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Sherwin Carlquist Claremont Graduate School

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#### POLLEN MORPHOLOGY OF RAPATEACEAE

SHERWIN CARLQUIST<sup>1</sup>

Claremont Graduate School, Claremont, California

#### INTRODUCTION

Several circumstances prompt the presentation of studies on pollen morphology of Rapateaceae at this time. First, recent explorations in the Guayana Highland region of northern South America have amassed excellent collections in this interesting monocotyledonous family. The family is restricted to South America with the exception of a monotypic genus in western tropical Africa (Maguire et al., 1958). Although there is no reason to believe that all new species in the family have been described, the remarkable collections of material certainly do furnish an extensive basis for pollen study which has not been available previously. Of great significance in this regard are the collections of Maguire and his associates at the New York Botanical Garden. Many of these collections included liquid-preserved portions. A second reason for presentation of pollen studies is the excellent condition in which pollen-bearing material of many species was preserved. Because the delicate nature of pollen grains of Rapateaceae, as described below, makes preparation of pollen-grain slides from dried material often unsatisfactory, liquid-preserved material is especially important. The collection of liquid-preserved material which Dr. Bassett Maguire has so kindly shared with me is unlikely to be matched in scope or quality, and makes mandatory the study of anatomical features, including pollen in this family. A third consideration in publication of palynological studies of Rapateaceae is the virtual absence of literature on morphology of rapateaceous pollens. As described later, the few descriptions of Erdtman (1952), which comprise the only literature on this topic at hand, contain inaccuracies. This results, in all likelihood, mostly from the fact that Erdtman was forced to work with dried materials. Without liquid-preserved materials, one cannot have a basis for understanding the shape or even many details of structure of these pollen grains. With preserved material, one can interpret, and allow for, the various degrees of artifact formation which inevitably result from any of the various ways of preparing dried material. Finally, Rapateaceae are an interesting family for palynological study because of the variety of pollen grains with respect to shape, size, morphology and fine structure, despite the relatively small size (16 genera; between 70 and 80 species) of the family. This variety can be compared with an up-to-date taxonomic system (Maguire et al., 1958) of the family, and can contribute to furthering taxonomic concepts. Moreover, the morphological diversity in rapateaceous pollen grains suggests stages and types of evolutionary patternings which require interpretation.

#### METHODS; NATURE OF POLLEN GRAINS

Pollen grains of Rapateaceae have an intine which is markedly thickened at apertural areas, as shown in the various photographs of fig. 1. This thickened intine area is also shown in drawings in fig. 9f, 11f, 13f, 14f, 16f, and 21f. It seems to be composed, by virtue of its staining and solubility reactions, of non-cellulosic anisotropic pectic compounds, as de-

<sup>&</sup>lt;sup>1</sup>This study has been aided by grants from the California Research Corporation and from the Research and Publication Fund, Claremont College.



Fig. 1. Photographs of sectioned pollen grains from liquid-preserved specimens.—a-b. Stegolepis sp., Steyermark & Wurdack 794. *a* represents a sectional equatorial view corresponding to the surface view shown for *S. squarrosa* in fig. 8a; likewise *b* corresponds to fig. 8c. Intine is comparatively thin, but shows with special prominence inside the aperture as a dark band (above in  $a_j$  near left in 3*b*. Shape



Fig. 2. Entire pollen grains, with long equatorial axis from left to right, to show aperture configurations; a-c from NaOH-treated material; d from liquid-preserved specimen.—a. *Stegolepis celiae*. Slightly overexpanded grain, showing gaping aperture; note that intine at apertural area has been dissolved. b. *Schoenocephalium cucullatum*, Maguire 41546. Somewhat shrunken grain, showing the trichotomosulcate apertural condition which is occasional in this genus.—c. *Spathanthus unilateralis*. Grains with forked aperture.—d. *Cephalostemon affinis*. Entire grain, showing the very wide apertural area, covered by linear or variously-shaped exine flakes. Nucleus of grain appears as a darker area, just left of center. —2a,  $\times$  1680; b,  $\times$  1000; c,  $\times$  1510; d,  $\times$  660.

of pollen grain nearly normal in *a*, slightly shrunken in *b*.—*c*–d. *Duckea squarrosa*, Maguire & Wurdack 34536. *c* is a sectional view corresponding to the polar surface view shown for *D*. *cyperaceoidea* in fig. 13a. Fig. 1d corresponds to fig. 13c. Note extremely thick intine (dark band) around equator of grain. Grain approximately normal in shape in *c*, shrunken in *d*.—*e*–f. *Rapatea* sp., Maguire 41540. The prominent intime which forms a circular band around the grain beneath the aperture is seen at right and left in *e*, and as a circle (entire dark ring) in *f*; *e* corresponds to surface view of *R*. *spruceana* in fig. 14b or c; *f* corresponds to fig. 14a.—All,  $\times$  1340.

scribed by Bailey (1960) in other angiosperms. As Bailey indicates, few reagents can preserve such non-resistant non-cellulosic materials. This is particularly critical in such Rapateaceae as Duckea, Cephalostemon, and Rapatea, where the only continuous layer connecting the two halves is the vulnerable intine which forms the wall layer over the zonal aperture. Even in those other genera where the aperture does not surround the grain, dissolution of the intine results in considerable distortion of the shape of pollen grains. All commonlyused reagents, such as acetolysis, strong hydroxide, etc., will dissolve this layer. Therefore, I availed myself wherever possible of Maguire's specimens collected in the living condition and fixed in an ethyl alcohol solution. This material was regarded as a reference point. Even in liquid-preserved material, some shrinkage does take place (e.g., fig. 1d), and judgment must be exercised in selecting for measurements, descriptions, and drawings those grains which may represent relatively unaltered conditions. Fixed material was sectioned and stained with a safranin-fast green combination according to the usual paraffin techniques. The safranin-fast green combination, although microchemically not specific, does differentiate the intine (green) from the exine (red) very clearly. Occasional preparations were treated with ruthenium red, following the suggestions of Bailey (1960). Sectioned material was of great help in interpreting the layers of the pollen grain. Probably only ultra-thin sections and electron microscopy can reveal with ultimate accuracy the nature of exine layers and the shape of lacunae within them. However, sectioned material was an indispensible complement to whole mounts, and a more accurate notion of exine structure was thereby gained. The writer attempted to correlate various appearances from all types of preparations, and by continued examination and re-examination, utilizing critical illumination, Erdtman's "L-O analysis" (Erdtman, 1952), and deep staining to bring out differences within the exine, has attempted to offer the best interpretations available with the light microscope.

