovary of *Arceuthobium americanum* consists of an outer whorl of four sterile and an inner whorl of four fertile carpels. These are much reduced forms of the Loranthaceae. A study of more primitive members of the family is desirable.

The appearance of traces directed downward in the ovary wall, especially of the inverted ones of *Phoradendron*, suggests that the inferior ovary is probably receptacular. The presence of X-traces in *Arceuthobium* and the complete absence of any indication of ventral carpellary strands in both genera are also suggestive of a receptacular inferior ovary. In the Santalaceae there is in general a gradual reduction in the connections of the ventral carpellary strand to the main traces. In some forms (e.g., *Anthobolus, Buckleya, Thesidium*) the ventral strands are entirely independent of the main vascular supply. In *Viscum* also the carpels are independent of the main vascular supply (Van Tieghem, 1869a).

RELATIONSHIPS WITHIN THE SANTALALES

The constitution of the Santalales and the relationships of the families included have been discussed by taxonomists for many years. The various groupings and arrangements suggested were discussed recently by Harms in "Natürlichen Pflanzenfamilien" (1935) and are not considered here in detail. In addition to the families considered here there are two others, the Opiliaceae and the Octoknemaceae, which are usually considered to belong to the Santalales. Both are closely related to the Olacaceae.

The Olacaceae together with the Opiliaceae were placed by Hutchinson (1926) in a separate order, the Olacales. In the Santalales he placed first the Loranthaceae, followed by the Santalaceae, the Grubbiaceae and the Myzodendraceae. On the basis of progressively increasing parasitism and of reduction in complexity of the ovule, Schellenberg (1932) considered the order of families in the Santalales to be the Olacaceae, the Grubbiaceae, the Santalaceae, the Myzodendraceae and the Loranthaceae. He considered the Grubbiaceae and the Myzodendraceae, however, as possibly convergent forms not directly related to the Santalales. The same arrangement is used in "Natürlichen Pflanzenfamilien" (1935). Rendle (1938) regarded the Myzodendraceae as a much reduced ally of the Santalaceae.

The Olacaceae is clearly the least advanced of the families of the Santalales described here. The number of floral whorls, the number of stamens, the more complete separation of the locules and the lack of fusion of petal and stamen traces in *Ochanostachys* and *Olax* are all indications of the more primitive nature of this family. Also, as indicated by Schellenberg (1932), the presence both of nonparasitic forms in this family and of species in which the ovules have two integuments covering the nucellus indicates that the Olacaceae should be placed lowest in the series.

It seems likely that divergent lines in the Olacaceae may have given rise to the Grubbiaceae and the Santalaceae. Within the Olacaceae both adnation and invagination have occurred to form two or three types of inferior ovary. The inferior ovary of *Grubbia* appears to be appendicular and thus would be derived from forms in which invagination of the floral axis has not occurred. The inferior ovary of *Grubbia* resembles very closely the superior ovary of *Aptandra* except that in the former the number of dorsal carpellary traces has been reduced to two and these appear only in the style. *Schoepfia* has an inferior ovary that is clearly appendicular and in this respect resembles *Grubbia.* There is not enough evidence available to suggest a direct connection between the Grubbiaceae and any given genus in the Olacaceae.

The Santalaceae was probably derived from the Olacaceae. This is the opinion of most taxonomists. There are similarities throughout both families in the structure of the ovary and of the ovules, especially with regard to placentation. A particularly striking similarity is the invagination of the floral axis, which is characteristic of the Santalaceae and which occurs in *Strombosia* and probably in *Anacolosa.* The receptacular inferior ovary resulting from invagination probably occurs rather infrequently in dicots. This together with similarities in ovary, ovule, placentation and parasitism seems to indicate that the primitive santalaceous flower may have been derived from the Olacaceae, possibly from the tribe Anacoloseae. It may be especially significant that *Strombosia,* which shows definite indications of invagination, has five carpels, five locules each with a suspended ovule, and strong dorsal carpellary traces, all of which are characteristic of the hypothetical primitive santalaceous flower. Since the inferior ovary of *Strombosia* is receptacular below and appendicular above, while the inferior ovary in the Santalaceae is receptacular throughout, the question arises as to the method of origin of the latter type. Before studying the floral anatomy of *Strombosia,* the authors had suggested (1942) that the receptacular inferior ovary in the Santalaceae might have originated by invagination of the floral axis to form a cup-shaped receptacle that subsequently became fused with the ovary. The structure of *Strombosia* suggests the possibility that the receptacular inferior ovary in the Santalaceae may have been derived from an inferior ovary which was receptacular below and appendicular above by a progressive increase in the amount of invagination. Conclusions regarding these two possibilities do not seem to be justified on the basis of evidence available at present. Additional studies in the Olacaceae are certainly desirable in determining the probable method of origin of the inferior ovary in the Santalaceae.

