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Introduction

Several reasons encourage the production of a study on the anatomy of the Rapateaceae at this time. First, the explorations of Maguire et al. (1958, 1965) at the New York Botanic Garden have, only recently, greatly widened our knowledge of this interesting family. Explorations sponsored by the New York Botanic Garden have covered many previously unknown areas of the Guayana Highlands of South America, a region to which the family is very nearly endemic. Epidryos reaches as far west as Panama, while the monotypic Maschalocephalus of Liberia is the lone non-American outlier of the family. Maguire's thorough systematic studies of this family have brought several new genera and many new species to light. Moreover, he has, during his explorations, realized the potential value of anatomical studies and prepared many liquid-preserved samples of species collected. A second reason for the study of the Rapateaceae is the current worldwide effort by students of monocotyledon anatomy to provide data which can be summarized in forthcoming volumes of C. R. Metcalfe's 'Anatomy of Monocotyledons'. Thirdly, the Rapateaceae is a family of considerable interest for phylogenetic and phytogeographic reasons and with good anatomical material, we are in a better position to assess the exact phylogenetic relationships. Also, anatomical materials prove of exceptional value for establishing subfamily, tribe, and generic criteria. In a few cases, good species characteristics are also yielded by anatomical study. The systematic and phylogenetic potential of internal characteristics in the Rapateaceae proved to be significant in the case of pollen (Carlquist, 1961a), and the present study shows also the value of the anatomical approach.

Relatively little data on anatomy of the Rapateaceae has thus far been accumulated, a fact related to the remoteness of areas inhabited by this family and the paucity of specimens collected. Most noteworthy among anatomical studies is that of Solereder & Meyer (1929) which includes information given earlier by van Tieghem (1887) and Boubier (1896). Very few species of the family were studied by these authors, and most of the data presented below is new.

As a basis for presentation, the subfamilies and tribes designated by Maguire et al. (1958) are used here:

Subfamily Saxofridericioideae
  Tribe Saxofridericieae: Saxofridericia, Philpsia, Amphiphylum, Stegolepis, Epidryos
  Tribe Schoenocephalieae: Kunhardtia, Guacamaya, Schoenocephalium

Subfamily Rapateoideae
  Tribe Rapateae: Rapatea, Duckea, Cephalostemon, Spathanthis
  Tribe Monotremae: Monotrema, Polarophyllum, Windsorina, Maschalocephalus

Materials and Methods

Most of this study is based upon the liquid-preserved materials given to me by Dr Bassett Maguire. Appreciation is expressed to him for this incomparable collection and for his interest in my studies. Species, collection data, and location of herbarium specimens for items in this collection which provided stem or root material, or both, are as follows:
Cephalostemon affinis Körnicke (Maguire et al. 41536, NY), Duckea cyperaceoides (Ducke) Maguire (Maguire et al. 41682, NY), D. flava (Link) Maguire (Maguire et al. 41492, NY), Guacamaya superba Maguire (Maguire et al. 41724, NY), Monotrema aemulans Körnicke (Maguire et al. 41659, NY), M. affine Maguire (Maguire et al. 41500, NY), M. xyridioides Gleason (Maguire et al. 41539, NY), Rapatea angustifolia Spruce ex Körnicke (Maguire, Wurdack & Keith 41911, NY), R. fankaewi Maguire (Tillett & Boyan 44862, NY), R. longipes Spruce ex Körnicke (Maguire, Wurdack & Keith 41727, NY), R. membranacea Maguire (Tillett & Boyan 43972, NY), R. paludosa Aubl. (Maguire et al. 41544, NY), R. spruceana Körnicke (Maguire, Wurdack & Keith 41728, NY; Maguire & Wurdack 41484, NY), R. yapacana Maguire (Maguire, Wurdack & Maguire 41540, NY), Saxofriderici inermis Ducke (Maguire et al. 42624, NY), S. spongiosa Maguire (Maguire, Wurdack & Bunting 37485, NY), Schoenocephalium coriaceum Maguire (Maguire et al. 43852, NY), S. cucculatum Maguire (Maguire et al. 41901, NY), S. teretifolium Maguire (Maguire et al. 41812, NY), Spanthanthus unilateralis (Rudge) Desv. (Maguire et al. 43852, NY), Siegolepis angustata Gleason (Maguire et al. 45129, NY), and S. celiae Maguire (Maguire, Wurdack & Bunting 42456, NY).

The above collections do not represent all genera within the family, and thus an attempt was made to supplement this collection with herbarium specimens so that in so far as possible a synoptical view of the genera within the family could be obtained. Root and stem material of Amphiophyllum and Kunhardtia proved impossible to secure. Herbarium specimens used for anatomical studies of roots and stems include the following:

Epidryos micrantherus Maguire (O. Haught 5378, US), Maschinocephalus dinkhae Gilg & K. Schum. (J. T. Baldwin, Jr. 13054, GH), Phelpsiella ptericaulis Maguire (Cowen & Wurdack 31058, NY), Polorphytum riparium Sandw. (Maguire & Fanshawe 23396, NY), Spanthanthus licolor Ducke (Maguire et al. 29326, NY), and Windsorsina guianonsis Gleason (Maguire 34143, NY).

The material of liquid-preserved roots and stems was embedded according to the usual paraffin techniques. A high-melting-point paraffin proved helpful in overcoming problems in sectioning caused by presence of sclerenchyma. Sections were stained with a safranin-fast green combination corresponding to Northen’s modification of Foster’s tannic acid-ferric chloride method (Johansen, 1940). The same techniques were used for herbarium materials, except that a preliminary expansion by soaking in 2.5 per cent aqueous NaOH was undertaken. The herbarium materials proved much less satisfactory than liquid-preserved specimens because perfect re-expansion of tissue was only rarely achieved, and primary walls were swollen somewhat by alkali treatment. Nevertheless, such specimens did provide reliable sources of anatomical data.

Both transverse and radial sections of stems and roots were prepared. This permitted not only a 3-dimensional view of cells and tissues, but also observation of perforation plates and pitting of vessel elements.

Reference is made below to deposits which fill lumina of cells, or occur as droplets within certain cells, or in intercellular spaces. For convenience, these deposits are termed “tannin-like”; they have been, in fact, regarded as tannins by Solereder & Meyer (1929). Sometimes these deposits appear grayish and granular, and thus suggest a phlobaphene nature. At other times, they appear homogeneous, and are yellowish in unstained material, bright red in material stained with safranin. These characteristics are ones which would be expected of resin-like materials. Sometimes, both characteristics are apparent. Obviously chemical studies of ergastic materials in the Rapateaceae are needed.

**Root Anatomy**

The material available for study provided a comprehensive survey of genera, but one could wish for a more complete representation of species.
Therefore, no attempt can be made here to suggest the full ranges of structures within the family, although much of this range is doubtless contained below. Unfortunately, the material of roots and stems of various sizes and ages was not available, with few exceptions, for each species. Therefore little reference is made, for example, to number of xylem and phloem poles in root steles, and information on the degree of lignification must be considered provisional. Only stems and roots judged to be relatively mature are, however, described here. In all cases, the descriptions reflect the study of material available.

