POLLEN STRUCTURE AND THE SYSTEMATICS OF THE NEOTROPICAL GESNERIACEAE

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The systematic study of the neotropical Gesneriaceae has increased greatly in the past decade, and as a result, a new system of classification has been proposed for the subfamily Gesnerioideae. The recent work of Wiehler (1971, 1973a, b, 1975a-g, 1976, 1977) has led to a redefinition of a number of genera and tribes of the neotropical gesneriads. Wiehler (1977) divides the neotropical gesneriads into three subfamilies: the exclusively neotropical Gesnerioideae, the austral Coroantheroideae with three genera in southern Chile, and the predominantly paleotropical Cyrtandroideae with one species found from Mexico to Ecuador and Venezuela. He further divides the neotropical Gesnerioideae into five tribes: Gesnerieae with one genus, Gloxinieae with 24 genera, Episcieae with 21 genera, Napeantheae with one genus, and Beslerieae with 7 genera. Skog (1976) recognized three genera in his recent treatment of the tribe Gesnerieae.

Wiehler (1977) makes the suggestion that a number of the genera of the Gesnerioideae were based on superficial characters, especially on characters that are concerned with the pollination biology of the species of a given genus. He suggests that certain corolla types are adapted to certain types of pollination systems, and that a number of genera as previously recognized are not natural genera, but are genera based on recognition of pollinator syndromes. In his new classification of the tribes and genera of the Gesnerioideae, Wiehler uses a number of diverse characters to support his scheme. They range from vegetative to reproductive, from hybrid viability to chromosome number, from fruit characters to stomatal apparatus. As with any new system of classification, his has not met with universal acceptance (Morley, 1976). The fact that pollen structure was not used in his classification (Wiehler, pers. comm.) prompted me to examine the pollen of several species of the Gesnerioideae to try to determine if pollen characters might be of use in either supporting or refuting his new system of classification.

As far as I can determine, no comprehensive survey of pollen structure in the Gesnerioideae, nor in the Gesneriaceae for that matter, has been published. Erdtman (1966, but based on his 1952 work) had examined only "about 20 species from 17 genera." Skog (1976) examined 27 examples from the tribe Gesnerieae and illustrated 19 taxa. He concluded that the pollen of the Gesnerieae is not very diverse, although there are some variations in surface features. Skog does not give any details of how the pollen he examined was prepared, but it is obvious from his photographs that some distortion of the pollen grains occurred either in the coating process or in the vacuum chamber of the scanning electron microscope. My own work with orchid pollen (Williams and Broome, 1976; Williams, unpublished) and the recent work of Lynch and Webster (1975) led me to the idea that careful treatment of gesneriad pollen was required to obtain useful results. The collapsed appearance of the pollen grains in Skog's work makes it difficult to observe portions of the grain. I have found the technique outlined below to give better resolution of the features of the pollen grains, as well as a more natural appearance.

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This paper reports on very preliminary results dealing with only 30 species of neotropical gesneriads of the subfamily Gesnerioideae. A new technique for the preparation of gesneriad pollen for observation with the scanning electron microscope is outlined. On the basis of these results it appears that pollen structure will be of immense importance in the systematics of the neotropical Gesnerioideae. Although these results are based mainly on the examination of two tribes of the Gesnerioideae, the Gloxinieae and the Episcieae, they suggest that an additional look at the pollen of the Gesnerieae may be in order, and that pollen structure may be quite useful in aiding in the delimitation of genera as well as in helping to understand the relationships of various genera within the five tribes and the relationships among the tribes themselves.

MATERIALS AND METHODS

Fresh pollen was collected from living flowers in the collection at the Marie Selby Botanical Gardens in Sarasota, Florida. The anthers were snipped from freshly opened flowers and stored in 70% ethyl alcohol until time was available for study. All pollen was acetolyzed following a modified acetolysis procedure as described below. Pollen was centrifuged in the 70% EtOH, then transferred to 5% KOH. These centrifuge tubes were placed in a 90°C water bath for 10 minutes, allowed to cool slightly, and poured through a fine mesh wire screen to remove the larger particles of debris. The pollen was centrifuged for 2-3 minutes in a clinical centrifuge, decanted, washed twice with distilled water with centrifuging, then washed twice with glacial acetic acid. Freshly prepared acetolysis mixture of one part concentrated sulfuric acid and nine parts acetic anhydride was poured into the tubes, and they were then kept in a water bath at 100°C for approximately five minutes. After slightly cooling, centrifuging, and decanting, the pollen was washed again with glacial acetic acid, centrifuged, washed twice with distilled water, and then transferred to 70% EtOH for storage.

Two different treatments were tried with acetolyzed pollen for examination with the scanning electron microscope. The first treatment involved critical point drying of the material. This procedure involved transferring the material from 70% EtOH through a graded series of alcohol changes (with centrifugation) into absolute ethyl alcohol, then into a graded series of alcohol:amyl acetate (100% EtOH, 3:1, 1:1, 1:3, 100% amyl acetate). The pollen was then placed into small tissue capsules (EM tissue processing capsules), and the capsules placed in a critical point drying apparatus. The amyl acetate was replaced with carbon dioxide, and what little pollen remained was mounted on the SEM stub. Pollen prepared in this manner was in good expanded shape for examination, but a great deal of the material appears to be lost in the process. In addition, it is sometimes difficult to clean the tissue processing capsules for re-use.