The Myzodendraceae was considered both by Skottsberg in "Natürlichen Pflanzenfamilien" (1935) and by Rendle (1938) as a reduced ally of the Santalaceae. While evidence obtained from the floral anatomy of *Myzodendron punctulatum* is not conclusive, it strongly suggests that the inferior ovary in *Myzodendron* is receptacular in nature. This would seem to indicate its relationship to the Santalaceae. Skottsberg, on the basis of the structure of the ovary and of the circular disk, suggested a relationship to *Arjona* and to *Quinchamalium. Myzodendron* is a very much reduced form and its origin is obscure. The only conclusion justifiable at present seems to be that there seem to be more reasons for relating it to *Arjona* and to *Quinchamalium* than to any other genera in the Santalaceae.

The Loranthaceae has been considered both as more primitive and as more advanced than the Santalaceae. The two species of this family that were studied are too advanced to indicate relationships. Studies are needed of the more primitive members of the family. The only conclusion possible here is that in *Phoradendron* and *Arceuthobium* the inferior ovary is probably receptacular. The advanced condition of the ovary in these forms, as evidenced by reduction and loss of traces, seems to indicate that the Loranthaceae is more advanced than the Santalaceae and was probably derived from it. According to Van Tieghem (1869a) the sepals of *Viscum* receive one dorsal trace and two lateral traces originating from commissural strands, as in *Thesium* and closely related forms. This fact alone, however, is hardly enough to connect the Loranthaceae with this particular series in the Santalaceae.

The Santalales, as treated here, has been considered as a member of the Celastrales (Pool, 1941), as a derivative of the Celastrales (Hutchinson, 1926), and as an ally of the Proteales (Rendle, 1938). No evidence based on floral anatomy is available from either the Celastrales or the Proteales to indicate the origin of the Santalales. It may be stated, however, that the Santalales apparently does not belong in the main line of development toward the Umbellales as in the Bessyian system. The inferior ovary in the Umbelliferae is appendicular (Jackson, 1933). It seems improbable that a receptacular inferior ovary could give rise to the type of ovary that has been interpreted as appendicular. At present it seems most likely that the Santalales constitutes a separate line of development and probably has not given rise to other orders. Whether this line originates from the Celastrales, the Proteales, or from some other order remains to be determined.

SUMMARY

Descriptions are given of the floral anatomy of the Santalaceae based on a study of twenty-four genera and forty species of the family. The inferior or partly inferior ovary of all species studied is considered to be receptacular. The ovary is embedded in tissues of the receptacle as a result of invagination of the floral axis. The receptacular inferior ovary probably occurs infrequently in the Angiosperms. Thus far the Santalales is the only order in which floral anatomy indicates the occurrence of such a type. The fol-

lowing characteristics may be considered as typical of the receptacular inferior ovary in the Santalaceae:

1. Inverted recurrent traces. These are characteristic of the more primitive receptacular inferior ovary and, when present, are a definite and easily recognizable indication of invagination.
2. Amphicribral condition of the main traces. It can be shown that the large, loosely arranged amphicribral strands in some species of the Santalaceae are the result of phylogenetic fusion of ascending and recurrent receptacular traces in the positions of the sepals. The traces between the sepal positions disappear near the top of the ovary in more primitive forms and low in the ovary in more advanced forms.
3. Downwardly directed residual tissue in the pith region of the pedicel. In the more primitive forms the carpellary traces originate from the inverted recurrent traces. The recurrent traces continue downward beyond the level of origin of the carpellary traces. It is because of invagination then that the residual tissue is directed downward instead of upward as in the appendicular type of inferior ovary.
4. Origin of the carpellary traces from a group of vascular tissue in the pith region, which connects upward and outward to the main vascular supply. In the more primitive forms the carpellary traces originate from the inverted recurrent traces low in the ovary, while in the more advanced forms the ascending and recurrent traces tend to become fused and the residual tissue tends to persist in the pith region. As a result of these two tendencies a saucer- or cone-shaped group of tissue, with the tip of the cone directed downward, persists in the pedicel and connects upward and outward to the main traces. In an appendicular type of inferior ovary the vascular tissue giving rise to the carpellary traces is in the form of a cone with the tip directed upward.
5. Lack of dorsal carpellary traces. This characteristic is of somewhat dubious value. It seems likely that in the Santalaceae dorsal carpellary traces may be lacking in some species because they have lost connections with the main vascular supply and have gradually disappeared through continued reduction in size. This should not be confused with the nonappearance of dorsal traces because of fusion with other traces.
6. Complete independence of the dorsal or ventral carpellary traces, or both, from the main vascular supply. This characteristic is even more dubious than the preceding, but it does appear in certain species of the Santalaceae. In many species there are only weak connections between the main traces and the carpellary traces, especially the ventral carpellary traces. In the more advanced species these connections disappear completely.

On the basis of evidence obtained in this study, it is postulated that the primitive santalaceous flower contained a partly or completely inferior ovary of the receptacular type. The ovary probably consisted of five carpels enclosing five locules, each containing a single ovule suspended from a central placental column. Because of invagination of the floral axis probably three rings of bundles were present in the ovary wall at the level of the locules, an outer ring of ascending receptacular bundles that were normally oriented, an intermediate ring of inverted recurrent receptacular bundles and an inner ring of dorsal carpellary traces that were normally oriented. The sepal and stamen traces originated near the top of the ovary or in the base of the floral tube. The dorsal and ventral carpellary traces originated near the ends of the recurrent traces in the base of the ovary. Residual tissue was present and was downwardly directed in the pith region of the pedicel below the level of origin of the carpellary traces.