**Tribe Monotremae** — *Monotrema xyridioides* (Figs. 1-6) serves conveniently for introducing root anatomy. This species demonstrates many features seen throughout the family as well as some peculiar to the genus. The roots of all the Rapateaceae may be considered in terms of exodermis, cortex and stele. The stele (Fig. 1) is delimited by a conspicuous endodermis which is composed, in all species of the Rapateaceae, by a single layer of cells with notably thickened walls. These cells appear square in transection, with a narrow lumen. In longitudinal section (Fig. 4) these endodermal cells are elongate, about four times as long as wide, with conspicuous simple pits. Within the endodermis is a single layer of cells which can readily be identified as pericycle. The cells of the pericycle are thin-walled adjacent to phloem poles, and thick-walled adjacent to protoxylem poles. The thick-walled cells bear wide pits so that the thickened portions appear as a series of fused bands, such as one might find in endothecial cells or trans-fusion cells. The phloem and xylem show typical monocotyledonous arrangements. The largest metaxylem vessels in xylem strands form a circle with reference to the stele as a whole, and no central vessels are present in the stele. The central portion of the stele is composed of fibroform sclereids. These are thicker-walled than the sclerenchyma which separates metaxylem of adjacent xylem bands.

The cortex of *M. xyridioides* may be said to consist of three regions. The outermost and innermost of these consist of cells, spheroidal in transection, elongate in longitudinal section, which retain their shape in mature roots and contain starch. Thus, the inner and outer cortical regions may be said to be starch sheaths. There are four layers of such cells outside the endodermis (Figs. 1, 4) and two layers inside the exodermis (Figs. 3, 6). In all the Rapateaceae, cells of the inner starch sheath are arranged in clear radial files. The central zone of the cortex in roots appears as a series of radially-arranged cells. These cells are of two types, and this portion of the cortex may be said to illustrate cellular dimorphism. One of the cell types is arm-parenchyma. Typically, each cell is provided with four arms: two radial and two tangential as seen in a transection of a root (Fig. 2). The arm-parenchyma cells are thin-walled and do not show lignification, but they do contain starch. The second cell type is large, thin-walled parenchyma cells, round as seen in transection, ovoid in a longitudinal section, which do not contain starch grains. These cells collapse at maturity whereas the arm-parenchyma cells are persistent. The pattern of cell collapse is not random, but occurs in such a way that radial plates (e.g., Fig. 14) are formed. Each of these plates is one, rarely two cells wide (Fig. 5). The arm-parenchyma cells appear less frequent than the ovoid collapsed cells, but actually they are present in equal numbers, for the two types alternate as superposed tiers (Fig. 5). This has the effect of formation of successive discs of arm-parenchyma cells separated by discs of collapsed cells, and thus the arm-parenchyma cells may provide a measure of mechanical support for the wide cortical regions of roots.

The exodermis of roots consists of an epidermis subtended by a single layer of hypodermal sclereids (Figs. 3, 6). The sclereids are very thick-walled, square in transection, elongate in longitudinal section, and resemble the cells of the endodermis.

Various cells of the root may contain a scattering of droplets of an unidentified substance, presumably partly or wholly...
Figs. 1-6 — *Monotremum xyridoides*, sections of roots. Fig. 1. Portion of stele and adjacent cortex from transection. Fig. 2. Portion of cortex in transection; note a group of persistent arm-parenchyma cells. Fig. 3. T.s. of exodermis showing sclerenchymatous hypodermis. Fig. 4. Radial section of root showing stele at left, cortex at right; collapsed and persistent parenchyma cells are also seen. Fig. 5. Tangential section of root cortex; files of persistent arm-parenchyma cells appear in stories separated by longer collapsed cells. Fig. 6. Exodermis from radial section of root, corresponding to the region shown in Fig. 3; at left note the elongate arm-parenchyma cells separated by large collapsed cells. Figs. 7-9. Exodermis from transections of roots, epidermis at right. Fig. 7. *Polarophyllum reparium*. Fig. 8. *Windsorina guianensis*. Fig. 9. *Machaloscelalus dinklagei*. All figures × 200.
tannin-like in nature. These droplets are common in the cortex.

The root anatomy in two other species of Monotrema, M. affine and M. aemulans, agrees closely with that of M. xyridioides. In M. affine tannin-like deposits occur as massive accumulations in particular cells and is thus idioblastic in occurrence, as it is in Rapatea (Figs. 10, 12). Solereder & Meyer (1929) gave a description of the roots of "Schoenocephalium arthrophyllum"; this species now proves to be M. arthrophylla (Maguire et al., 1958). The description of root anatomy of this species by Solereder & Meyer is rather vague, but falls within the structure outlined above for M. xyridioides.

The other genera of Monotremaceae show many similarities to the type of structure reported for M. xyridioides. In Polarophyllum riparium (Fig. 7) the exodermis is much thicker than in Monotrema. Two layers of thick-walled sclereids, and often two layers of thin-walled sclereids, underlie the epidermis. The outer cortex consists of about three layers of spheroidal (starch-sheath) cells; the inner starch-sheath portion of the cortex consists of about five layers. The endodermis is as in Monotrema. The pericycle, however, is one or two cells wide and is composed of relatively thick-walled sclereids. Extremely thick-walled sclereids compose the central portion of the stele.

In Windsorina guianensis the exodermis (Fig. 8) consists of about five or six layers of sclereids. The cortex is as in Potarophyllum riparium. Windsorina is distinctive in the high degree of sclerification of the stelar region. Beneath the endodermis, which is like that of Monotrema, the entire stele consists of thick-walled fibroform sclereids except for the xylem and phloem strands. These sclereids surround xylem and phloem bands completely. The one or two layers of pericycle are thick-walled and resemble closely the stelar sclereids. Luma of all sclereids contain deposits of tannin-like nature.

Maschalocephalus dinklagei shows great similarity to Windsorina guianensis in root anatomy. The exodermis (Fig. 9) is thicker, however, consisting of up to ten layers of sclereids. The cortex is as in Polarophyllum riparium, and the endodermis as in Monotrema. The walls of the thick-walled pericycle showed borders on some pits, suggesting a transfusion-cell function. This appears an extreme development of the band-like thickenings mentioned for pericyclic cells of Monotrema xyridioides. Sclerification of the stele in Maschalocephalus dinklagei is somewhat less extreme than observed in Windsorina guianensis, but the resemblance is close.

TRIBE RAPATEEAE — The only species of this tribe for which root anatomy has previously been studied is Rapatea paludosa (Boubier, 1896). Boubier's description was repeated by Solereder & Meyer (1929). Good material of this species was available to me also, and an amplified description is given here for the sake of completeness. In my material the epidermis (Fig. 11) had collapsed so that the outer surface of the root consisted of about four hypodermal layers of thin-walled sclereids. On the outermost of these, staining reactions suggest a degree of suberization. Some of the sclereids are idioblastic by virtue of content of tannin-like materials. Internal to the hypodermal sclerenchyma are one or two layers of thin-walled ovoid cells constituting an outer starch sheath. The central portion of the cortex has a composition identical to that described above for Monotrema xyridioides. The inner cortex (Fig. 10) consists of nine or ten layers of thin-walled cells, clearly arranged in radial rows, which are rich in starch. These inner starch-sheath cells are round as seen in transection (rectangular in longitudinal section) and associated with prominent intercellular spaces. Some of the starch-sheath cells, as well as some of the arm-parenchyma cells, are idioblastic by virtue of their content of tannin-like substances. The endodermis consists of sclereids with walls thickened equally on all sides. There is a single layer of pericycle whose cells are thin-walled adjacent to phloem bands, but those near xylem bands bear thickenings. These thickenings appear like fused bands because the pits occupy
as much space on the wall as the thickenings and the wall appears composed of intersecting bands. These cells, which may be likened to transfusion cells, are identical to some which abut on larger metaxylem vessels. In the phloem, sieve tubes, companion cells and parenchyma occur in a scattered fashion. Sieve tubes are relatively narrow in diameter. Each of the xylem bands is sheathed by a layer of thin-walled smaller sclereids of the same sort which occupy the center of the stelar region. Most of the xylem bands terminate in one of the large metaxylem vessels which form a circle around the stele, although some terminate in a smaller vessel. In addition, there is an occasional central vessel isolated in the center of the stele (Fig. 10).