A second procedure was tried which gave better results with little loss of material. Pollen was treated as described above through the stages into 100% amyl acetate. Scanning electron microscope stubs were prepared by placing a small piece of double-sided sticky tape on the top of the stub, and then placing a 13 mm round glass cover slip on the tape. A small drop of the pollen was then placed on the coverslip and allowed to air dry (while kept under a cover to prevent contamination). One aspect of this treatment is that too much pollen is detrimental in that it prevents the grains from spreading out on the cover slip, thus hindering a good look at several views of the grains

The SEM stubs prepared in this manner are then given the usual gold-palladium coating and examined with the SEM. One advantage of this method is that the cover slip can be teased off the stub with a little solvent (chloroform, acetone, etc.) and inverted and mounted in any of several mounting media on regular glass slides for a permanent record. In addition, pollen taken directly from the 100% amyl acetate may be dried onto a glass microscope slide (under a cover) and a cover slip mounted with a medium such as Euparal.

A comparison of unacetolyzed and acetolyzed material indicated that acetolysis is usually necessary for comparative work. In addition, drying the pollen onto the SEM stub directly out of 70% EtOH usually did not give acceptable results.

Voucher slides were prepared as above and are deposited at FSU. Vouchers of the plant material used are at SEL. A list of localities and collection data is available on request. The species studied are listed in Table 1.

The purpose of this paper is to provide a brief survey of the Gesnerioideae (the main group of neotropical Gesneriaceae) in order to determine the usefulness of pollen structure in the systematics of this subfamily. Detailed descriptions and measurements of the pollen grains will be given in a later paper when I have finished a more comprehensive survey of approximately 200 species in this subfamily.

RESULTS AND OBSERVATIONS

The diversity of pollen types found in this survey can be seen in Figures 1-57. The pollen grains of the Gloxinieae are fairly uniform. They are generally isopolor; tricolpate-tricolporate, with three mesocolpia, two apocolpia; mainly prolate to prolate spheroidal; sexine variously reticulate, the reticulations often reduced or closed along edges of mesocolpia. The main differences seem to be in the degree of reticulation of the sexine, the size of the lumina of the sexine, and whether or not the edges of the mesocolpia are reticulate or solid. In the non-mesocolpial areas the foot layer appears to be non-baculate or smooth, although *Gloxinia perennis* appears to have a slightly verrucate foot layer (Figure 1). There is some difference in the polar views of the grains (Figures 1-4, 6, 10), but it is not yet clear if these differences are real differences or artifacts of the method of preparation.

One representative each of the Napeantheae (Figure 11) and the Beslerieae (Figure 12) are shown for comparison. The pollen grains of both of these species are similar to the pollen grains of the Gloxinieae in having isopolar, reticulate grains. The mesocolpia of these two species are not so wide as those of most of the Gloxinieae, nor do the mesocolpia extend quite so far into the polar areas of the grains.

The Episcieae showed the greatest diversity in shape, size, and ornamentation of the pollen grains (Figures 13-57). Some of the genera, such as *Alsobia* and *Rufodorsia* (Figures 13-21) have grains not unlike those found in representatives of the Gloxinieae, Napeantheae, and Beslerieae. *Alsobia* and *Rufodorsia* do differ from genera of the other tribes in having definitely baculate foot layer in the luminal areas (Figure 21). Some luminal baculi are also found in *Episcia lilacina* (Figure 24), although the foot layer may actually be more verrucate than baculate in this species. *Episcia cupreata* also appears to have a foot layer that is at least minutely verrucate (Figure 28). The two species of *Episcia* and other genera of the Episcieae studied begin to show more differences from the other three tribes surveyed. Within *Episcia* there are marked differences in the two species studied (Figure 22-25, 28).

