

Pollen Morphology and the
Relationship of the
Plumbaginaceae, Polygonaceae,
and Primulaceae to the
Order Centrospermae

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ABSTRACT

Nowicke, Joan W., and John J. Skvarla. Pollen Morphology and the Relationship of the Plumbaginaceae, Polygonaceae, and Primulaceae to the Order Centrospermae. *Smithsonian Contributions to Botany*, number 37, 64 pages, 200 figures, 5 tables, 1977.—Three families, Plumbaginaceae, Polygonaceae, and Primulaceae, are considered to be related to or derived from the Order Centrospermae by various authors. These three families have anthocyanin pigments in contrast to the betalains found in all but two families in the Centrospermae. In addition, all three are known to have starch-type sieve-tube plastids in contrast to the protein type found in all centrospermous families. Examination of the pollen of 134 species by SEM, TEM, and light microscopy revealed great diversity, especially in the Polygonaceae, but not the spinulose and tubuliferous/punctate ectexine, which characterizes the vast majority of the centrospermous taxa. Recent evidence argues against a close relationship of the Plumbaginaceae, Polygonaceae, and Primulaceae with the Centrospermae, and the absence of any pollen types common to the three families further suggests that they are not closely related to each other.

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Pollen Morphology and the Relationship of the Plumbaginaceae, Polygonaceae, and Primulaceae to the Order Centrospermae

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Introduction

The Centrospermae (Caryophyllales) represents one of the most controversial orders in the angiosperms. This group of at least 10 families, which in the past has been cited as one of the few natural orders based mostly on morphological characteristics, has unique N-containing pigments, the betalains, and a distinctive structure in the sieve-tube plastids. Both Cronquist (1968) and Takhtajan (1969) unite the betalain families, Aizoaceae, Amaranthaceae, Basellaceae, Cactaceae, Chenopodiaceae, Didiereaceae, Nyctaginaceae, Phytolaccaceae, and Portulacaceae, as well as two anthocyanin families, Caryophyllaceae and Molluginaceae, in the order Caryophyllales (\pm Centrospermae). Both authors include *Halophytum ameghinoi* Spegazzini (a betalain taxon) and the Gyrostemonaceae in this order: Cronquist (1968) treats *Halophytum* as a monotypic genus in the Chenopodiaceae while Takhtajan (1969) gives it family status; Cronquist regards the

Gyrostemonaceae as part of the Phytolaccaceae, and Takhtajan separates it as a distinct family. Takhtajan recognizes the Tetragnoniaceae as a separate family while Cronquist includes it in the Aizoaceae. *Dysphania* is treated as a member of the Chenopodiaceae by both authors; and finally Takhtajan also places the Hectorellaceae and the Bataceae in this order.

Thorne (1968) in a synopsis of angiosperm classification has placed the betalain families in a suborder, Chenopodiinae, one of two constituting the order Chenopodiales. He recognized the Gyrostemonaceae and the Halophytaceae as distinct families but treated the Molluginaceae as a subfamily in the Aizoaceae, the Achatocarpaceae as a subfamily in the Phytolaccaceae, and *Dysphania* as a member of the Chenopodiaceae. The other suborder, Caryophyllinae, consists of two families, the Caryophyllaceae and the Polygonaceae. The next order, Batidales, consists of only the Batidaceae, but Thorne apparently regards this family as somewhat related to the Chenopodiales since both orders are united under a superorder, Chenopodiiflorae.

Mabry, Taylor, and Turner (1963) and Behnke and Turner (1971) have treated the betalain fami-

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lies as a distinct group, separate from, yet closely allied to, the two anthocyanin families, Caryophyllaceae and Molluginaceae.

Evidence from ultrastructural research on sieve-tube plastids (Behnke and Turner, 1971; Behnke, 1976) and pollen morphology (Nowicke, 1975; Skvarla and Nowicke, 1976) has reinforced the close tie between the betalain families and the Caryophyllaceae and the Molluginaceae. In an investigation of these plastids (colorless leucoplasts found in the sieve-tubes) of the above-mentioned families (Behnke and Turner, 1971) and the Magnoliidae and Ranunculidae (Behnke, 1971), two main types were found: plastids accumulating only starch and designated as the S-type; and plastids accumulating at least some protein, variously deposited, and designated as the P-type. The betalain families and the Caryophyllaceae and the Molluginaceae all had the P-type plastid in which proteinaceous filaments formed a peripheral ring usually around a crystalloid. Within the above-mentioned families, Behnke (1976) was able to distinguish three groups based on the crystalloid: globular, the most common; polygonal, found in the Caryophyllaceae and in two other genera, *Limeum* (Molluginaceae) and *Stegnosperma* (Phytolaccaceae); and crystalloid-free, having only the ring, found in two families, the Amaranthaceae and the Chenopodiaceae.