Rapatea spruceana (Figs. 12, 13) shows several points of difference. The exodermis (Fig. 13) is thicker than that of R. paludosa. Excluding epidermis, which was collapsed in the material studied, it consists of about six layers of thin-walled sclereids some of which contain massive accumulations of tannin-like material. Internal to the hypodermis, one or two thin-walled cell layers are present. The inner cortex (Fig. 12) consists of ten to twelve layers of cells ovoid in transsection. Some of these are tannin-bearing idioblasts, and most contain starch grains. These cells not only decrease in diameter towards the stele, they also grade into thick-walled sclereids much like those of the endodermis. Two to seven layers of the inner cortex adjacent to the endodermis are composed of such sclereids. These sclereids, in fact, have very prominent pits and all of them can be referred to the transfusion-cell-like cells described above for R. paludosa, as can pericycle cells in R. spruceana. Longitudinal sections of the inner cortex show that (as in the other Rapateaceae) the inner cells near the endodermis are longer as well as narrower, while the outer ones near the central cortex (aerenchyma) are shorter as well as wider. Most xylem bands in the stele of R. spruceana terminate in the large metaxylem vessels. Xylem bands are not accompanied by sclereids which occur only in the central portion of the stele. The central sclereids are very thick-walled and intrude among the larger metaxylem vessels which are, however, mostly sheathed by thin-walled parenchyma. Central vessels were not observed.

Rapatea longipes proved similar to R. paludosa in most respects. It differed, however, in possessing the following features. Three layers of sclereids compose the exodermis. Two sclerenchymatous layers (like those of R. spruceana) are adjacent to the endodermis in the innermost part of the cortex. No central vessels were observed in the stele. Starch grains in the inner starch sheath are mostly spherical with a single hilum, as observed in other Rapateaceae, but a few twin starch grains were also seen. Arm-parenchyma cells of the central cortex often have lignified secondary walls.

In Rapatea yapacana a thin-walled epidermis was observed and this explains why it was rarely seen intact in the roots of Rapatea species. The exodermis of R. yapacana is composed of about six layers of thin-walled sclereids. Arm-parenchyma cells of the central cortex were observed to have rather thick lignified walls. The inner cortex is composed of seven or eight layers of thin-walled cells with an additional layer of sclereids just outside the endodermis. The endodermis is relatively thin-walled but sclerenchymatous. No thick-walled cells were observed in the single layer of pericycle. The lack of thicker walls in the central portion of the stele may be due to immaturity of the root studied, but this explanation does not appear likely in view of the presence of sclerenchyma elsewhere in the root. A unique feature of the roots of R. yapacana was the occurrence in the central portion of the stele of many narrow vessels, much narrower than the large metaxylem vessels which terminate xylem bands.

The roots of Rapatea angustifolia conform in all major features to the pattern described for R. paludosa. Distinctive features observed in R. angustifolia included the apparent suberization of the outermost layer of hypodermal sclereids.
Figs. 10, 11 — *Rapatea paludosa*, portions of root in t.s. Fig. 10. Portion including part of stele and inner cortex, at right bands formed of collapsed cells may be seen; note central vessels in stele, sclereids in the single layer of endodermis, and dark cells contain tannin-like deposits. Fig. 11. Exodermis; radial plates of cortex at left. Figs. 12, 13. *R. spruceana*. Fig. 12. Portion from transection of root showing sclerenchymatous inner cortex and part of stele. Fig. 13. Exodermis from transection of root. Fig. 14. *Duckea flava*, exodermis and outer cortex from transection of root. Fig. 15. *Cephalostemon affinis*, exodermis from transection of root; note the single sclerenchymatous layer. All figures × 215.
One or two layers of the inner cortex adjacent to the endodermis have thick lignified secondary walls. Sclereids of the stelar center and around xylem bands are very thick-walled, unlike the relatively thin-walled sclereids in these locations in *R. paludosa* roots.

The roots of *Rapatea fanshaweii* possess a rather thick exodermis which contains six or seven layers of thin-walled sclereids, some of these are idioblastic in content of tannin-like materials. Ten to twelve layers of ovoid cells compose the inner cortex; a few cells are tannin-idioblasts. An interesting feature of the inner cortex cells is that their walls gradually increase in thickness towards the stele. The three or four innermost layers could be called sclereids by virtue of the staining reactions which suggest lignification. The endodermis is composed of thick-walled sclereids and their small lumina are circular in outline. Xylem bands are sheathed in thick-walled sclerenchyma; such cells also compose the central portion of the stele. In the root sectioned, four central vessels were observed. An interesting feature shown by this root was the occasional interpolation of small strips of xylem into the otherwise well-defined phloem areas.

*Rapatea membranacea* showed a type of root anatomy identical to that of *R. angustifolia*. The interpolated xylem strips in phloem areas mentioned for *R. fanshaweii* were also observed in *R. membranacea*.

Many of the above features could also be observed in the roots of *Duckea*. *D. flava* has an epidermis composed of large, relatively persistent cells (Fig. 14). In comparison, the four layers of thin-walled exodermis sclereids are composed of small cells. An outer starch sheath is notable for large size of cells. The middle cortex is composed of collapsed spheroidal and persistent, but thin-walled, arm-parenchyma as in the above genera. The inner cortex is ten to twelve layers in thickness. The innermost of these layers is thick-walled and lignified. The endodermis is composed of thick-walled lignified square cells. All cells of the single pericycle layer are thin-walled. The ground tissue of the stele is also thin-walled. Within the central region of the stele are a few small vessels, reminiscent of the condition described above for *Rapatea yapacana*.

*Duckea cyperaceoides* differs from *D. flava* by possessing only two layers of thin-walled exodermis sclereids, internal to which is a single layer of large thin-walled cells. Some arm-parenchyma cells of the central cortex have thick lignified walls. The ovoid cells of the inner cortex (starch sheath) are thin-walled and occur as about seven layers. These contain either starch or, idioblastically, tannin-like materials. The stele is as in *D. flava*.

The roots of *Duckea squarrosa* proved very similar to those of *D. cyperaceoides*. A difference of interest occurred in the inner cortex. In *D. squarrosa* this region consists of four to six cell layers; the outer layers contain large intercellular spaces so that the cells have an appearance much like arm-parenchyma of the central cortex, and appear to form a transition to those cells.

The roots of *Cephalostemon affinis* proved similar to those of *Duckea* and *Rapatea*. The exodermis, however, is a very thin one (Fig. 15). Beneath the small and thin-walled cells of the epidermis is only a single layer of thin-walled hypodermal sclereids. The central region of the cortex contains both arm-parenchyma cells and collapsed spheroidal cells, but in the root examined both were rather collapsed and appeared similar to each other. The inner cortex is composed of about six layers of ovoid cells and the outer ones are like arm-parenchyma, as in *Duckea squarrosa*. Some cells in this region are idioblasts containing massive tannin-like deposits. The endodermis is composed of relatively thin-walled lignified cells which are square in outline as seen in a transection. The pericycle is a single layer of thin-walled cells. The large metaxytem vessels of the xylem bands form a close-packed ring; large vessels of adjacent bands are, in fact, in contact with each other. Internal to the metaxytem vessels the central region of the stele is composed of very thick-walled sclereids.