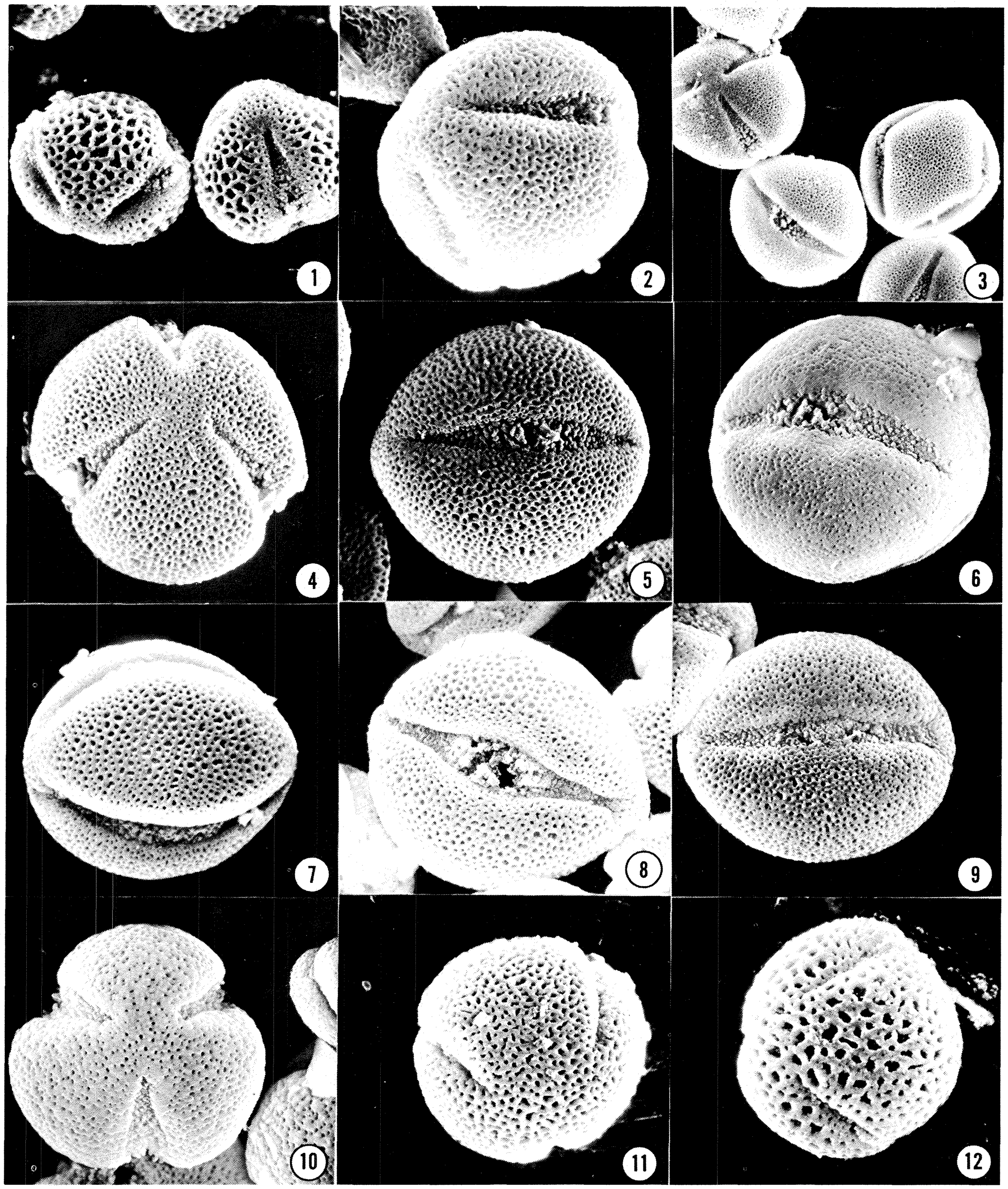

Plate 1

Figures 1-12. Representative examples of pollen of the Gloxinieae, Napeantheae, and Beslerieae. 1. *Gloxinia perennis*, polar and more or less equatorial views, × 1450. 2. *Bellonia aspera*, polar-equatorial view, × 3650. 3. *Sinningia canescens*, polar and equatorial views, × 930. 4. *Moussonia elegans*, polar view, × 1880. 5. *Moussonia elegans*, equatorial view, × 2000. 6. *Kohleria spicata*, equatorial view, × 1900. 7. *Kohleria digitaliflora*, equatorial view, × 1563. 8. *Kohleria digitaliflora*, equatorial view, × 1610. 9. *Kohleria allenii*, equatorial view, × 1450. 10. *Kohleria allenii*, polar view, × 1700. 11. *Napeanthus costaricensis*, polar view, × 2300. 12. *Gasteranthus acropodus*, polar-equatorial view, × 2325.

The sizes of the mesocolpia are quite different, with the mesocolpia of *E. cupreata* greatly reduced (Figure 28). Compare the polar views of *E. lilacina* and *E. cupreata* in Figures 22 and 25, for example, as well as the type and degree of reticulation of the sexine. In the species of *Nautilocalyx*, *Drymonia*, and *Codonanthe* studied, the reticulate sexine is extremely fine with very small lumina. In *Nautilocalyx porphyrotrichus* (Figure 26, 29) and *Drymonia serrulata* (Figures 27, 30) the mesocolpia are more rounded towards the polar ends of the grains, whereas in *D. killipii* (Figure 33) the mesocolpia are definitely angular at the poles. *Codonanthe luteola* (Figures 34-35) also has a very finely reticulate sexine. The grains of *Codonanthe luteola* are more oblate to oblate spheroidal than prolate, and the mesocolpia are greatly reduced in length. In addition, there is no sharp delimitation of the mesocolpia from the surrounding sexine (Figure 35). *Cobananthus calochlamys* (Figures 31-32) has an almost pertectate appearance of the sexine.

In the columneoid complex of genera composed of *Bucinella*, *Columnea*, *Dalbergaria*, *Pentadenia*, and *Trichantha* I found the greatest diversity of pollen types (Figures 36-57). The pollen grains of the three species of *Columnea* (Figures 36-39) examined are extremely different from the grains of *Dalbergaria*, *Bucinella*, *Pentadenia*, and *Trichantha* (Figures 40-57). *Columnea* (Figures 36-39) has prolate grains, whereas *Dalbergaria* has prolate spheroidal grains (Figures 40-45). *Pentadenia* (Figures 46-47, 49-50) and some species of *Trichantha* (Figures 48, 51-52, 55) have oblate spheroidal grains, while the two species of *Bucinella* have definitely oblate grains (Figures 53-54, 56-57).

Not only the general shape of the grains, but also the type and degree of reticulation of the sexine varies from species to species in the *Columnea* complex (sensu lato). Also, the size, shape, and ornamentation of the mesocolpia vary among the various species of the *Columnea* alliance. *Columnea* (sensu stricto) has grains that are definitely prolate, and the sexine (or tectum) is minutely pitted, almost pertectate in the case of *Columnea gloriosa* (Figures 36, 39). There is no noticeable differentiation of the sexine adjacent to the mesocolpia in *Columnea;* the same holds true for several other species of *Columnea* examined but not illustrated.