Many of the collections utilized herein were not available as liquid-preserved material. Such specimens include all collections for which an herbarium other than the New York Botanical Garden herbarium is cited in Table 1, as well as some specimens from that institution. For dried specimens, a warm 0.5% NaOH solution was used. After expanding for one or two hours, material was washed, dehydrated in an ethyl alcohol series, stained in safranin, and mounted in Canada Balsam. This method, to be sure, often did dissolve intine, like other clearing agents. Grains with zonal apertures often parted into two halves. However, the relatively gentle clearing action did leave some grains nearly intact or did not appreciably dissolve the protoplast. For example, the spherical nature of grains of *Rapatea* could be demonstrated from the spherical shape of the protoplast, to which one or both halves of the exine could still be found attached. Although clearing agents were desirable to reveal the fine structure of the exine, which is resistant, some preparations gave little or no information about the true shape of the grain. Such preparations were not used in formulating Table 1.

Erdtman (1952) has evidently used acetolysis or some other clearing reaction to obtain his preparations of pollen grains of Rapateaceae. Interestingly enough, the two species which he illustrates, *Cephalostemon angustatus* and *Rapatea spectabilis*, both have zonal apertures, so that the two halves of the grains must have come apart in his preparations. Comparison of my figures to Erdtman's suggests that this is the case. As one instance, Erdtman's figures do not show exine flakes on the apertures, although he does mention such flakes as present in *Cephalostemon*. Such flakes were observed in all the genera of the present study. Moreover, apertural regions in *Cephalostemon* and *Rapatea* are wide (see fig. 14, 15, 16), not narrow, as in Erdtman's drawings.

Thus, Erdtman's figures must represent an attempt to reconstruct entire pollen grains in these two genera from dissociated halves. The writer has preparations which, like those Erdtman probably obtained, would suggest the shapes Erdtman has figured. Thus, for example, Erdtman figures *Rapatea spectabilis* grains as markedly equatorially flattened, suggesting a

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subdisciform shape. One can find such shapes as this (e.g., fig. 3e) in cleared preparations because if the intine and protoplast are dissolved, the two halves of the grain separate and tend to collapse from a cup-like form into a flattened pocket-like form. Although I cannot



Fig. 3. Surface view of pollen grains which show finer type of exine sculpturing.—a. Saxofridericia compressa, Maguire et al. 42180.—b. Stegolepis pauciflora.—c. Epiphyton micranthera.—d. Rapatea sp., Fernandez 2167, portion of exine from torn grain.—e. Rapatea spectabilis.—f. Ampbiphyllum rigidum. —g. Phelpsiella ptericaulis, Cowan & Wurdack 31352.—All photographs except d show a high focus of surface, so that cavities appear dark, muri light, except for d, in which the reverse is true, owing to a closer focus. Scale in upper left shows 10  $\mu$  division.

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FIGURE 4

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categorically deny that grains such as Erdtman figures might ever occur other than as an artifact, my fixed preparations clearly showed quite a different condition in *Rapatea*, as shown in fig. 1e-f, and fig. 14. My cleared preparations also showed that pocket-shaped exine halves were artificial in their shape.

This discussion of alteration of pollen-grain shape and even structure by various reagents is undertaken not because Erdtman's widely-circulated book may give readers an erroneous impression of rapateaceous pollens, but because insufficient emphasis has, in my opinion, been placed on the fact that morphological pollen studies are highly influenced by methods



Fig. 5. Saxofridericia compressa, Maguire, Wurdack & Bunting 37054.—a. Polar view.—b. Equatorial view, long axis.—c. Equatorial view, narrow axis.—d. "Paradermal" optical section of exine showing reticulum. This view, as in succeeding figures, shows subsurface pattern of the sculptured layer (sexine).—e. Optical section of pollen-grain wall showing, from left to right, intine (black line), nexine (unsculptured, stippled), and sexine (sculptured, stippled).—The 20  $\mu$  scale applies to views of entire grains. The 5  $\mu$  scale applies to views of pollen grain walls (d and e). The same scales are used in all drawings in this paper for these respective type of views.

of preparation. Although various reagents may reveal differentiation among layers by differrential solubility (Erdtman, 1960; Carlquist, 1960), such methods are inadvisable where the grain is severely damaged. In dealing with delicate grains, the least possible treatment seems to be best (e.g., Xyridaceae, Carlquist, 1960). One can also say that no single method of preparation is likely to reveal all the palynological data one may desire. Although Erdtman (1952, p. 9) gives a list of angiosperm families which are not resistant to acetolysis (and therefore, in all likelihood, many other commonly-used techniques), this list does not include Rapateaceae and Xyridaceae. These families should certainly be added.

Fig. 4. Surface view of pollen grains which show coarser types of exine sculpturing. Analysis of these shows that these prominent ridges overlie finer types of sculpture.—a. Monotrema xyridioides, Maguire et al. 34644.—b. Maschaloeephalus dinklagei.—c. Windsorina guianensis, Maguire et al. 32142.—d. Duckea cyperaceoidea, Maguire 37586.—e. Potarophytum riparium.—f. Cephalostemon gracile.—In fig. 4b and c, a high focus shows ridges as light, depressions between them as dark. In remainder, a lower focus shows the reverse. Scale at right indicates two 10  $\mu$  divisions.

One may well ask, however, how one can ascertain if a pollen grain of Rapateaceae is in a "normal" or "unaltered" condition. Fixed material seems to offer the best suggestions, although not without exceptions. Attention should be called to the fact that the aperture, covered by a pectic (and presumably somewhat hygrophilic) intine layer, is subject to desiccation. If desiccation occurred, what alterations in the grain shape would occur? A grain would probably become more elongated, parallel to the long axis of the sulcus, and narrower, according to the considerations of Wodehouse (1935: e.g., his comparative illustrations of Phoenix dactylifera, Pl. IV, fig. 5-6). The aperture would perhaps also shrink. In some preparations of rapateaceous grains I gained the impression that apertures could, in fact, shrink, bringing the exine flakes closer together and thus perhaps protecting the grain from further desiccation. The aperture, in a fresh and turgid grain, probably does not have closely-fitting flakes of exine, however, judging from fixed preparations in which even somewhat shrunken grains showed well-separated exine flakes on apertures (e.g., fig. 2d). Consequently, slightly bulging apertures are considered normal in grains, and are figured in this manner in the drawings. Needless to say, the only way to obtain a true picture of pollen-grain shape in this family would be to examine fresh material, and because of the remote areas in which most species grow, such examinations would be extremely difficult to make.