The roots of *Spathanthus unilateralis* are very close to patterns described for
Rapatea. Beneath the thin-walled (and usually collapsed in mature roots) epidermis are four layers of thin-walled sclereids. There are no ovoid cells comprising an outer starch sheath; directly underneath the hypodermal sclereids are the radial plates composed of collapsed spheroidal cells and arm-parenchyma. The inner cortex consists of six or seven layers of cells ovoid in outline. Only the innermost layer contains cells which have thicker lignified walls. The endodermis cells are square in outline and have relatively thin lignified walls. The pericycle is thin-walled except adjacent to protoxylem poles where the cells have prominent pits as in Rapatea spruceana. The central portion of the stele is composed of thick-walled sclereids, and such sclereids are also present (as in Rapatea angustifolia) adjacent to xylem bands.

Spathanthus bicolor agrees with S. unilateralis in root anatomy except that internal to the hypodermal sclereids two layers of thin-walled ovoid cells were observed.

Tribe Schoenocephalieae — Guacamaya superba (Figs. 16-18) illustrates several features characteristic of this tribe. The exodermis of a mature root (Fig. 17) is covered by an epidermis composed of persistent thick-walled cells showing some degree of suberization. Beneath the epidermis are five to seven layers of hypodermis; the interior layers of cells are larger and thicker-walled and all of these could be called sclereids. Internal to the sclerenchyma are two to three layers which, like the comparable region of root cortex in Rapatea, are thin-walled, contain starch, and can be called an outer starch sheath. The central portion of the cortex of Guacamaya (Fig. 18) does not consist of radial plates. This feature, in fact, differentiates Monotremaeae and Rapateaee on the one hand from Schoenocephalieae, and Saxofridericieae on the other. The central cortex is composed of not two, but three kinds of cells: arm-parenchyma, collapsed spheroidal cells, and tannin-bearing idioblasts. Although the spheroidal cells collapse so that their walls are oriented in a radial direction, they do not form continuous radial bands. The arm-parenchyma cells also are not symmetrical with four arms as they are in Rapateaee and Monotremaeae. The arm-parenchyma and collapsed parenchyma cells tend to alternate in successive layers when viewed in longitudinal sections, but they are not so precisely layered as shown for Monotremea in Figs. 1-6. The tannin-bearing idioblasts appear narrow and round in transection; in longitudinal section they are quite long and form vertical series. The arm-parenchyma cells in Guacamaya superba are thin-walled, but the walls do become lignified. The spheroidal parenchyma cells prior to collapse are shown for Saxofridericia inermis in Fig. 20, and it offers a close comparison with that of Fig. 18. Surrounding the stele of Guacamaya superba are ten to twelve layers of cells round in transection, oriented in radial rows (Fig. 16). These cells are elongate in longitudinal section. Many of the cells are filled with tannin-like compounds; such cells are, in fact, so frequent that one hesitates to designate them as idioblastic in this species. None of these inner cortex cells have thick lignified walls. The endodermis is composed of extremely thick-walled and lignified cells. As seen in a transection these cells are markedly elongate radially, and they have very small lumina. Internal to the endodermis are two layers of relatively thin-walled pericyclic cells which are lightly lignified and bear pits. The large number of alternating xylem and phloem bands in the stele of Guacamaya is shown in Fig. 16. Of the xylem bands, fewer than half terminate inwardly in the very large metaxylem vessels; the remainder terminate in smaller metaxylem vessels. The vessels are sheathed by a single layer of parenchyma cells which have pitted walls and are reminiscent of the cells discussed above for Rapatea paludosa. They recall the transfusion-cells. The ground tissue of the stele consists of sclerenchyma whose cells are thick-walled just internal to the wide metaxylem vessels than in the center of the root. This thick-walled sclerenchyma also occurs between the large metaxylem vessels. A feature of
Figs. 16-18—Guacamaya superba. Fig. 16. Stele from t.s. of root; dark cells of inner cortex contain tannin-like deposits. Fig. 17. Exodermis from t.s. of root, epidermis above; note layers of sclereids. Fig. 18. Portion of cortex from root transection; three types of cells are evident: persistent arm-parenchyma, collapsed spheroidal parenchyma, and idioblasts containing tannin-like substance. Fig. 19. Schoenocephalium cucullatum, portion of stele and adjacent cortex from root transection. Fig. 20. Sasaofridecia inermis, portion of cortex from transection of maturing root; the three types of cells mentioned in Fig. 18 are present, but the large spheroidal parenchyma cells have not yet collapsed. Fig. 16. × 56; Figs. 17-20. × 140.
particular interest in the phloem of roots of Guacamaya — as well as other Schoenocephalieae and Saxofridericieae — is the large diameter of metaphloem sieve tubes. These are visible in Fig. 16, but have been better illustrated for Guacamaya superba earlier (Carlquist, 1961b).

Schoenocephalium cucullatum (Fig. 19) serves to illustrate the stelar features of Schoenocephalieae well. There are fewer and smaller metaxylem vessels than in Guacamaya superba. The exodermis of S. cucullatum consists of a layer of persistent epidermal cells, three or four layers of sclereids, and one or two layers of thin-walled cells (outer starch sheath). Otherwise, the roots of S. cucullatum match closely features described for Guacamaya.

The same pattern may be seen in Schoenocephalium tertifolium. Among distinctive features of this species, however, are a thinner exodermis, one or two layers of hypodermal sclereids, and one or two layers of outer starch sheath. The entire central portion of the root stele is very thick-walled sclerenchyma; only a single layer of pericycle was observed.

In S. coriaceum (Figs. 21, 22) a thin exodermis is also evident. The pericycle is mostly two cells in thickness, but because of radial orientation of these cell pairs one suspects that the two layers originate from a single layer by tangential divisions rather late in ontogeny. In Fig. 22 is shown a portion of the pericycle three or four cells in thickness. This pericycle is undoubtedly associated with the formation of a nearby lateral root. Such divisions associated with lateral roots were reported in the roots of Rapaetea by van Tieghem & Douliot (1891). The extremely wide metaphloem sieve tubes and the very thick-walled sclereids of the central region of the stele are shown for S. coriaceum in Fig. 21.

Epidryos micrantherus shows many points of similarity in root anatomy to Schoenocephalium coriaceum. The exodermis consists of a rather persistent epidermis, three layers of hypodermal sclereids, and about four outer starch sheath layers. The central portion of the cortex contains the same three types of cells as in Guacamaya. The inner cortex consists of five or six layers of ovoid cells. Of these, the inner two may have thick lignified walls. The endodermis is composed of radially elongate cells. The center of the stele is sclerenchymatous, and the walls of sclereids are thicker near the large metaxylem vessels than in the center of the stele.

Tribe Saxofridericieae — The roots of this tribe agree in most respects with those of the Schoenocephalieae, requiring little additional illustration. Saxofridericia spongiosa (Fig. 23) has a thick exodermis. Beneath the persistent epidermis are six to eight layers of hypodermal sclereids. The outer three are relatively thin-walled, whereas the inner three or four are thick-walled. An outer starch sheath of two or three cell layers is present. The middle cortex consists of the three cell types described for Guacamaya. The inner cortex of S. spongiosa is exceptionally thick. It is composed of 16 to 18 layers of cells, elliptical (tangentially widened) in transection. Some of these contain tannin-like substances idioblastically. The endodermis is like that of Guacamaya. Only a single layer of pericycle is present; cells of this layer have pitted lignified walls. The phloem bands contain exceptionally wide sieve-tube elements in late metaphloem. Of the xylem bands, only about half terminate inwardly in the largest size of metaxylem vessels. The ground tissue of the stele consists of thick-walled sclereids which sheathe the xylem bands. The central portion of the stele consists of somewhat thin-walled sclereids.