The pollen grains of *Dalbergaria puyana* (Figures 40-43) have a very reticulate sexine with a very smooth foot layer. The portions of the sexine adjacent to the mesocolpia are thickened and appear tectate. In addition, the polar areas are also tectate to slightly pertectate and appear very different from the reticulate areas between the mesocolpia. The columellae are very short and form an almost continuous layer. *Dalbergaria aureonitens* (Figures 44-45) has pollen grains that are quite distinct from *D. puyana.* The pollen grains of *D. aureonitens* are more flattened, the lumina of the sexine are more rounded, the sexine is reticulate with small perforations in the surface, the foot layer is slightly verrucate, the columellae are extremely short, and the mesocolpia are very short. The polar areas are not tectate, but are pertectate with fairly large openings. In polar view the grains are distinctly triangular in shape.

Pentadenia spathulata (Figures 46, 49), *P. zapotalana* (Figures 47, 50), *Trichantha dissimilis* (Figures 48, 51), and *T. filifera* (Figures 52, 55) resemble *Dalbergaria aureonitens* in the shape and ornamentation of the pollen grains. The mesocolpia are reduced in length; the polar areas are pertectate to reticulate, rather than tectate; the columellae are reduced in height and not readily apparent; and the sexine adjacent to the mesocolpia is usually

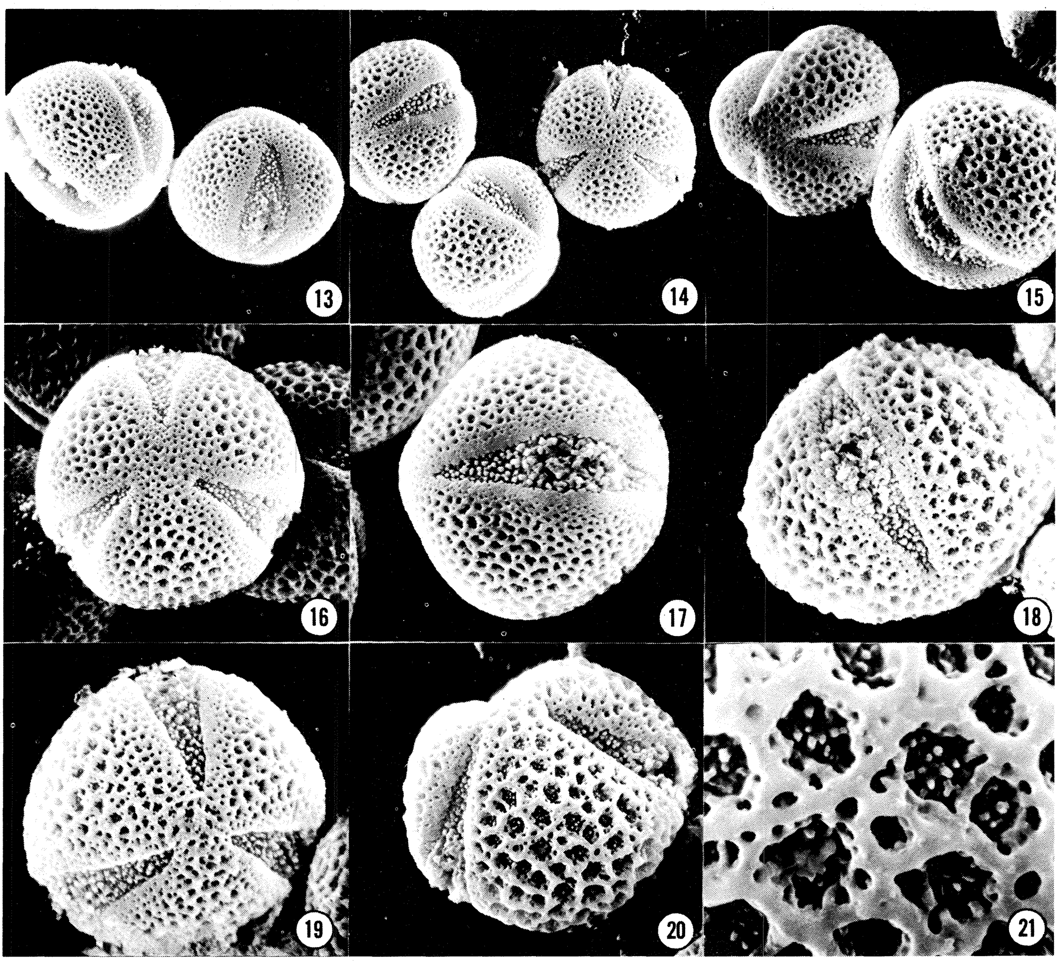

Plate 2

Figures 13-21. Representative examples of pollen of the Episcieae. 13. *Alsobia dianthiflora*, equatorial and equatorial-polar views, × 688. 14. *Alsobia punctata*, polar and polar-equatorial views, × 800. 15. *Alsobia punctata*, polar and equatorial views, × 975. 16. *Alsobia punctata*, polar view, × 1350. 17. *Alsobia punctata*, equatorial view, × 1375. 18. *Rufodorsia major*, equatorial view, × 1713. 19. *Rufodorsia major*, polar view, × 1625. 20. *Rufodorsia major*, polar-equatorial view, × 1593. 21. *Rufodorsia major*, close up showing baculate foot layer, × 6500.

thickened tectate. The foot layer in these species of *Pentadenia* and *Trichantha* appears smooth. The minute pores in the tectum seen in *D. aureonitens* around the mesocolpia (Figure 45) are also found in *Trichantha dissimilis* (Figures 48, 51) and *T. filifera* (Figures 52, 55). These small openings are found to a lesser degree in *Pentadenia zapotalana* (Figure 50). The grains of these species of *Pentadenia* and *Trichantha* are more oblate than prolate, and have a distinctly triangular shape in polar view (Figures 46-49).