Examination of the pollen of 177 species (Nowicke, 1975) by light microscopy and SEM revealed that 85% had a similar type of ectexine pattern or sculpture, which was described as spinulose and the tectum perforate, the openings described as tubules or punctae. This was the predominant ectexine pattern in every betalain family and in the Caryophyllaceae and the Molluginaceae; in some families, i.e., the Phytolaccaceae and the Molluginaceae, this pattern was the only one found. Examination of selected taxa by TEM (Skvarla and Nowicke, 1976) revealed that the predominant pollen-type in the betalain families and in the Caryophyllaceae has a similar, sometimes identical, wall structure.

Pollen of the Achatocarpaceae, Bataceae, Gyrostemonaceae, and Theligonaceae was also examined, but none of the species in these small families has the spinulose and tubuliferous/punctate ectexine described above. The Bataceae, Gyrostemonaceae, and Theligonaceae all have the starch-type plastid and lack the betalain pigments. Thus the evidence

from palynology, pigmentation, and plastid structure indicates that these three families are not closely related to the Centrospermae. The relationship of the Achatocarpaceae, a family unknown with regard to pigmentation, to the Centrospermae is more obscure—the pollen morphology does not, in Nowicke's opinion (1975) support a close tie, but on the other hand the two genera that comprise the family, *Achatocarpus* and *Phaulothamnus*, do have the P-type of plastid (Behnke, 1976).

The Gyrostemonaceae have in fact been the subject of a multidisciplinary study (Goldblatt, et al., 1976) in which all lines of evidence, including cytological, argue strongly against any relationship of this family to the Centrospermae.

Although there is almost universal agreement on treating the betalain families as a closely related group, the precise definition of the order Centrospermae, i.e., to include or exclude the Caryophyllaceae and Molluginaceae, may never be resolved to everyone's satisfaction. Of more interest in view of the accumulating data on the Centrospermae (*sensu lato*) is the question of the derivation of the families Plumbaginaceae, Polygonaceae, and Primulaceae from this order.

Takhtajan (1969) considers the Polygonales, containing only the Polygonaceae, as near the Caryophyllales, especially the Portulacaceae and Basellaceae, and probably derived from the same stock as the Caryophyllales (Centrospermae). His views on the Plumbaginaceae are similar: nearest to Portulacaceae and Basellaceae and probably derived from the same stock as Caryophyllales. He does admit that the pollen morphology of the Plumbaginaceae is different—apparently from that of Portulacaceae and Basellaceae.

According to Cronquist (1968:185), "both the Polygonaceae and Plumbaginaceae are pretty clearly related to the Caryophyllales. Both have a single, basal, bitegmic, crassinucellate ovule in a compound, unilocular ovary, and both have trinucleate pollen. These characters are not known to occur in combination outside the subclass Caryophyllidae. The Polygonaceae are further bound to the Caryophyllales by similarities in the pollen and by a more or less transitional group of genera which are variously referred to the Caryophyllaceae or treated as a separate family, Illecebraceae. The Plumbagina-

ceae are somewhat more isolated but may also be derived from the Caryophyllaceae."

In one respect the system of Thorne (1968) parallels those of Cronquist (1968) and Takhtajan (1969) in that all three authors consider the Polygonaceae as related to the Caryophyllaceae. Although Thorne treats the Primulales and Plumbaginales as adjacent orders indicative of some relationship, they are far removed from the Chenopodiales, at least in his linear sequence.

Philipson (1975) in a review paper on evolutionary lines in the dicotyledons states that there is general agreement to exclude the Primulaceae from the subclass Caryophyllidae (sensu Cronquist, 1968). "Almost as universal is the acceptance of the Polygonaceae as at least peripheral to the group. The position of the Plumbaginaceae remains more debatable" (Philipson, 1975:74).

Hutchinson (1959:117) regarded the Caryophyllales (Elatinaceae, Molluginaceae, Caryophyllaceae, Ficoidaceae, and Portulacaceae) as "a prolific herbaceous group which has given rise to apetalous orders such as Polygonales, Chenopodiales, and perigynous petaliferous families as Lythrales, besides sympetalous groups as Gentianales and Primulales." The Illecebraceae are given family status and included as the only other family in the Polygonales. It is noteworthy that Hutchinson included *Herniaria*, *Paronychia*, and *Scleranthus*, as well as *Illecebrum*, among the genera listed at the end of the family description. He united the Primulaceae and Plumbaginaceae as the order Primulales, closely related to the Caryophyllaceae and perhaps the Saxifragaceae. The Primulaceae, Polygonaceae, and Plumbaginaceae contain the anthocyanin pigments, and the last two, at least, are known to have the starch-type of plastid (Behnke and Turner, 1971) and apparently the Primulaceae also has this type (Behnke, pers. comm.).