The material of Saxofridericia inermis differed from S. spongiosa in the following ways: exodermis containing about five layers of hypodermal sclereids, the outer two layers thick-walled; inner cortex composed of eight to nine cell layers; and presence of two pericyclic layers.

Stegolepis angustata (Fig. 24) contains several notable anatomical features. The exodermis is relatively thin; beneath the epidermis are one or two layers of thin-walled sclereids, and internal to these about two layers of parenchyma. The
Figs. 21, 22—Schoenocephalium coriaceum. Fig. 21. Portion of stele (below) and adjacent cortex (above) from t.s. of root; portion of a perforation plate is visible within one of the vessels. Fig. 22. Exodermis and adjacent cortex from t.s. of root; idioblasts stain darkly. Fig. 23. Saxofridericia spongiosa, exodermis from transection of root, thick-walled sclereids are centrally placed in the exodermis. Fig. 24. Stigolpis angustata, portion of stele and adjacent cortex, beside the xylem bands are cells with thickenings on the xylem side only; note also the pattern of thickenings on endodermal cells and the thicker walls of cells of cortex at extreme right. Fig. 25. Stigolpis celtiae; note prominently sclerenchymatous layers outside the endodermis; walls of the endodermis stain darkly perhaps because of suberization. Figs. 21-23, 25. × 170; Fig. 24. × 200.
central portion of the cortex contains not three, but four types of cells: arm-parenchyma; collapsed spheroidal cells; narrow thin-walled cells, circular in transection, which occur singly; and narrow thick-walled cells, circular in transection, which occur in clusters. This last type is also represented as the outer portion of the inner cortex (Fig. 24, extreme right). The inner cortex contains about ten layers of such non-lignified cells followed by eight layers of thin-walled parenchyma, and (next to the endodermis) one or two layers of thin-walled sclereids. The endodermal cells are unique among the Rapateaceae studied: they are large, radially elongate, and bear thickenings — maximum on the internal faces, tapering on the radial walls, and absent on outer walls. Two or three layers of thin-walled pericycle are present. The central portions of the stele are thick-walled sclerenchyma. Cells which sheath the xylem bands are unique in the family (Fig. 24); they bear thick lignified walls only on the wall faces which are adjacent to xylem.

Stegolepis celiae (Fig. 25) has an exodermis like that of Saxofridericia spongiosa: two outer layers of hypodermal sclereids, and three inner layers of thick-walled sclereids followed by three layers of outer (starch sheath) cortical parenchyma. The middle cortex contains the three types of cells mentioned for Guacamaya. The inner cortex of Stegolepis celiae is like that of S. angustata in possessing three types of cells. The outermost of these are two or three layers of thick-walled non-lignified cells. Internal to these are three to four layers of thin-walled parenchyma cells, elliptical in outline, and two to four layers of sclereids. These sclereids are not of the same nature as in other Rapateaceae, where they are elliptical in outline and associated with large intercellular spaces. Inner cortical sclereids of S. celiae (Fig. 25) are polygonal in outline, closely packed, and the layers adjacent to the endodermis have extremely thick walls. The endodermis, however, is relatively thin-walled and stains much more deeply than the inner cortical sclereids perhaps because of suberization. One or two layers of thin-walled pericycle cells are present. Those adjacent to xylem have slightly thicker pitted lignified walls. Metaphloem sieve tubes are very wide. The ground tissue of the stele is composed of moderately thick-walled sclereids; those in the center of the root are thin-walled.

The roots of *Phelpsiella ptericaulis* have about five layers of hypodermal sclereids — the outer three are thin-walled and the inner two thick-walled. The ovoid cells of the outer cortex occur as about three layers, those of the inner cortex as eight to ten. Idioblasts bearing the dark-staining tannin-like substances occur in both cortical regions. The endodermal cells are square in transection and have very thick walls. A single layer of pericycle is present. The center of the stele is thick-walled sclerenchyma which extends outward between the larger metaxylem vessels.

**Systematic Distinctions**—The differences and similarities among the major groupings within the Rapateaceae with respect to root anatomy may be summarized in the form of a key. Obviously, much information cannot be included within such a key but it does serve to underline the usefulness of root anatomy alone to the systematics of this family.

Central cortex composed of three types of cells which are not arranged in clear radial plates at maturity; sieve-tube elements of metaphloem very wide

... Saxofridericioideae

Cells of inner cortex mostly not filled with tannin-like compounds, such cells occurring idioblastically

... Saxofridericieae

Cells of inner cortex which are filled with tannin-like contents abundant, often more numerous than cells lacking such contents

... Schoenocephalieae

Central cortex composed of two types of cells, arranged in radial plates; metaphloem sieve-tube elements narrow

... Rapateoideae

Exodermis composed of thin-walled hypodermal sclereids...Rapateae. Exodermis composed of thick-walled hypodermal sclereids...Monotremeae
Figs. 26-28 — Portions of stem transections. Fig. 26. *Monotropa xyridoides*, endodermis-like layers form a light band (at right), cortex at extreme right. Figs. 27, 28. *Guacamaya superba*. Fig. 27. Vascular core of stem and, at right, innermost cortex; endodermal-like layers consist of sclereids (gray, outside the bands of light, radially-aligned cells). Fig. 28. Section from near center of vascular core of stem showing a slime cavity (extreme left) and an amphivasal bundle (above, right). All figures x 70.
Stem Anatomy

The stems of the Rapateaceae vary from narrow, with conspicuous internodes, to broad, short, and "acaulescent". An example of the former is *Rapaea angustifolia*: stems of mature plants are 1/2 to 1 cm in diameter, and internodes may be several millimeters in length. In other taxa, such as *Guacamaya superba*, the stems may be 5 cm in diameter. Most stems of the Rapateaceae are very condensed, and thus provide great difficulty in interpretation of paths of vascular bundles. The histological features do vary from species to species, but offer less numerous criteria for systematic purposes than do roots.

The data on vessels are given in a later section. Trichomes were observed on some stems, and are noted below. However, the trichomes of the Rapateaceae are best observed on leaf primordia and will be described in detail in a later paper dealing with leaf anatomy of the family.

Differences with respect to prominence of sclerenchyma described below are, in part, the result of different ages of stems in the material available. Because of the nature of this material, the age of plants and the part of the stem from which a segment came could not always be determined.