Bucinella nariniana (Figures 53,56) and *B. paramicola* (Figures 54, 57) have the most distinctive pollen grains of those I examined. The grains are definitely oblate and triangular in polar view. *Bucinella nariniana* has a reticulate sexine, small or short columellae, a smooth foot layer, very short and reduced mesocolpia, and slight thickenings of the sexine adjacent to the mesocolpia. *Bucinella paramicola* has a tectate to slightly pertectate sexine, reduced mesocolpia, and apparent thickenings of the sexine adjacent to the mesocolpia.

In many species examined in this survey, an apparent pore was found in the mesocolpial region (Figures 3, 5-6, 8-9, 13-20, 22, 24, 26, 28, 31-34, 36-42, 45, 50). Although such pores were present in the majority of the pollen grains examined, it is possible that these pores are artifacts.

DISCUSSION

Pollen structure has long been used in taxonomic and systematic work, and it is not necessary here to give a detailed review of the literature on the use of pollen in modern systematics. An excellent review of the subject can be found in the recent book by Ferguson and Muller (1976). The work reported here provides evidence that the neotropical Gesnerioideae contain several divergent types of pollen, and that this diversity of pollen types will be of value in establishing and delimiting genera and possibly higher taxonomic groups in the Gesnerioideae. It is possible that within certain groups pollen structure will be more important than in other groups. In addition to the taxonomic use of pollen, the relationship of pollen type to pollinator type should be mentioned. This last aspect will be discussed first.

Taylor and Levin (1975) conducted an extensive survey of pollen in the Polemoniaceae and found that there was no apparent relationship between the structure or sculpturing of the pollen grains and the type of pollinator. They found that species thought to be reasonably closely related, but which differed in the type of pollinator (for example, bat pollination versus hawkmoth pollination), had similar pollen grains. In addition, they failed to find supporting evidence that pollen structure and environmental factors were related.

Within the Gesnerioideae there also appears to be a lack of correlation between pollen structure and type of pollinator, as well as a great deal of diversity of pollen types in groups with the same type of pollinator. Within the *Columnea* alliance, for example, all species studied are probably hummingbird pollinated, but there is a great deal of diversity between *Columnea* and the other genera, such as *Bucinella*, *Pentadenia*, *Dalbergaria*, and *Trichantha* (Figures 36-57). Since pollen structure is thought to be a rather conservative feature, it is probable that the pollen diversity represents a good indication of relationship, and that corolla shape and color represent adaptations to or modificiations for hummingbird pollination. We hope to be able to elaborate on this subject when the more extensive survey of the subfamily is completed.