Although the present study is not cytological in scope, liquid-preserved material also served to reveal the fact that all fixed pollen grains at the shedding stage were uninucleate in this family.

The drawings are so organized as to provide comparable views, at the same scales of magnification, for a species from each genus. In only one genus, Rapatea, was enough distinction of one species from others found to warrant figuring more than a single species. For each species, a polar view (a) with aperture above (if other than zonisulculate) is shown. Two equatorial views, one showing the long axis (b), and one showing the grain viewed from the narrow axis, aperture at right (c), are shown for each species illustrated. In the exine-pattern drawings (rectangle), the nature of lacunae *within* the sculptured layer of the exine is shown. Irregularities in the surface of the exine are also suggested in some of these (e.g., fig. 16), as indicated in the legends for those particular drawings. The scales of magnification are the same in all drawings, and are shown in fig. 5. Likewise, photographs of exine patterns (fig. 3, 4) are all presented at a single magnification. These photographs are presented to show by photographic means some of the exine features which are analyzed in the drawings. In order to obtain greater depth of focus, exine photographs were made with a "high-dry" ( $\times$  40) objective, using a long bellows extension. The way in which high or close focus influences lightness or darkness of solid and lacunar portions of exine respectively is indicated in legends for these figures. No specimens are cited in photographic plates if only one collection of a particular species was studied. All documenting specimens are listed in Table 1. The writer felt that exine analysis by means of the sectional view, the parallel-to-surface view, and photographs were sufficient, and that successive drawings of various levels of focus within sexine would have been superfluous. Exine flakes are shown on drawings of entire grains by means of dense stippling, despite the fact that areas of exine adjacent to an aperture do not have such dense stippling (although they are just as thick, if not more so). Palynological terminology follows that of Erdtman (1952).

#### MATERIALS AND ACKNOWLEDGMENTS

Without the excellent material provided me by Dr. Bassett Maguire of the New York Botanical Garden, this study would not have been attempted. Sincere appreciation is expressed to Dr. Maguire both for this material and for his interest in my studies of Rapateaceae. Additional materials were provided from the U. S. National Herbarium, through



Fig. 6. *Phelpsiella ptericaulis*, Cowan & Wurdack 31352.—a. Polar view.—b. Equatorial view, long axis.—c. Equatorial view, narrow axis.—d. Reticulate pattern of exine.—e. Section of pollen-grain wall. —Scales for magnification given in fig. 5.

the kindness of Dr. William L. Stern, curator, Division of Woods, Smithsonian Institution. The location of specimens documenting this study is given by the abbreviations, following those of Lanjouw and Stafleu (1959), in Table 1.

Names of the taxa are in accordance with those of the latest treatment of the family (Maguire et al., 1958), and the reader may consult that account for details as to gross morphology and taxonomy of the genera with the exception of the larger genera *Rapatea* and *Stegolepis*. Dr. Maguire is expected to treat these two genera in forthcoming issues of



Fig. 7. Amphiphyllum rigidum, Steyermark 58249.—a. Polar view.—b. Equatorial view, long axis.—c. Equatorial view, narrow axis.—d. Reticulate pattern of exine.—e. Section of pollen-grain wall.—Scales for magnifications given in fig. 5.



Fig. 8. Stegolepis squarrosa, Maguire et al. 33033.—a. Polar view.—b. Equatorial view, long axis. c. Equatorial view, narrow axis.—d. Reticulate pattern of exine.—e. Section of pollen-grain wall.— Scales for magnifications given in fig. 5.

the Memoirs of the New York Botanical Garden, and names for collections cited here as *Rapatea* sp. and *Stegolepis* sp. will probably be given when those studies appear. The *Rapatea* figured in fig. 15 is seemingly to be proposed by Dr. Maguire as a new species, which may bear a name commemorating the collector.

The materials of the present study cover all of the known genera, and although only about half of the species in *Stegolepis* and *Rapatea* are represented, variation among species in these genera, as in other genera in Rapateaceae, does not appear to be so conspicuous that data on additional species in these two genera might greatly alter the picture presented herein.

Comparisons of pollen grains of Rapateaceae with those of other monocotyledons have been furthered by the examination of pollen slides furnished me by the California Research Corporation, La Habra, through the good offices of Dr. A. R. Loeblich, paleontologist of that organization.

#### MORPHOLOGY

Table 1 lists the specimens studied, and the dimensions of the grains. Arrangement of the table is alphabetical, but arrangement of drawings corresponds to groups of genera similar with respect to pollen morphology and follows, with some exceptions, the order of genera presented by Maguire et al. (1958).

Because grains of Rapateaceae are, with the exception of *Rapatea*, bilaterally symmetrical, three measurements are necessary. There is no pretense of statistical accuracy in these measurements, and some degree of estimation was required in a few cases. In all preparations, only a few grains showed what I would call a "true" shape and size, unaltered by shrinkage or chemical treatment. Thus, measurements are based on one or more grains in a more natural condition. Measurement of a large number of grains which show various degrees of distortion would only result in an average artifact, a procedure which seems patently inadvisable.

Measurements of Rapateaceae given by Erdtman (1952) have been included in Table 1. These may be distinguished from dimensions given by the writer by the fact that Erdtman's dimensions are placed in italics. RAPATEACEAE

#### SIZE

Variations in size are quite marked in rapateaceous pollen grains. Aside from inconstancy in dimensions within species, which evidently does exist to some degree, one can cite extremes in size. The large grains of *Cephalostemon* (fig. 16) contrast, for example, with the small grains of *Spathanthus* (fig. 17). The genera which possess elongate grains with a sulcus fusiform in outline show a rather small range in size: the length of the longer equatorial axis is between 30 and 45  $\mu$  in *Amphiphyllum* (fig. 7), *Phelpsiella* (fig. 6), *Kunhardtia* (fig. 9), *Saxofridericia* (fig. 5), and *Stegolepis* (fig. 8). The grains with elongate apertures, widened into germ pores at both ends, are predominantly larger in size; grains



Fig. 9. Kunhardtia rhodantha, Maguire & Maguire 35400.—a. Polar view.—b. Equatorial view, long axis.—c. Equatorial view, narrow axis.—d. Reticulate pattern of exine.—e. Section of pollen-grain wall.—f. Section of pollen-grain wall containing a transection of sulcus. The wide black area represents the thick intime associated with the aperture, on which flakes of exine are borne.—Scales for magnifications given in fig. 5.

of Maschalocephalus (fig. 21), Monotrema (fig. 18), Potarophytum (fig. 19), and Windsorina (fig. 20) all exceed 50  $\mu$  in length. Assessment of variation within genera is difficult because one cannot be sure how much dimensions may be influenced by maturity and methods of preparation. Nevertheless, most species of *Rapatea* have small grains (fig. 14), but one (fig. 15) has appreciably larger grains.