**TRIBE MONOTREMEEAE — Monotrema xyridoides** (Fig. 26) serves conveniently to introduce the features which are found throughout the family, as well as some characteristics of the tribe. On the epidermis of this species, uniseriate slime-producing trichomes, averaging three cells in length, were observed. The epidermal cells did not show any peculiarities. The wide cortex in this species is composed of thin-walled cells, round in a transectional view and elongate in longitudinal section. These cortical cells are associated with abundant intercellular spaces and contain many starch grains, mostly simple but a few paired or compound ones. Crystal sand — presumably composed of silica — was observed in cortical parenchyma. Leaf traces within the cortex are sheathed by thin-walled parenchyma. At the inner margin of the cortex are several layers of sclereids (thin-walled cells in younger portions of the stem as shown in Fig. 26). These cells must be regarded as endodermal in nature. The sclereids are intercontinuous with and histologically similar to the single layer of sclerenchymatous cells which form endodermis of lateral roots. Because the Rapateaceae often grow in marshy situations, an endodermis-like layer in stems might not be unexpected. The endodermis is two to five (mostly three) layers thick, and tangential (periclinal) divisions are frequent. These tangential divisions — where such cells are thin-walled — suggest a site of origin for lateral roots, and this possibility was, in fact, confirmed in various species of the Rapateaceae. Internal to the endodermal layers is the stelar region which consists of numerous crowded bundles. The parenchyma which intervenes between the bundles is thin-walled and like that of the cortex in *M. xyridoides*. Some stelar parenchyma cells in this species contain the dark-staining idioblastic compounds. As would be expected, bundles which supply the leaves a short distance above the plane of section (which are therefore leaf traces) are located not at the periphery, but in the center of the stele. These bundles are collateral in organization. Such leaf traces do, of course, turn sharply outward in their nearly horizontal course into leaves, and oblique portions of such leaf traces may be seen in stem transections in various portions of the stele as well as in the cortex. The remainder of the bundles are amphivasal, or transitional between amphivasal and collateral. An exception to this is provided by a girdle of extremely contorted bundles which lie just underneath the endodermal region (Fig. 26, right). These bundles, although tortuous in course, tend to be oriented predominantly horizontally (tangentially) and not vertically. This seems curious because these bundles cannot be considered leaf traces. Moreover, where leaf traces traverse the endodermal region, their xylem and phloem strands are not in contact with the contorted bundles. There is, however, a clear
explanation for the girdle of sub-endodermal bundles. Lateral roots are initiated in the endodermal region of the stem. Sections of various rapateaceous stems which show basal portions of lateral roots illustrated that the contorted bundles are intercontinuous with xylem and phloem of the steles of lateral roots. Some of the Rapateaceae, such as several species of *Rapatea*, have long internodes and form lateral roots at nodes. Sections of internodes of such species (e.g., Fig. 29) do not show a transverse girdle of subendodermal bundles. This confirms the close relationship between the lateral roots and subendodermal bundles. The highly contorted nature of this subendodermal vascular cylinder is significant, because vascular tissue of this cylinder contacts many bundles of the outer stelar region providing intimate contact between stem and root vascular tissue. Although these facts on the course of vascular bundles are set forth here for *Monotremum xyridioides*, these considerations apply to all the Rapateaceae with the exception of internodes in species with long internodes.

*Monotremum aemulans* agrees with the pattern described for *M. xyridioides* but, in addition, possesses idioblasts containing tannin-like compounds in cortical as well as stelar regions. *M. affine*, of which an older stem was available for study, showed clear suberization of the outermost endodermal layer as well as deposits of tannin-like materials in intercellular spaces of outer cortex.

The stems of *Potarophytum riparium*, *Maschalocephalus dinklagei*, and *Windsorina guianensis* showed the same features mentioned for *Monotremum xyridioides*. In *P. riparium* relatively thick-walled endodermal sclereids were observed. The epidermis of *M. dinklagei* stems contained many idioblasts bearing tannin-like compounds.

**Tribe Rapateaeae — Rapatea longipes** (Fig. 29) shows many points of resemblance to the pattern described for *Monotremum xyridioides*. In *R. longipes*, however, parenchyma cells of the stelar region are, in part, thick-walled and lightly lignified. Bundles which, by virtue of their position and collateral nature can be designated as leaf traces (e.g. Fig. 5, center, above), are sheathed in fibers. Other bundles are sheathed by thin-walled parenchyma. The endodermal zone is composed of notably thick-walled sclereids. Although most of the cortex is thin-walled, a zone of sclereids which are relatively thin-walled is present in the outer cortex, separated from the epidermis and endodermal region by non-lignified parenchyma. No silica was observed in stelar or cortical parenchyma, but cells of both regions are rich in starch grains. Features of epidermis and hypodermis were well demonstrated by *R. longipes* (Fig. 32). Long uniseriate slime-producing trichomes form a prominent feature of the epidermis. Droplets of an unidentified substance can be seen prominently in these trichomes. Some epidermal cells contain massive deposits of the dark-staining tannin-like materials. The remaining epidermal cells contain numerous small silica bodies. Epidermal cells bearing these silica bodies show an accumulation of suberin-like material along their inner walls. Underlying the silica-bearing epidermal cells are two or three layers of fibers. Features such as these have been illustrated for leaves of *Rapatea* (Carlquist, 1961b).

The stems of *Rapatea spruceana* proved identical to those of *R. longipes* except that in the stem studied, sclereids in the outer cortex appeared in the form of scattered cells rather than as a continuous band. In *R. fanshaweii* such cortical sclerechyma was not seen, but most of the ground tissue of the stelar region could be called thin-walled sclerechyma which fades into the sclereids of the endodermal region.

The stems of *R. yapacana* are basically like those of *R. longipes*. Peculiarities in the material of *R. yapacana* examined include the following: the central portion of the ground tissue of the stelar region consists of thick-walled sclereids, whereas peripheral portions of stelar ground tissue consist of thin-walled sclereids; endodermal cells are thick-walled sclereids; and cortical parenchyma is wholly non-lignified thin-walled parenchyma.

The stems of *R. angustisola* are referable to the descriptions given above for
Fig. 29 — *Rapatea longipes*, t.s. stem showing vascular core (left) and cortex (right); dark-staining sclereids delimit the two zones and suggest presence of a sort of stem endodermis. Fig. 30. *Spathanthus unilateralis*, t.s. stem; the portions shown and their arrangement correspond to the stem of Fig. 29; mottled appearance of photograph is caused by the abundance of starch grains and silica bodies. Fig. 31. Same, portion of cortex; a vascular strand surrounded by thick-walled fibers (lower left); parenchyma cells are filled with starch grains (bila appear black) and silica bodies. Fig. 32. *Rapatea longipes*, surface of stem from transsection, two uniseriate trichomes with a few tannin-like deposits are shown; the epidermis contains minute silica bodies, epidermal idioblasts containing the tannin-like compounds stain darkly; hypodermal fibers are also shown. Fig. 33. *R. angustifolia*, surface of stem from t.s., three strands of narrow hypodermal fibres are seen. Figs. 29, 30. × 70. Figs. 31-33. × 190.
R. fanshawei. They are much narrower and contain fewer bundles than in other species. The outer cortex (Fig. 33) also reveals a somewhat different pattern. The fiber strands are very narrow, and only a single strand of silica-body-bearing epidermal cells is adjacent to each of these fiber strands.

The stem of R. membranacea available for study was like that of R. longipes, but showed (perhaps because of immaturity) less lignification. Only a few lignified parenchyma cells were present in stelar ground tissue, and fibers were present around only a few leaf traces.

The stems of Cephalostemon affinis are referable to the description given above for Monotremum xyridioides. The cortical cells contained droplets of unidentified substances, and endodermal cells were sclerenchymatous. Trichomes and epidermal cells with silica bodies, as in Rapatea longipes (Fig. 32), were observed.

The stems of Duckea flava and D. squarrosa also conform to the pattern described for Monotremum xyridioides. In both species of Duckea the unidentified substances were present not only in cortical cells but in parenchyma of the stelar region as well. Older vessels were occluded with these deposits.