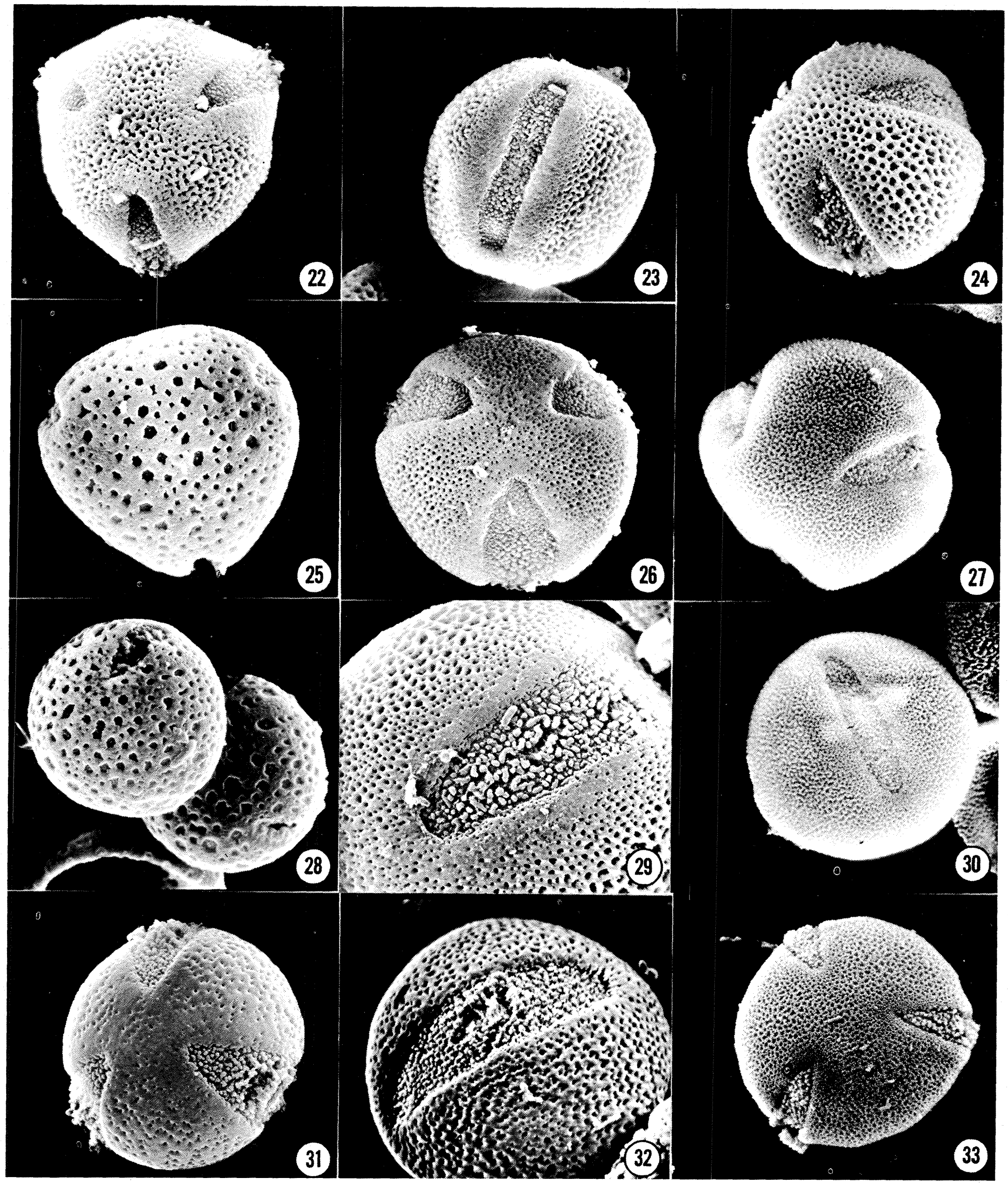

Plate 3

Figures 22-33. Representative examples of pollen of the Episcieae. 22. *Episcia lilacina*, polar view, × 1350. 23. *Episcia lilacina*, equatorial view, × 1350. 24. *Episcia lilacina*, polar-equatorial view, × 1015. Note the variation in sculpturing in these three grains, part of which is due to the angle of the photograph. 25. *Episcia cupreata*, polar view, × 1063. 26. *Nautilocalyx porphyrotrichus*, polar view, × 1088. 27. *Drymonia serrulata*, polar view, × 1300. 28. *Episcia cupreata*, polar-equatorial view, × 883. 29. *Nautilocalyx porphyrotrichus*, close up of mesocolpial region near the polar area, × 1813. 30. *Drymonia serrulata*, equatorial view, × 1300. 31. *Cobananthus calochlamys*, polar view, × 1088. 32. *Cobananthus calochlamys*, equatorial view, × 1450. 33. *Drymonia killipii*, polar view, × 1000.

The systematic value of pollen structure apparently varies from group to group. Within the Gloxinieae the length of the mesocolpia, the type of reticulation of the sexine, and the degree of thickening around the mesocolpia appear to be of taxonomic use at the specific level, but the sample size used was not large enough to determine if definite differences exist at the generic level within the Gloxinieae.

Many features of the pollen in the Episcieae seem to be of use at the specific and generic levels, as well as among some groups above the generic level. *Alsobia* and *Rufodorsia* are similar in having a baculate or verrucate foot layer. *Drymonia* and *Codonanthe* are similar in having extremely fine, closely spaced reticulations of the sexine and in having moderately to greatly reduced mesocolpia. *Columnea* stands out from all other genera examined in having rather oblong pollen with a pertectate sexine, and differs from the *Bucinella*, *Dalbergaria*, *Pentadenia*, *Trichantha* complex in having little differentiation around the mesocolpia. The grains of the species of *Columnea* examined are definitely different from those found in *Bucinella*, *Dalbergaria*, *Pentadenia*, and *Trichantha.* At least on the basis of this sample, *Columnea* seems adequately distinct to be separated from *Bucinella* or *Dalbergaria*, *Pentadenia*, and *Trichantha.*

The group of genera composed of *Dalbergaria*, *Pentadenia*, and *Trichantha* seem to be closely related in the structure of the pollen. At least two distinct trends appear in the pollen of these genera. One trend is from more or less rounded, prolate spheroidal grains to distinctly oblate, triangular grains. The second trend seems to be from grains having a reticulate sexine to those having an almost complete tectum. Although at this time it is not clear in which direction either of these trends evolved, I would postuate that those species with oblate grains with reduced mesocolpia are derived from species with prolate or prolate spheroidal grains. In addition, I would postulate that the tectate type of grain found in *Bucinella paramicola* is probably a derived condition from something resembling the reticulate pattern found in *B. nariniana.* In both of these cases much more work will need to be done to provide support or refutation of these hypotheses.