#### SHAPE

Shape of pollen grains may be discussed independently of apertural configurations. Thus, for example, both *Epiphyton* and *Rapatea* have subsphaeroidal grains, but apertures are quite different in the two genera.

In addition to similarities in size, similarities in shape unite the group of genera Saxofridericia (fig. 5), Phelpsiella (fig. 6), Amphiphyllum (fig. 7), Stegolepis (fig. 8; fig. 1 a-b), and Kunhardtia (fig. 9). As shown in these various figures, grains of these genera tend to have an oval outline in all three views, although the grains are prominently elongate

SPECIES	COLLECTION AND HERBARIUM	EQUATORIAL AXIS, LONG, $\mu$	EQUATORIAL AXIS, NARRO <b>W, µ</b>	POLAR AXIS, $\mu$
Amphiphyllum rigidum Gleason	Stevermark 58349 (NY)	37	15	24
Cephalostemon affinis Körnicke	Maguire et al. 41536 (NY)	96	66	66
Cephalostemon angustatus Malme	Malme 1710	85	40	40
Cephalostemon gracilis (Poep. & Endl.)	Ducke 11182 (NS)	78	45	43
R. Schomb.	Ducke 19430	96	45	38
Duckea cyperaceoidea (Ducke) Maguire	Maguire 37586 (NY)	58	46	43
	Maguire 35697 (NY)	38	20	26
Duckea flava (Link) Maguire	Maguire & Wurdack 34492 (NY)	56	43	59
· · · · · · · · · · · · · · · · · · ·	Maguire et al. 41660 (NY)	59	40	49
Duckea squarrosa (Willd. ex. Link) Maguire	Maguire & Wurdack 34536 (NY)	49	43	36
Epiphyton micranthera Maguire	Haught 5378 (US)	53	50	53
Guacamaya superba Maguire	Maguire & Wurdack 35619 (NY)	69	40	48
. , .	Maguire et al. 41724 (NY)	50	40	43
Kunhardtia rhodantha Maguire	Maguire & Maguire 35400 (NY)	46	33	33
Maschalocephalus dinklagei Gilg. &				
K. Schum.	J. T. Baldwin, Jr. 13051 (GH)	79	49	42
Monotrema aemulans Körnicke	Maguire et al. 41654 (NY)	53	33	33
Monotrema affine Maguire	Maguire et al. 41500 (NY)	53	33	36
Monotrema bracteatum Maguire	Maguire et al. 41547 (NY)	50	26	26
Monotrema xyridioides Gleason	Maguire et al. 34644 (NY)	63	34	40
-	Maguire et al. 41539 (NY)	56	36	40
Phelpsiella ptericaulis Maguire	Cowan & Wurdack 31352 (NY)	38	23	26
	Phelps & Hitchcock 518 (NY)	33	17	21
Potarophytum riparium Sandw.	Maguire & Fanshawe 23396 (NY)	69	40	40
Rapatea circasiana H. García-Barriga &	Schultes & Cabrera 19680 (US)	28	28	40
L. E. Mora	Schultes & Cabrera 14449 (US)	28	28	42
Rapatea elongata Schulze				
Rapatea maju H. García-Barriga &				
L. E. Mora	García-Barriga 14364 (US)	28	28	33
Rapatea paludosa Aubl.	Maguire et al. 41544 (NY)	35	35	41
Rapatea pycnocephala Seub.	Macedo 4022 (US)	30	30	35
Rapatea spectabilis Pilg.	Ferreyra 1175 (US)	28	28	33
	Klug 1683	20	35	40
Rapatea spruceana Körnicke	Maguire et al. 41848 (NY)	36	36	40
	Maguire et al. 41765 (NY)	33	33	36
Rapatea sp.	Fernández 2167 (US)	50	50	55
Rapatea sp.	Maguire 41540 (NY)	30	30	36

#### TABLE 1. Dimensions of pollen grains of Rapateaceae

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#### EQUATORIAL AXIS, NARROW, µ EQUATORIAL AXIS, LONG, $\mu$ POLAR AXIS, µ COLLECTION AND HERBARIUM SPECIES Maguire, Wurdack & Bunting Saxofridericia compressa Maguire 37054 (NY) 50 50 55 Maguire et al. 42180 (NY) 43 23 25 Saxofridericia inermis Ducke Maguire et al. 42624 (NY) 30 15 18 Saxofridericia regalis R. Schomb. Maguire 23301 (NY) 41 25 26 Stevermark 60209 38 Maguire, Wurdack & Bunting Saxofridericia spongiosa Maguire 37485 (NY) 43 32 34 Saxofridericia subcordata Körnicke Ducke 23634 27 14 19 Schoenocephalium coriaceum Maguire Maguire et al. 41455 (NY) 53 40 40 Schoenocephalium cucullatum Maguire Maguire et al. 41546 (NY) 56 42 43 Maguire et al. 41901 (NY) 48 42 43 Schoenocephalium teretifolium Maguire Maguire et al. 37560 (NY) 51 43 49 Maguire et al. 47812 (NY) 46 30 33 Spathanthus bicolor A. Ducke Schultes & Cabrera 19909 (US) 23 14 16 Spathanthus unilateralis (Rudge) Desv. Maguire 32140 (NY) 33 20 23 Krukoff 9124 37 26 16 Maguire et al. 37138 (NY) Stegolepis celiae Maguire 27 22 26 Maguire et al. 42115 (NY) 31 21 23 Maguire et al. 42333 (NY) 37 20 21 Stegolepis ferruginea Baker Maguire & Fanshawe 23320 (NY) 40 30 31 Stegolepis gleasoniana Steyermark Steyermark 58040 (US) 31 18 20 Stegolepis guianensis Kl. & Körnicke Maguire 33406 (US) 35 19 23 Stegolepis neblinae Maguire Maguire, Wurdack & Bunting 37159 (NY) 40 30 31 Stegolepis parvipetala Steyermark Stevermark 59514 (US) 29 17 22 Stegolepis pauciflora Gleason Steyermark 58330 (US) 36 24 22 Stegolepis ptaritepuiensis Stevermark Maguire 33303 (US) 38 24 26 Stegolepis pungens Gleason Maguire et al. 29660 (US) 30 18 20 Steyermark 58224 41 Stegolepis squarrosa Maguire Maguire et al. 33033 (NY) 41 24 26 Stegolepis sp. Steyermark & Wurdack 794 43 21 28 Windsorina guianensis Gleason Gleanson 272 (NY) 76 45 39 Maguire et al. 32142 (NY) 83 47 43

#### TABLE 1. Dimensions of pollen grains of Rapateaceae

parallel to the aperture. The narrow equatorial axis may exceed the polar axis. Some grains in these genera do not appear oval in outline, but have flattened sides (e.g., *Amphiphyllum*, fig. 7; *Kunhardtia*, fig. 9). More prominent flattening of the sides of the grains is probably related to shrinking of grains.