The stems of Spathanthus unilateralis (Figs. 30, 31) seem similar to those of Rapatea, but offer several well-marked peculiarities. Silica bodies were observed in the epidermis but, unlike the epidermal condition in Rapatea, no underlying hypodermal fibers were observed. Although a few droplets of tannin-like substances were seen in cortical and stelar parenchyma, idioblasts were absent. All parenchyma cells are relatively thin-walled and non-lignified. Leaf traces, both in cortical and stelar regions, are encased in thick strands of fibers (Fig. 31, lower left). The endodermal region consists of thin-walled sclereids. A very distinctive feature of the stem of Spathanthus unilateralis is the presence in parenchyma not only of abundant starch but even of silica. This silica occurs in the form of one body per cell and has a rough, granular or erose outline.

The stems of S. bicolor showed the same basic features, but less sclerenchyma in leaf traces. Silica bodies were not observed, but each parenchyma cell possessed a nest of silica sand. These features (also observed in Monotremum) suggest an earlier stage in ontogeny than in the stem of S. unilateralis. The endodermal region, however, consisted of very thick-walled sclereids.

Tribes Schoenocephalieae — Guacamaia superba (Figs. 27, 28) demonstrates several interesting features of this tribe. Although uniseriate slime-producing trichomes were observed on the epidermis, silica bodies were absent in epidermal cells. Cortical parenchyma is thin-walled, although in the stem studied a band of sclerified parenchyma was present a short distance beneath the stem surface. Both cortical and stelar parenchyma are starch-rich. Some parenchyma cells in both zones contain massive tannin-like deposits (Fig. 27). These cells are numerous, and occur in patches rather than idioblastically. An endodermal region is well-marked. About three layers of thick-walled sclerenchyma overlie several thin-walled layers in which periclinal divisions are evident. A fibrous sheath is present around leaf traces, both in stelar and cortical regions, but such sheaths are lacking on most bundles.

A highly distinctive feature of Guacamaia stems is the presence of what can be called slime cavities (Fig. 28, left). These cavities may be present in the stelar and cortical regions and many extend from one region into the other. Some cavities appear to run vertically in the stem, others horizontally or in various directions. In the material available I was not able to follow the course of these cavities completely. A feature of especial interest is the presence of uniseriate trichomes on the cavity walls. These are slime-producing trichomes like those on the exterior surface of the plant, but have much shorter stalks. The typical trichome lining these canals has a 3-celled stalk shorter than the globose head cell. A slimy deposit was observed in the canals. The secretory
canals of Guacamaya appear to be an internal version of the external epidermis and its slime-producing hairs. The presence of hairs in both places suggests the possibility that the cavities communicate with the outer surface, or at least that the cavities are formed at an early point in ontogeny when protoderm capable of forming trichomes can be initiated on the cavity. In other words, these cavities are probably schizogenous in origin and are formed near the apical meristem of the stem. The examination of leaf bases in Guacamaya and other genera in which cavities are present shows that the cavities do not, seemingly, extend into leaves.

The stems in the genus Schoenocephalium are virtually identical to those of Guacamaya. The stems of S. coriaceum differ only in their rather more numerous tannin-filled cells, while less sclerenchyma (perhaps because of immaturity) was observed on leaf traces of the stem of S. teretifolium.

The stems of Epidryos micrantherus also showed the same features mentioned for Guacamaya, except that slime cavities were not observed in the material examined; further studies are needed to see if they occur in Epidryos.

TRIBE SAXOFRIDERICIEAE — The stems of Stegolepis celsae agree with those of Guacamaya except that slime canals or cavities are absent and ground tissue of the stelar region, although thin-walled, is lightly lignified. In Stegolepis angustata the endodermal region is not sclerenchymatous, and the parenchyma of the stelar region, although thin-walled, is lignified as is cortical parenchyma. In S. angustata tannin deposits in intercellular spaces were observed in various portions of the stem.

The stems of Phelopsyillaptericaulis follow the pattern described for Stegolepis celsae, but tannin-filled cells were particularly abundant in the outer portion of the cortex. The stems of Saxofridericia were not available for study.

SYSTEMATIC CONSIDERATIONS — As with roots, in respect to stem anatomy the four tribes of the family may be arranged in the form of a key to summarize differences and similarities within the family:

| Tannin-filled parenchyma cells present as packets of cells in both cortical and stelar regions | Saxofridericioideae |
| Slime canals and cavities absent; stelar parenchyma lightly lignified | Saxofridericioideae |
| Slime canals and cavities present; stelar parenchyma not lignified | Schoenocephalioideae |
| Tannin-filled parenchyma present as idioblasts in stelar region and cortex, or absent | Rapateoideae |
| Epidermis containing silica bodies; epidermis containing silica bodies (in some genera) associated with hypodermal strands of fibers | Rapateoideae |
| Epidermis of stem lacking silica bodies; hypodermal fiber strands absent | Monotremae |

Spathanthus is noteworthy for possessing silica bodies or silica sand within the parenchyma cells. This characteristic is not shared by the other Rapateaeae, but is present in Monotrema. Lack of lignification on stelar parenchyma cells is also common to Spathanthus and Monotremaeae. Spathanthus differs from the other Rapateaeae in lacking hypodermal fiber strands.

The presence of slime canals and cavities seems to be a good criterion for the tribe Schoenocephalioideae.

Vessels

Little has been reported concerning occurrence of vessels in the Rapateaceae. The family was not included in Cheadle's (1942) survey of monocotyledon xylem. The only data given by Solereder & Meyer (1929) is the report of simple perforations in vessels of roots of Monotrema arthropylla (reported by those authors as Schoenocephalium arthropylla).

The occurrence of vessels in the Rapateaceae is summarized below. Taxa upon which this report is made are the same as those on which the details...
of root and stem anatomy are described above, and all taxa for which either stem or root material was available were included in this survey.

**Tribe Saxofridericéeae** — Roots: vessels with scalariform perforation plates, up to 20 bars. Stems: vessels with scalariform perforation plates.

**Tribe Schoenoecephalicieae** — Roots: vessels with scalariform perforation plates; in wide metaxylem vessels, the perforation may not be merely scalariform, but have several longitudinal series of perforations, each series like a scalariform perforation plate (the fragment of a perforation plate in Fig. 21 is two to three perforations wide). Stems: vessels with scalariform perforation plates.

**Tribe Raptiveae (except Spathantheus)** — Roots: vessels with three to ten narrow bars on perforation plates. Stems: perforation plates scalariform (or variously multiperforate if vessels tortuous), bars narrow. *Spathantheus*: vessels with simple perforation plates in roots; in stems, perforation plates of vessels are simple or with a few vestigial bars which usually do not cross the perforation.

**Tribe Monotremeae** — Roots: vessels with simple perforation plates occur in larger metaxylem vessels; smaller vessels possess scalariform perforation plates with five to twenty bars. Stems: vessels with simple perforation plates.

In Saxofridericéeae and Schoenoecephalicieae observation of vessels in stems proved very difficult, for the same reasons that Cheadle (1942) found observation of vessels in stems of Bromeliaceae difficult. Scalariform perforations were seen in stems of the two tribes, however, an occurrence which would be expected on the basis of Cheadle's (1942) considerations, for vessels were observed in inflorescence axes of these two tribes.

In roots of the Raptiveae, protoxylem vessels are mostly transitional in pitting; metaxylem vessels possess wide elliptical pits in scalariform arrangement exclusively. In stems most vessels have transitional or scalariform pitting on lateral walls.