ACKNOWLEDGEMENTS

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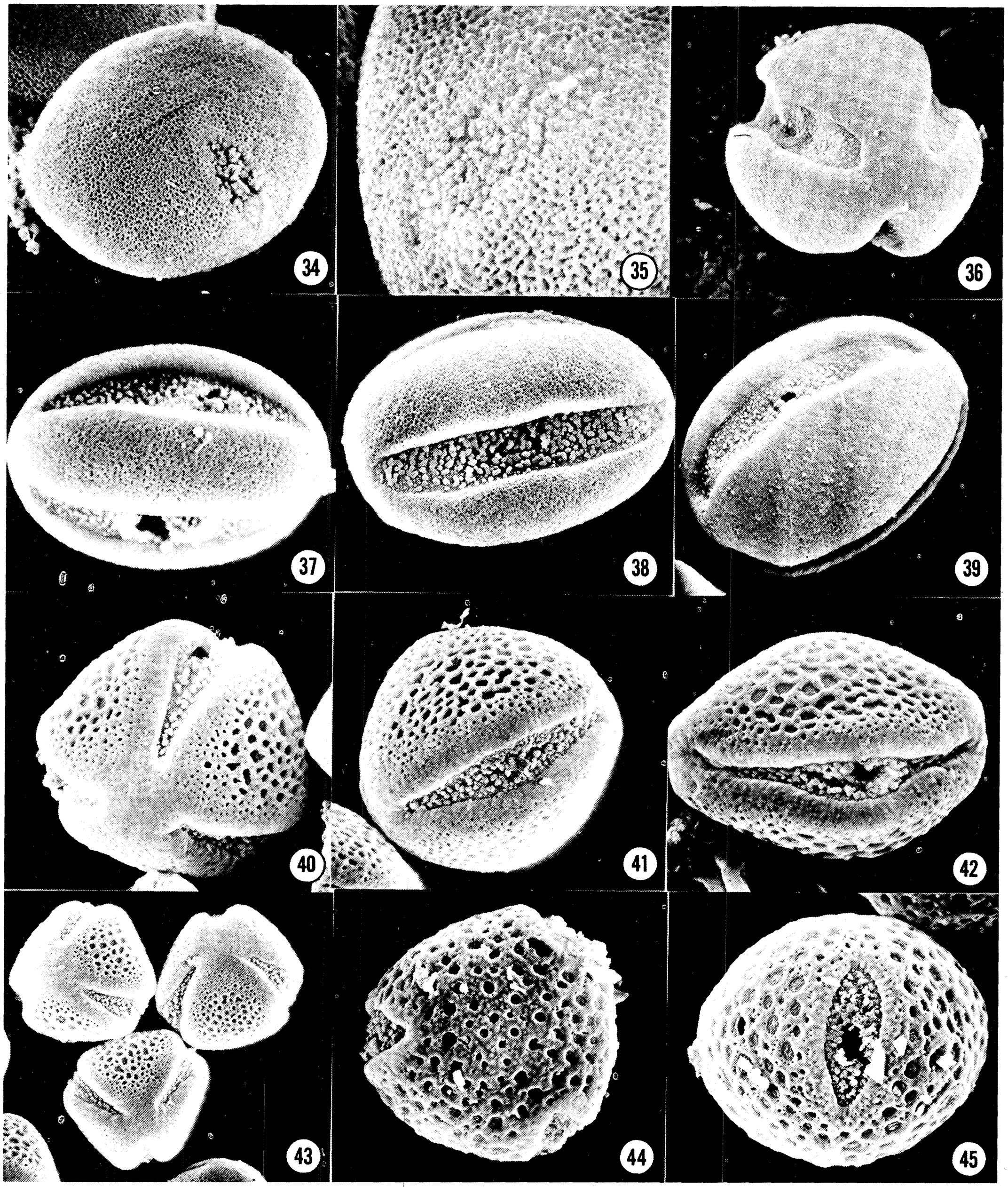

Plate 4

Figures 34-45. Representative examples of pollen of the Episcieae. 34. *Codonanthe luteola*, equatorial-polar view, X 800. 35. *Codonanthe luteola*, close up of the mesocolpial area, X 1830. 36. *Columnea gloriosa*, polar view, X 1000. 37. *Columnea maculata*, equatorial view, X 1013. 38. *Columnea nicaraguensis*, equatorial view, X 1050. 30. *Columnea gloriosa*, equatorial view, X 1013. 40. *Dalbergaria puyana*, polar view, X 1300. 41. *Dalbergaria puyana*, equatorial view, X 1213. 42. *Dalbergaria puyana*, equatorial view, X 1300. 43. *Dalbergaria puyana*, polar and polar-equatorial views, X 675. 44. *Dalbergaria aureonitens*, polar view, X 1033. 45. *Dalbergaria aureonitens*, equatorial view, X 1088.

TABLE 1: SPECIES OF GESNERIOIDEAE EXAMINED IN THIS SURVEY

SPECIES	GREENHOUSE ACCESSION NUMBER (SEL)	ORIGIN
	Tribe Gloxinieae Fritsch	
Bellonia aspera L.	G-1032	Hispaniola
Gloxinia perennis (L.) Fritsch	W-2070	Pachitea, Peru
Kohleria allenii Standley & L. O. Williams	G-1317	Puntarenas, Costa Rica
Kohleria digitaliflora (Linden & André) Fritsch	W-1727	Cauca, Colombia
Kohleria spicta (Kunth) Oersted	G-331	Cartago, Costa Rica
Moussonia elegans Decaisne	G-724	Oaxaca, Mexico
Sinningia canescens (Mart.) Wiehler	W-1985a	hort.
	Tribe Napeantheae Wiehler	
Napeanthus costaricensis Wiehler	W-1701	San José, Costa Rica
	Tribe Beslerieae Bartling & Wendland	
Gasteranthus acropodus (Donn. Smith) Wiehler	W-2164	Bocas del Toro, Panamá
	Tribe Episcieae Endlicher	
Alsobia dianthiflora (Moore & Wilson) Wiehler	G-111	Guerrero, Mexico
Alsobia punctata (Lindl.) Hanst.	G-722	Oaxaca, Mexico
Bucinella nariniana Wiehler	W-1642	Nariño, Colombia
Bucinella paramicola Wiehler	W-1634	Nariño, Colombia
Cobananthus calochlamys (Donn. Smith) Wiehler	W-830	Alta Verapaz, Guatemala
Codonanthe luteola Wiehler	W-1630	Panamá, Panamá
Columnea gloriosa Sprague	W-2131	Veraguas, Panamá
Columnea maculata Morton	W-1592	Colón, Panamá
Columnea nicaraguensis Oersted	G-949	Coclé, Panamá
Dalbergaria aureonitens (Hooker) Wiehler	W-1820	Aragua, Venezuela
Dalbergaria puyana Wiehler	W-2040	Pastaza, Ecuador
Drymonia killipii Wiehler	W-1726	El Valle, Colombia
Drymonia serrulata (Jacq.) Mart.	W-1077	Miranda, Venezuela
Episcia cupreata (Hooker) Hanst.	W-1833	Mérida, Venezuela
Episcia lilacina Hanst.	W-2221	hort.
Nautilocalyx porphyrotrichus (Leeuwenb.) Wiehler	W-1814	Bolivar, Venezuela
Pentadenia spathulata (Mansf.) Wiehler	W-2165	Pichincha, Ecuador
Pentadenia zapotalana Wiehler	W-2167	Los Rios, Ecuador
Rufodorsia major Wiehler	W-1131	Panamá, Panamá
Trichantha dissimilis (Morton) Wiehler	W-1177	Colón, Panamá
Trichantha filifera Wiehler	W-1631	El Valle, Colombia