The relatively larger pollen grains of *Guacamaya* (fig. 10) and *Schoenocephalium* (fig. 11; fig. 2b) are distinctly oval, with no indication of flattening of sides. Grains of *Schoenocephalium* with trichotomosulcate apertures (fig. 2b) tend to be subsphaeroidal. *Epiphyton* (fig. 12) has very nearly sphaeroidal grains. Of the genera with zonisulculate apertures,



Fig. 10. *Guacamaya superba*, Maguire & Wurdack 35619.—a. Polar view.—b. Equatorial view, long axis.—c. Equatorial view, narrow axis.—d. Exine pattern, showing very small lacunae (scrobiculi).— e. Section of pollen-grain wall.—Scales for magnifications given in fig. 5.

only *Rapatea* (fig. 14, 15; fig. 1e-f) has grains clearly subsphaeroidal in shape. *Duckea* (fig. 13; fig. 1c-d) often has clearly oval grains, although some (see Table 1) tend to be subsphaeroidal. *Cephalostemon* grains (fig. 2d; fig. 16) are markedly elongate, with walls parallel to the long axis appearing flatter.

Grains of *Spathanthus* (fig. 2c; fig. 17) are oval, but not much longer than wide. They are more like grains of *Guacamaya* (to which genus *Spathanthus* is not closely related) in shape.

The similarities among the grains of genera with elongate apertures widened at either end are evident. Thus, *Monotrema* (fig. 18), *Potarophytum* (fig. 19), *Windsorina* (fig. 20) and *Maschalocephalus* (fig. 21) all have elongate ovoid grains. The likeness among the three latter genera is particularly marked.

#### APERTURES

Shape.—There seems little doubt that the single aperture (sulcus), fusiform in outline, is basic in Rapateaceae as it is elsewhere in the monocotyledons. This type of aperture occurs in more genera of the family than does any other type. Examples of this simple sulcus may be found in Saxofridericia (fig. 5), Phelpsiella (fig. 6), Amphiphyllum (fig. 7), Stegolepis (fig. 2a; fig. 8), Kunhardtia (fig. 9), Guacamaya (fig. 10), Schoenocephalium (fig. 11), and Epiphyton (fig. 12).



Fig. 11. Schoenocephalium cucullatum, Maguire et al.41546.—a. Polar view.—b. Equatorial view, long axis.—c. Equatorial view, narrow axis.—d. Exine pattern, showing very small lacunae.—e. Section of pollen-grain wall.—f. Section of pollen-grain wall containing a transection of the sulcus. Thick black portion is intine associated with aperture, on which there are flecks of exine, as seen in a-c.—Scales for magnification given in fig. 5.

Variations on this type include a greatly elongate fusiform sulcus, which may extend more than halfway around the grain, as in *Schoenocephalium* (fig. 11). The aperture may be somewhat rounded at each end, as in *Phelpsiella* (fig. 6). Another variation is the occurrence, in both species of *Schoenocephalium*, of trichotomosulcate apertures. Grains with these apertures (fig. 2b) are not mere abnormalities, but occur with some frequency in all preparations of pollen of this genus. The more common simple sulcus must be considered the basic type in this genus, however. The occurrence of both simple monosulcate and tricho-



Fig. 12. *Epiphyton micranthera*, Haught 5378.—a. Polar view.—b. Equatorial view, showing face view of aperture.—c. Equatorial view, showing side view of aperture.—d. Pattern of exine. Lightly-stippled parts represent depressions, darker portions ridges, although both areas contain lacunae.—e. Section of pollen-grain wall. Scales for magnification given in fig. 5.

tomosulcate grains in a genus or species is not unprecedented. Erdtman (1952), for example, reports both conditions in grains of *Jessenia bataua* (Palmae), and figures a trichotomosulcate condition for *Acanthorbiza mocinni*, also of that family, in which the trichotomosulcate condition is apparently characteristic. Judging from Cranwell's (1953) figures of *Collospermum* (Liliaceae) grains, both monosulcate and trichotomosulcate conditions can obtain in that genus.

When monosulcate grains of Rapateaceae are shrunken or collapsed, the simple fusiform sulcus tends to be nearly closed (fig. 3f).

One line of advancement from the monosulcate type is the extension of the furrow around the grain, producing a circular, or zonisulculate aperture. In the grain of *Duckea* pictured in fig. 13, the aperture is wider on one side than on the other. This condition, which is in fact common in *Duckea*, suggests that the attainment of the zonisulculate condition has, in fact, been recent, and that the face on which the sulcus is narrower represents the face distal from the original center of the monosulcate aperture. The intine associated with apertures in *Duckea* (fig. 1v–d) is equally prominent on both sides of the grain, however. Despite the differences in their shape, *Rapatea* (fig. 1e–f; fig. 14, 15) and *Cephalostemon* grains (fig. 2d; fig. 16) also have zonisulculate apertures. In fully turgid grains of both of



Fig. 13. *Duckea cyperaceoidea*, Maguire 37586.—a. Polar view.—b. Equatorial view, long axiso—c. Equatorial view, narrow axis.—d. Pattern of exine.—e. Section of pollen-grain wall.—f. Section of pollen-grain wall showing approximately half of the apertural zone in transection.—Scales of magnifications given in fig. 5.

these genera, apertural areas are probably rather wide (fig. 1e; 2d), although the aperture in *Cephalostemon* is certainly exceptionally wide.