In an effort to resolve the limits and relationships of the Centrospermae, pollen of Plumbaginaceae, Polygonaceae, and Primulaceae were examined by light microscopy, SEM, and TEM. For purposes of comparison and the reader's convenience, we have included a brief discussion and a SEM and TEM of a species from several betalain families, and from the Caryophyllaceae and Molluginaceae.

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or another, but Janice Bittner at the Smithsonian Institution and William Chisoe at the University of Oklahoma deserve special thanks for their fine technical assistance and helpful suggestions. The scanning electron photographs were prepared by the Scanning Electron Microscope Laboratory at the Smithsonian Institution. We also wish to thank Aaron Goldberg and Stanwyn G. Shetler for their critical review and Clara Ann Simmons for her assistance in the preparation of the manuscript. This research was supported in part by BMS grant 75-19846 to John J. Skvarla.

Materials and Methods

Pollen of 20 species in the Plumbaginaceae (Table 3), 85 in the Polygonaceae (Table 4) and 29 in the Primulaceae (Table 5) was examined by light microscopy, scanning electron microscopy (SEM), and transmission electron microscopy (TEM). Also examined and included are 38 additional taxa from the centrospermaous families (Table 2). Pollen samples were removed from herbarium material and acetolyzed according to procedure outlined in Erdtman (1966). Samples for the SEM were vacuum-coated with gold, and examined and photographed with a Cambridge Stereoscan MK IIA microscope. Samples for the TEM were incorporated into agar, dehydrated through increased concentrations of ethyl alcohol, and subsequently embedded in araldite-epon resins (Skvarla, 1973). Some pollen samples were stained in 0.125% OsO₄ in 0.1 M sodium cacodylate buffer for two hours prior to agar incorporation. Thin-sections were made with diamond knives, collected on uncoated grids and stained with uranyl acetate and then lead citrate. Electron microscope observations were made with a Philips model-200 transmission electron microscope. Slides of all samples are deposited at the Palynological Laboratory, Department of Botany, Smithsonian Institution.

This study is a comparison of the pollen morphology of three families, Plumbaginaceae, Polygonaceae, and Primulaceae, with the pollen of the Centrospermae, and detailed measurements and/or descriptions are not given. The species examined are listed in Tables 2-5; the names were taken from the herbarium labels or the most recent annotations. The identifications would have to be mis-

taken at the level of family to be significantly misleading in this type of study, but all vouchers and geographical locations are given in Tables 2–5.

Results of Pollen Analyses

Pollen analysis of the Plumbaginaceae, Polygonaceae, and Primulaceae revealed diverse forms within each family, especially the Polygonaceae, but no distinctive pollen type(s) was common to all three families. For this reason each family will be discussed separately following a review of the Centrospermae.

CENTROSPERMAE

FIGURES 1–28

The common pollen types in the Centrospermae are illustrated in Figures 1–6: 3-colpate, pantoporate, and pantocolpate, all with a spinulose and tubuliferous/punctate ectexine. With the exception of some taxa in the Caryophyllaceae which are 3-colporoidate, the apertures in the Centrospermae pollen are simple. The most variable class of apertures is that of pantoporate. *Anredera scandens* (Figure 3) is usually 6-porate, with one pore on each plane of the roughly cube-shaped grain. *Gymnocarpus fruticosum* pollen (Figure 4), with large, sunken pores in a geometric pattern, contrasts sharply with that of *Chenopodium ambrosioides* (Figure 5), which has numerous small pores.

Figures 7 through 12 illustrate at high magnification ($\times 7500$) the ectexine surface, spinulose, and tubuliferous/punctate, which characterizes the vast majority (85%) of the centrospermous taxa. *Hamatocactus septispinus* pollen (Figure 12) has the largest perforations among the species examined by SEM.

Figures 13 through 18 illustrate specialized or unusual forms, but at least one species, *Cardionema ramosissima* (Figure 16), has the typical ectexine. Two other taxa, *Psilotrichum amplum* (Figure 13), considered unusual because of the stellate aperture plates, and *Herniaria glabra* (Figure 15), in which the grains have a rare tetrahedral shape, also have the common ectexine pattern but a modified version of it—the spines and perforations are much reduced.