From this primitive type there appear to have been two main lines of development as shown by the floral anatomy of pistillate and perfect flowers (Plate XV). In one line of development the number of carpels was early reduced to three (*Colpoon*). The number of locules was in most cases reduced to one by the disappearance of the partitions between the locules (*Darbya, Santalum*). This left a free central placental column composed entirely of carpellary tissue. The double ring of ascending and recurrent receptacular traces was gradually replaced by large, loosely arranged amphicribral strands in the positions of the sepals. These amphicribral strands appear only near the top of the ovary in the more primitive forms such as *Darbya* and result from a gradual reduction in the number of ascending and recurrent traces between the sepal positions. In more advanced forms in this series (*Pyrularia, Comandra, Geocaulon*) there are few or no traces between the sepal positions. The amphicribral condition here results partly from the presence of inverted traces inside each sepal trace and partly from the rotation to the inverted position of the marginal strands of each sepal trace. In *Nanodea,* the most advanced species in this series, the number of carpels is reduced to two. *Osyris* and *Acanthosyris* represent a side line in development from this series and were probably derived from *Santalum* or some closely related form. *Buckleya* probably represents another side line from this series but its affinities are more uncertain.

The second line of development in the Santalaceae is characterized by an early reduction in the number and size of the recurrent traces. In the more primitive members of this series, five carpels have been retained but in the more advanced forms the number of carpels is reduced to three and in some species to two. This series can be divided into two subgroups distinguished by a difference in the nature of the traces received by the sepals. In one group, consisting of *Henslowia, Jodina,* and *Myoschilos,* each sepal receives a single trace, which branches tangentially to form a stamen and a sepal trace. The sepal trace then branches radially to supply the sepal. In the other group, consisting of *Choretrum, Leptomeria, Thesium, Thesidium* and *Omphacomeria,* each sepal receives three traces, one dorsal sepal-stamen trace and two lateral traces. The lateral traces in the adjacent margins of the sepals are derived from a single receptacular trace in the commissural position. In *Thesidium* these commissural traces disappear before they reach the sepals. *Osyridocarpus, Quinchamalium* and *Arjona* show indications of commissural traces and are probably related to this series.

The ovary in *Anthobolus* and in *Exocarpus* is partly inferior though it appears to be essentially superior. The relation of these genera to the rest of the Santalaceae is uncertain. Their floral anatomy is rather advanced. The pistillate flowers show some similarity to *Santalum* but the structure of the staminate flowers of *Exocarpus* suggests that of the perfect flowers of *Choretrum* and *Leptomeria,* which belong to a different series from *Santalum.* There is also the possibility that *Anthobolus* and *Exocarpus* were derived directly from the primitive santalaceous species and would thus be related to the two main series only by a common origin.

The relationships within the Santalales suggested in Plate XV are based almost exclusively on the floral anatomy of pistillate or perfect flowers. The primary purpose of this chart is to show the paths of development of the receptacular inferior ovary. The chart gives some indication of phylogeny within the group since floral anatomy is one of the best indices of relationship.

A few species of the Olacaceae, Grubbiaceae, Myzodendraceae, and Loranthaceae were studied because of their probable relationship to the Santalaceae. The Olacaceae is the most primitive family of the Santalales. A single species of each of seven genera was available. The species of *Ochanostachys, Olax, Heisteria,* and *Aptandra* that were studied have a superior ovary. *Schoepfia californica* has an appendicular inferior ovary. *Strombosia philippinensis* has an inferior ovary, which is receptacular below the level of the base of the locules and appendicular above. *Anacolosa luzoniensis* possibly has a receptacular inferior ovary with the calyx freed below the ovary so that it does not enter into its formation. In view of the confusion regarding the relation of bracts to floral parts in this family, however, it may be that the structure that is termed calyx is actually composed of bracts and that the calyx is then incorporated in the inferior ovary. There are thus two and possibly all three types of inferior ovary in the Olacaceae. The tribe Anacoloseae, including *Strombosia* and *Anacolosa,* seems to be the group of the Olacaceae most closely related to the Santalaceae since, like the Santalaceae, it is characterized by invagination of the floral axis.

The Grubbiaceae has an appendicular inferior ovary and hence can be considered neither as a progenitor nor as a derivative of the Santalaceae. It appears to have been derived from the Olacaceae. Thus in addition to having two and possibly three types of inferior ovary, the Olacaceae may also have given rise to two families, one of which has a receptacular, the other an appendicular inferior ovary.

Both the Myzodendraceae and the Loranthaceae apparently have a receptacular inferior ovary and were probably derived from the Santalaceae. The Myzodendraceae is probably more closely related to *Arjona* and *Quinchamalium* than to any other genera in the Santalaceae. The relationship of the Loranthaceae to the Santalaceae could not be determined on the basis of the floral anatomy of *Phoradendron* and *Arceuthobium,* the only genera of which material was available.

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