A second line of advancement must certainly be said to be represented by the grains of *Spathanthus* (fig. 17). Although Erdtman (1952) reports grains of *Spathanthus unilateralis* as "1-sulcate", careful examination of grains of both species in this genus revealed that all have a second, identical sulcus, which occurs on the reverse side of the grain. In fact, the two faces of the grain are identical, and one cannot tell which is distal and which proximal. The sulci in *Spathanthus* grains tend to be fusiform in outline, but may be somewhat irregular in shape, as shown in fig. 17. They may even show abnomalities such as forking of the aperture (fig. 2c). Such irregularities seem to underlie the instability which might be associated with a bisulculate condition. A similar instability, paired with tendency to produce more than one sulcus, occurs in the monocot genus *Xyris* (Erdtman, 1952). Bisculculate grains have also been figured in a species of Amaryllidaceae, *Crinum americanum* (Erdtman, 1952), in which a monosulcate condition also occurs.

A third line of evolution is probably represented by the four genera in which the elongate sulcus widens at both ends, narrows in its central portion, and produces what are functionally germ pores at either end of the sulcus. This type of sulcus, which was not found by Erdtman in the family, occurs in *Monotrema* (fig. 18), *Potarophytum* (fig. 19), *Windsorina* (fig. 20) and *Maschalocephalus* (fig. 21). These genera also share such similarities as exine patterning and have been grouped by Maguire et al. (1958) as a tribe, Monotremeae.

This grouping was based on evidence other than the pollen, which Maguire did not include in his studies. This type of sulcus is apparently infrequent in monocots. It has, however, been reported in *Crinum americanum* by Erdtman (1952). Although a number of species of Amaryllidaceae and Bromeliaceae are bisulculate, they characteristically show two isolated sulculi which are not connected as a single sulcus. In the writer's pollen collection, slides of *Sabal exul* (Palmae) showed monosulcate and bisulculate grains as well as a few showing degrees of transition.

Associated Intine.—The fact that the intine widens prominently at the apertural area has been mentioned above, and is shown photographically in fig. 1, as well as in certain drawings (fig. 9f, 11f, 13f, 14f, 16f, and 21f). The thickened intine follows the outline of apertures very closely in all species. Thus, thickened intine is present only on one side of a



Fig. 14. *Rapatea spruceana*, Maguire et al. 41765.—a. Polar view.—b-c. Equatorial views. Because the grain is radially symmetrical, all equatorial views are identical.—d. Pattern of exine.—e. Section of pollen-grain wall.—f. Section of pollen-grain wall containing a transection of the apertural zone.— Scales of magnifications given in fig. 5.

grain which has a monosulcate condition (fig. 1a-b), but is present in a band around grains which are zonisulculate (fig. 1c-f). The thickness of this intine can be rather modest, as in *Stegolepis* (fig. 1a-b) or quite marked, as in *Cephalostemon* (fig. 16f). Because various methods of preparation tend to destroy non-cellulosic intine, relatively little literature clearly indicates its presence. A thick intine is characteristic of a family supposedly related to Rapateaceae, Xyridaceae. In this latter family, *Achlyphila, Abolboda* (inner portion of wall ?) and probably *Xyris* show such intine (Carlquist, 1960). Erdtman (1952) indicates the probability of thick intine in Musaceae, a fact confirmed by my preparations of *Strelitzia* (placed in Musaceae by Erdtman). The methods used by Wodehouse (1935) evidently did not alter intine condition appreciably, and he reports intine thickened beneath the aperture in a wide variety of monocot families, including Gramineae and Palmae. The figure of Wodehouse (1935, p. 84) of thick intine in *Potamogeton natans* is particularly clear.

Thickened intine associated with apertural areas is probably a fairly general phenomenon, and has been insufficiently appreciated by those dealing with acetolyzed or otherwise cleared grains. Attention is called to the fact that thickened intine may occur at apertures in gymnosperms (e.g., *Welwitschia*: Wodehouse, 1935) as well as primitive dicots (e.g., *Liriodendron:* Bailey, 1960) and advanced dicots (*Argyroxiphium*: Carlquist, 1959). *Exine Flakes.*—All of the Rapateaceae studied showed a tendency to have a coating of



Fig. 15. *Rapatea* sp., Fernández 2167.—a. Polar view.—b-c. Equatorial views. Because the grain is radially symmetrical, all equatorial views are identical.—d. Pattern of exine; lacunae are not merely depressions of exine, but are subsurface spaces.—e. Section of pollen-grain wall.—Scales of magnifications given in fig. 5.

scattered exine flakes over the apertures. This is shown in the various drawings and may be clearly seen in the photograph of *Cephalostemon affine* (fig. 2d). These exine flakes generally correspond in thickness to the nature of the exine wall in any particular species. Thus, they are thick in *Cephalostemon* (fig. 16f) and thin in *Rapatea* (fig. 14). In shape, exine flakes may be various. Basically, they are circular or elliptical, and they may appear to be aggregated into bar-like aggregations (fig. 2d). Finer patterning, such as lacunae (scrobiculi) within the exine flakes, suggests that they have homology to the sculptured layer (sexine). In the four genera with dual germ pores, *Monotrema, Potarophytum, Windsorina*, and *Maschalocephalus*, there is some tendency for the flakes to be less frequent or absent in the center of the germinal areas (cf. fig. 19–21).



FIGURE 16

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The presence of exine flakes over apertural areas is common in certain angiosperm families, including both dicots and monocots. In monocots, one may cite Alismataceae (Wodehouse, 1936), Restionaceae (Cranwell, 1953), Commelinaceae (Rowley, 1959; van Zinderen Bakker, 1953), Liliaceae (Cranwell, 1953; Erdtman, 1952), Iridaceae (Hyde and Adams, 1958), Cyperaceae (Cranwell, 1953), and in *Xyris* (unpublished), which belongs to a family supposedly related to Rapateaceae, Xyridaceae. Thus, this condition is undoubtedly quite widespread in monocots. In Rapateaceae, it may be a means of protecting



Fig. 17. Spathanthus unilateralis, Maguire 32140.—a. Polar view.—b-d. Equatorial views, long axis. Because an aperture is present on either face, these views look very similar.—c. Equatorial view, narrow axis.—e. Pattern of exine.—f. Section of pollen-grain wall.—Scales of magnifications given in fig. 5.

the rather wide, vulnerable apertures from desiccation. Thus, a broad band of intine can be exposed, although the surface of exposed intine would be cut down considerably by the presence of exine flakes. Also, contraction of the apertural area seems to bring the flakes closer together, forming an even more effective covering of the intine.

#### EXINE

In attempting to elucidate the nature of exine patterns, one must consider: (1), the nature of the unsculptured layer (nexine); (2), the basic nature of the sculptured layer (sexine); and (3), the variations in sculpturing which have taken place within the family, as well as other alterations in the sexine.