**Taxonomy and Phylogeny within the Raptiveae**

The fact that the system of Maguire et al. (1958) for tribes within the family has been cited above as a means of summarizing anatomical data shows clearly that this system is, in general, confirmed by distribution of anatomical characteristics. A possible exception might be formed by *Spathantheus*. This genus, placed in the Raptiveae by Maguire, has certain exceptional characteristics. To be sure, root anatomy suggests similarity to *Raptivea*, a similarity also claimed (without detailed evidence) by Soleder & Meyer (1929). However, the presence of silica bodies or silica sand in stem parenchyma of *Spathantheus* is a feature shared only by Monotremeae. *Spathantheus* resembles Monotremeae rather than Raptiveae in the presence of simple perforation plates in vessels. The lack of tannin-bearing idioblasts in *Spathantheus* is seemingly a distinctive feature. Peculiarities of pollen grains (Carlquist, 1961a) also suggest the distinctive nature of *Spathantheus*. Further anatomical evidence may prove decisive in demonstrating whether or not *Spathantheus* is best retained in the Raptiveae.

The criteria for recognition of genera and species are not offered as abundantly by root and stem anatomy as by pollen grains in the Raptiveae. In Monotremeae the genera can apparently be differentiated with respect to exodermis structure, a characteristic which is also distinctive in *Cephalosienmon* of the Raptiveae. Peculiar root cortex features might be used to define the genus *Stegolepis*, as well as species within it. Width of exodermis and degree of sclerification of inner cortex may be specific criteria in *Raptivea*. Presence or absence of central vessels in the stele seems a good species characteristic in the Raptiveae, as does degree of sclerification of the stele.

The arrangement and sequence of subfamilies and tribes for the family erected by Maguire et al. (see p. 17 of this article) suggest that Saxofridericéeae retain more unspecialized characteristics, whereas Monotremeae contain the most
numerous specialized features. This sequence proved clearly justified on the basis of pollen. Features of root and stem anatomy offer fewer criteria. The most significant of these is to be found in occurrence of vessel types, and Saxofridericieae and Schoenocephalieae prove equally primitive in this respect. Rapateae are intermediate in this respect, whereas Monotremaeae are the most highly specialized. The precise pattern of radial plates in root cortex of Monotremaeae and Rapateaeae marks these tribes as specialized in this respect. The trimorphism of cells in root cortex of Saxofridericieae and Schoenocephalieae could be interpreted as a specialization as compared with the dimorphism of root cortex cells in Rapateaeae and Monotremaeae, but probably this characteristic has little phylogenetic significance.

**Relationships of the Rapateaceae**

Hamann (1961) has given an extensive summary of characteristics of the various families of the Farinosae and the views of various workers concerning the interrelationships of these families. These views need not be repeated here, for Hamann's review is very thorough. Using a system of "similarity quotients," he found that the Rapateaceae show most numerous resemblances to the Commelinaceae, Xyridaceae, Bromeliaceae, and Liliaceae, in that order. Other families show less numerous resemblances. The Liliaceae seem less significant as a source of affinity using Hamann's method because Liliaceae is a large and polymorphic family and might be expected to contain a greater variety of characteristics than a small family. The Xyridaceae and Bromeliaceae appear particularly significant because these two families have a maximum of diversity within the same geographic region in which the Rapateaceae are best represented, northern South America.

The roots of the Rapateaceae do find many points of resemblance to those of the Xyridaceae, especially *Abolboda* (Carlquist, 1960). There are several points of difference. In the Xyridaceae the phloem and xylem are scattered throughout the stele. The roots of Eriocaulaceae (Malmanche, 1919) are very similar in stelar characteristics, but lack pericycle. The Bromeliaceae may offer some of the closest matches (Solereder & Meyer, 1929), particularly when more genera of that family are known anatomically than have as yet been investigated. A feature of interest which occurs in several families in addition to the Rapateaceae is the presence of transverse plates of arm-parenchyma alternating with collapsed parenchyma tiers in root cortex (e.g. Eriocaulaceae: Malmanche, 1919; Xyridaceae: Carlquist, 1960).

The ergastic materials (tannin, silica bodies) of the Rapateaceae occur also in the Bromeliaceae. The presence of both simple and compound starch grains characterizes many families of the Farinosae. Interestingly, the schizogenous slime cavities such as found in Schoenocephalieae of the Rapateaceae have also been reported in the Bromeliaceae (Solereder & Meyer, 1929). Slime-producing uniseriate trichomes occur in both the Rapateaceae and Xyridaceae.

The roots of *Abolboda* of the Xyridaceae (Carlquist, 1960) show many points of resemblance to those of the Rapateaceae, but these similarities may derive from similar habit and ecology rather than deep-seated phylogenetic resemblances.

Stems of *Abolboda* of the Xyridaceae (Carlquist, 1960) show many points of resemblance to those of the Rapateaceae, but these similarities may derive from similar habit and ecology rather than deep-seated phylogenetic resemblances.

The levels of specialization of vessels in the Rapateaceae fall between that of the Bromeliaceae (more primitive than Rapateaceae) and the Xyridaceae (more specialized than Rapateaceae) and are about the same as the Commelinaceae (Cheadle, 1942).

In conclusion, the anatomical data presently available suggest that the closest affinities of the Rapateaceae are to be found among the Bromeliaceae and Xyridaceae, and — to a lesser extent — Commelinaceae, Eriocaulaceae and even Mayacaceae. The constellation of characteristics so far reported for the Rapateaceae mark the family as distinct from other families of monocotyledons. It is a natural family which shows affinities to more than one other family.
Summary

The extensive explorations by Maguire and his associates have provided excellent liquid-preserved material of the Rapateaceae, a family in which only a few species have hitherto been available for anatomical study. The scheme of Maguire for tribes and subfamilies of the family is used as a framework for anatomical studies of stems and roots, as was done earlier for pollen. Anatomical data support Maguire's classification, and the details of root and stem anatomy, respectively, are summarized in the form of keys. Roots of Rapateaceae have a well-developed sclerenchymatous exodermis within which is a starch sheath. Internal to this is the central cortex which consists of two or three kinds of cells, according to the tribe. These cells are: arm-parenchyma; spheroidal parenchyma cells which collapse at maturity; and idioblasts which contain a tannin-like substance. In the tribe Rapateoideae arm-parenchyma and collapsed cells are arranged in alternating superposed radial plates. In Saxofriderioidae idioblasts are present in addition. The inner cortex of roots of Rapateaceae is composed of spheroidal cells, arranged in radial files, which contain starch and exhibit various degrees of secondary thickening on walls. The endodermis is ordinarily one cell-layer thick. The ground tissue of the stele exhibits various degrees of sclerification. Central vessels may or may not be present. Exceptionally wide sieve tubes occur in Saxofriderioidae. The stems show a broad outer cortical tissue of thin-walled cells containing various amounts of starch. An endodermal region, usually consisting of two to five layers of sclereids, surrounds the vascular core. The vascular core consists of amphivasal bundles and, in the center, collateral bundles (leaf traces). Various degrees of sclerification occur in ground tissue of the vascular core. Noteworthy features in stems include presence of slime canals in Schoenoecephalaeae, and conspicuous silica bodies throughout the stems of Spathanthus. Vessels of roots and stems of Rapateaceae have scalariform perforation plates except in Monotremaeae (plates simple in stems) and Spathanthus (plates simple in roots and stems).

Anatomical distinctions lend themselves to generic definition in some cases. Spathanthus is highly distinctive in various respects, but may be provisionally placed in the Rapateaceae. Within the family, Schoenoecephalaeae and Saxofriderioidae appear relatively primitive, Monotremaeae most specialized, and Rapateaceae intermediate. From the evidence of roots and stems, Rapateaceae forms a natural family which shows numerous resemblances to the families Bromeliaceae and Xyridaceae.

Literature Cited