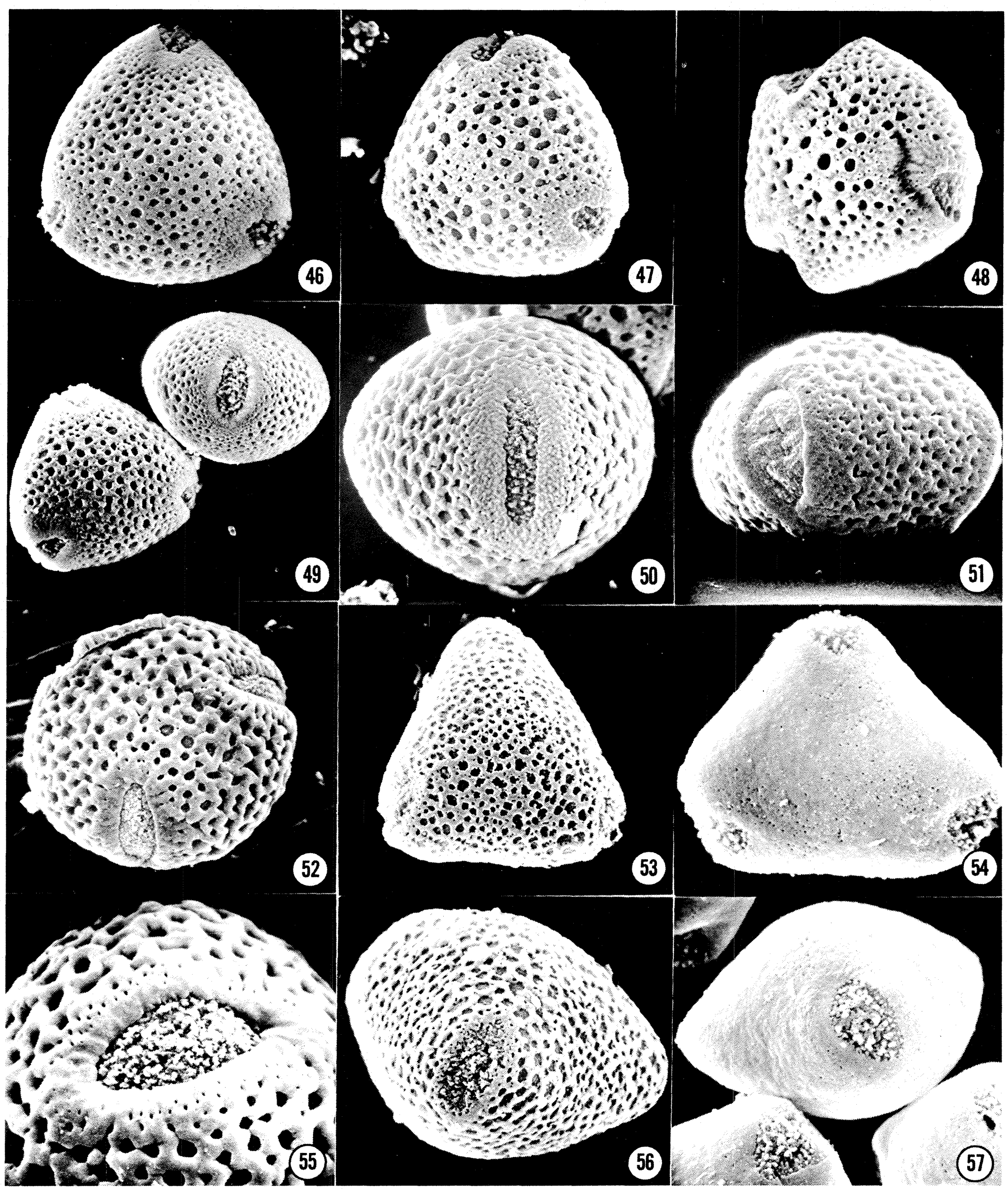

Plate 5

Figures 46-57. Representative examples of pollen of the Episcieae. 46. *Pentadenia spathulata*, polar view, X 1015. 47. *Pentadenia zapotalana*, polar view, X 1000. 48. *Trichantha dissimilis*, polar view, X 850. 49. *Pentadenia spathulata*, polar and equatorial view, X 725. 50. *Pentadenia zapotalana*, equatorial view, X 1240. 51. *Trichantha dissimilis*, equatorial view, X 950. 52. *Trichantha filifera*, polar-equatorial view, X 1000. 53. *Bucinella nariniana*, polar view, X 1000. 54. *Bucinella paramicola*, polar view, X 1225. 55. *Trichantha filifera*, close up view of the mesocolpial area, X 2000. 56. *Bucinella nariniana*, equatorial view, X 1225. 57. *Bucinella paramicola*, equatorial view, X 1225.

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