Nexine shows relatively little variation in Rapateaceae. In nearly all the genera, nexine is approximately half, or a little less, the total exine width. Exceptions to this include *Potarophytum* (fig. 19), *Windsorina* (fig. 20), and *Maschalocephalus* (fig. 21), where nexine is much less than half the exine width. In *Windsorina*, nexine is extremely narrow.

Fig. 16. *Cephalostemon affinis*, Maguire et al. 41536.—a. Polar view.—b. Polar view, long axis.—c. Equatorial view, narrow axis.—d. Pattern of exine; darker areas represent ridges, lightly-stippled areas depressions; both contain lacunae.—e. Section of pollen-grain wall.—f. Section of pollen-grain wall showing part of transection of apertural zone.—Scales of magnifications given in fig. 5.

The nature of sculpturing in exine was studied by observation of staining and nonstaining areas in deeply-stained exine, by observation of sections, and by "L-O analysis" (Erdtman, 1952). By means of these approaches, I reached the conclusion that the sculptured layer, or sexine, is composed of a solid phase in which small lacunae are located. In most cases, these lacunae do not appear to extend to the surface of the grain, but are closed in their outward extent by a surface film of exine. Such closure of these lacunae was not clearly observed in *Phelpsiella* (fig. 6). Lacunae in *Windsorina* (fig. 20) are absent, unless one could term the large pit-like depressions in sexine lacunae in the same sense as the tiny lacunae in other genera. These major sculpturing features seem more like major sculpturing in other genera, such as *Cephalostemon*. Closure of the tiny lacunae is undoubtedly a late event in pollen-wall formation, and therefore its absence in *Phelpsiella* is not of major im-



Fig. 18. *Monotrema aemulans*, Maguire et al. 41654.—a. Polar view.—b. Equatorial view, long axis. c. Equatorial view, narrow axis.—d. Pattern of exine.—e. Section of pollen-grain wall.—Scales for magnifications given in fig. 5.

portance. It would merely mean a dropping-out of terminal closure of these lacunae. Pollen grains of *Phelpsiella* did appear to be mature, however. With the exception of these two genera, then, the appearance of small lacunae (scrobiculi) did appear to be of universal appearance in the family. High focus of these scrobiculi shows them as dark spots against a light background, and deeper focus shows them light against a dark background ("O-L pattern" of Erdtman, 1952). The background in which the scrobiculi are embedded may be termed a reticulum, or muri.

If the sculptured portion of the exine were composed of a series of more or less united rods ("bacula") surrounding the lacunae, one would expect an "L-O pattern", and one would also expect to be able to see such rod-like units in other ways. In fact, careful analysis by all methods did not reveal the presence of such structures. The sexine, disregarding the scrobiculi, appears quite homogeneous and does not appear to be made up of tiny units. Thus, I was unable to confirm Erdtman's report of "clearly baculate" for *Cephalostemon*, in which both cleared walls and sectioned material were particularly convincing. In all other

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cases studied by Erdtman (1952), he reports an "O-L" pattern, which accords with the presence of the scrobiculi or foveolae, but does not indicate minute rod-like structures united into a reticulum. Personal demonstration of rapateaceous pollen grains to other palynologists, using phase microscopy as well as ordinary techniques has also failed to confirm presence of rod-like units. I am quite willing to concede that in many monocots, rod-like structures, whether "bacula" or "pila", do occur. Examination of about thirty species of Palmae, for example, suggests that a pilate condition may be basic to sexine formation in that entire family.

Supposing then, that the sexine is basically composed of scrobiculi embedded in homogeneous wall material, we may examine variations which occur with reference to this layer. First, these scrobiculi vary in size. Two genera, *Schoenocephalium* (fig. 11d-e; fig. 2b) and



Fig. 19. Potarophytum riparium, Maguire & Fanshawe 23396.—a. Polar view.—b. Equatorial view, long axis.—c. Equatorial view, narrow axis.—d. Pattern of exine.—e. Section of pollen-grain wall.— Scales for magnifications given in fig. 5.

*Guacamaya* (fig. 10d-e) have particularly small scrobiculi, only slightly above the limit of resolution of a light microscope. The genera with simple monosulcate apertures mostly have relatively even walls containing lacunae which are larger, and which therefore may be termed scrobiculi or foveolae, depending on their size. These are shown photographically for *Saxofridericia* (fig. 3a), *Stegolepis* (fig. 3b), *Rapatea spectabilis* (fig. 3e), *Amphiphyllum* (fig. 3f), and *Phelpsiella* (fig. 3g). They are shown in drawings of these genera, as well as in those of *Kunhardtia* (fig. 9) and *Spathanthus* (fig. 17).

Lacunae were found to be conspicuously larger in one species of *Rapatea* (fig. 3d; 15d-e). Likewise, large foveolae were observed in *Monotrema* (fig. 4a; 18) and *Maschalocephalus* (fig. 4b; 21). In *Maschalocephalus* curious reversions of the prevailing O-L pattern within these foveolae proved to be caused, as sections proved, by irregularities within the foveolae.

Pits and ridges within the foveolae (fig. 21e) cause such change in appearance with change in focus.

Grains of several of the genera of Rapateaceae were found to have scrobiculi, but also to have major patterns of sculpture imposed upon the surface. That is to say, there are both thick and thin areas of sexine, both of which contain scrobiculi. I have attempted to indicate this both in the sectional view and in the patterned view for *Epiphyton* (fig. 12), Duckea (fig. 13), and *Cephalostemon* (fig. 16). These are shown photographically in fig. 3c, 4d, and 4f, respectively. In *Epiphyton* and *Duckea*, the thick portions of the wall take the form of large reticulate ridges. There are similar ridges in *Monotrema* (fig. 4a; fig. 18), in which large foveolae are present instead of small scrobiculi. In *Cephalostemon*, the thick portions



Fig. 20. *Windsorina guianensis*, Maguire et al. 32143.—a. Polar view.—b. Equatorial view, long axis. c. Equatorial view, narrow axis.—d. Pattern of exine.—e. Section of pollen-grain wall.—Scales of magnifications given in fig. 5.

of the sexine are, in surface view, fusiform in shape and arranged parallel to the long axis of the grain.

In *Potarophytum* (fig. 4e; 19), scrobiculi were seen in the major ridge-like portions of the sexine, but no scrobiculi could be seen in the intervening spaces, which must (if lacking in sexine material) therefore be pit-like. Likewise, the sexine of *Windsorina* (fig. 4c; fig. 20) shows a series of ridges, evidently separated by pits which extend inward to the nexine; no scrobiculi could be observed in these ridges.

In many Rapateaceae, patterning of exine (i.e., ridges, scrobiculi) becomes finer adjacent to apertures. This can be seen, for example, in fig. 4c. Sexine is also often thinner near apertural areas. May 15, 1961]

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Evidently, if these observations are correct, a great deal of re-patterning of exine has occurred in Rapateaceae. Some of these distinctive patterns are obviously related to generic distinctions.



Fig. 21. Maschalocephalus dinklagei, J. T. Baldwin, Jr., 13051.—a. Polar view.—b. Equatorial view, long axis.—c. Equatorial view, narrow axis.—d. Pattern of exine; blank spaces are interpreted as actual pits, not lacunae within the exine.—e. Section of pollen-grain wall.—f. Small portion of aperture in sectional view, showing thickness of intine and appearance of exine flakes.—Scales of magnifications given in fig. 5.

#### TAXONOMIC AND EVOLUTIONARY CONCLUSIONS

The system of Maguire et al. (1958) for Rapateaceae arranges the genera within the following subdivisions:

Subfamily Saxofridericioideae

Tribe Saxofridericieae: Saxofridericia, Phelpsiella, Amphiphyllum, Stegolepis, Epiphyton.

Tribe Schoenocephalieae: Kunhardtia, Guacamaya, Schoenochephalium. Sub family Rapateoideae

Tribe Rapateeae: Rapatea, Duckea, Cephalostemon, Spathanthus.

Tribe Monotremeae: Monotrema, Potarphytum, Windsorina, Maschalocephalus.

Obviously, a totality of evidence concerning variations within Rapateaceae must be assembled before this or any other scheme of subdivisions within the family can ultimately satisfying. The evidence from anatomy of other portions of the plant should be extremely valuable, and cytology may also offer some information. However, similarities and differences which evidence from *pollen alone* suggests may be set up in the form of a key:

А.	Grains with one sulcus (or two identical sulci), fusiform in outline.
	B. Sulcus 1, about the length of the grain or shorter.
	C. Scrobiculi larger (ca5–1.5 $\mu$ in diameter).
	D. Grains sphaerical, containing thick areas which form a reticulum as seen in surface view
	DD. Grains oblong; wall relatively even, with- out markedly thick and thin areas
	CC. Scrobiculi smaller (less than $.3\mu$ in diameter); wall relatively even as seen in sectional view.
	D. Sulcus about as long as grainSchoenocephalium
	DD. Sulcus shorter than length of grainGuacamaya
	BB. Sulci 2, identical, parallel with long axis of grain and on opposite sides of grainSpathanthus
AA.	Grains zonisulculate
	B. Grains subsphaerical, wall about 1 $\mu$ in thickness, rela- tively even as seen in sectional view
	BB. Grains oblong, wall with thick areas which form a series of ridges.
	C. Ridges separate from each other, fusiform in outline, parallel with long axis of grain; grains more than 70 $\mu$ in length
	CC. Ridges forming a reticulum; grains less than 60 $\mu$ in length
AAA.	Grains with a single sulcus which is widened into a germ pore at each end and narrowed in the middle.
	B. Grains smaller (less than 65 $\mu$ in length)
	BB. Grains larger (more than 65 $\mu$ in length).
	C. Wall with both large pits and scrobiculi Potarophytum
	CC. Wall with large pits, scrobiculi not evidentWindsorina
	CCC. Wall containing subsurface foveolae, irregular in
	trema

Emphasis should be placed on the fact that the four main groups set up by Maguire— Saxofridericieae, Schoenocephalieae, Rapateeae, and Monotremeae, do emerge from this key as natural groups, with certain exceptions in their generic constitution. On account of the importance in aperture morphology in separating out the main groups, and also the significance of exine in this regard, one might tend to elevate Rapateeae and Monotremeae to subfamilial level. The distinctive apertures of Monotremeae do not seem to be more closely related to those of Rapateeae than to those of Saxofridericieae.

Pollen morphology tends to emphasize distinctions of certain genera, and on account of these distinctions such genera would be difficult to place in any larger group. Because each of the furrows in *Spathanthus* grains is like the single one in grains of genera of Saxofridericieae, and because exine pattern in this genus is like that of Saxofridericieae, the writer would tend to suggest that there is some affinity between *Spathanthus* and that group.

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*Spathanthus* is a highly distinctive plant in its gross morphology, as well as in its pollen grains, and would be difficult to place in any group containing more than one genus in addition to it.

*Kunhardtia*, on the other hand, shows more affinities to Saxofridericieae than to Schoenocephalieae in shape and size of grains and in the size of scrobiculi within the exine, characteristics in which the two other genera placed by Maguire in Schoenocephalieae, *Guacamaya* and *Schoenocephalium*, do agree.

*Epiphyton*, like *Spathanthus*, is distinctive in its large spherical grains, with ridged walls. Maguire and his collaborators (1958) emphasize the epiphytic habit and trans-Andean (Panama and Colombia) distribution of *Epiphyton* as unique features within the family. Palynology tends to enforce the isolated position of this genus.

The sulcus morphology, shape, and exine characteristics of grains of Saxofridericieae seem to be less specialized than do these features in the three other subtribes, and thus Saxofridericieae also resemble generalized monocot pollen-grain characteristics more closely. Consequently, grains of the tribes other than Saxofridericieae, at least Rapateeae and Monotremeae, seem clearly advanced, and these two tribes probably represent independent lines of evolution from the basic type. This would agree with the phylogeny implied in the arrangement of the genera by Maguire et al. (1958).

The necessity of correlating evidence from other studies, particularly anatomy, cannot be too strongly emphasized. The writer hopes to contribute such additional evidence in future papers, and combine it with material already at hand in pollen morphology and gross morphology of the family.

With regard to what evidence pollen morphology offers concerning relationships of Rapateaceae, one can mention an affinity with the genus Xyris. Although I have studied pollen of only a few species of Xyris, similar scrobiculi (furnishing a similar O-L pattern), and similar monosulcate aperture with exine flakes (despite curious variations in sulcus morphology) may be found in Xyris. The closeness of Xyris pollens to those of Rapateaceae, in fact, may be more compelling than similarities between Xyris pollen and that of the other xyridaceous genera *Abolboda*, *Orectanthe*, and *Achlyphila*. Further palynological and anatomical studies of Xyris are needed to see if that genus is, in fact, related to Rapateaceae, and whether or not the other three genera of Xyridaceae deserve segregation as a separate family (already proposed), Abolbodaceae.

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