The internal structure of the exine in various centrospermous pollen types is illustrated in Figures 19–28. Characteristically in the centrospermous taxa, the ectexine is well developed while the endexine, with few exceptions (e.g., *Mesembryanthemum variabile*, Figure 19; *Herniaria glabra*, Figure 24), is developed only in the region of the aperture. Apertures with spine-shaped flecks of ectexine are common in the Centrospermae and in this study are illustrated by *Opuntia* (Figure 22), *Limeum* (Figure 26), and *Gymnocarpus* (Figure 23). Representative pollen from nine families of the Centrospermae were examined by TEM. Comparison of these data with those of earlier TEM work in the Centrospermae (Skvarla and Nowicke, 1976) allows us to expand our knowledge of this order, and a brief summary for each family is presented below.

AIZOACEAE.—*Mesembryanthemum variabile* pollen (Figure 19) is considerably different from that of *M. crystallinum* (Skvarla and Nowicke, 1976, fig. 13) in possessing a thinner tectum and columellae, as well as an extremely thick foot layer and a narrow but consistent endexine. *Mesembryanthemum*, however, is a large and unsatisfactory genus and structural variation is not unexpected. The exine stratification of *M. variabile* bears a striking similarity to that of *Boerhavia erecta* of the Nyctaginaceae (Skvarla and Nowicke, 1976, fig. 30).

AMARANTHACEAE.—The pollen of this family has been shown with SEM and TEM to be highly pleomorphic (Nowicke, 1975; Skvarla and Nowicke, 1976). The exine structure of *Psilotrichum amplum* (Figure 20) extends this pleomorphism by indicating a complete absence of endexine.

BASELLACEAE.—Some pollen in this family is unique in having a cuboidal shape (Nowicke, 1975; Skvarla and Nowicke, 1976). The structure of *Anredera scandens* pollen (Figure 21), is quite different from that of *Basella alba* (Skvarla and Nowicke, 1976, fig. 19) but similar to that of *Boussingaultia gracilis* (Roland, 1968, pl. 8: fig. 4), a more typical member of the family.

CACTACEAE.—The structure of *Opuntia lindheimeri* pollen (Figure 22) is consistent with other examples of the Cactaceae. Comparison of this micrograph with one of *Alluaudia* (Skvarla and Nowicke, 1976, fig. 28) again underscores the close relationship of the Cactaceae and Didieriaceae.

CARYOPHYLLACEAE.—The two taxa examined, *Gymnocarpus fruticosum* (Figure 23) and *Herniaria glabra* (Figure 24), correspond in exine structure to that previously noted for the family (Skvarla and Nowicke, 1976, figs. 41–48). Additional comments on *H. glabra* will be given later.

CHENOPODIACEAE.—The exine structure of *Chenopodium ambrosioides* (Figure 25) agrees with other examples in the family: thick tectum with few spines and a thin foot layer.

MOLLUGINACEAE.—The exine structure of this family has not been previously examined. Pollen of *Limeum viscosum* (Figure 26) appears similar to the pollen of *Cometes surattensis* of the Caryophyllaceae (Skvarla and Nowicke, 1976, fig. 41), as well as to *Mesembryanthemum crystallinum* of the Aizoaceae (Skvarla and Nowicke, 1976, fig. 13). These relationships are of interest in the context of the introductory remarks concerning the Molluginaceae.

NYCTAGINACEAE.—*Abronia angustifolia* (Figure 27) pollen morphology differs from that of previous taxa examined by lacking an endexine. As indicated earlier (Skvarla and Nowicke, 1976), however, the Nyctaginaceae display a spectrum of exine morphology.

PORTULACACEAE.—The exine morphology of *Naiocrene parvifolia* (Figure 28) is similar to that of other taxa examined in the family, most notably *Calyptridium umbellatum* (Skvarla and Nowicke, 1976, fig. 38).

Several taxa whose placement or affinities are in dispute were also examined. *Geocarpon minimum* (Figure 9), the single species of this monotypic genus, has an ektexine pattern that is characteristic of the order Centrospermae, but the presence of anthocyanins would seem to restrict the family placement to Caryophyllaceae or Molluginaceae. Two more monotypic genera, *Hectorella* and *Lyallia*, have been united as a separate family, Hectorellaceae (Philipson and Skipworth, 1961), or included in the Caryophyllaceae (Eckhardt, 1964). Material of *Hectorella* was not available, and a pollen sample of *Lyallia kerguelensis* yielded only 10–12 grains, all of which were 3-colpate with a spinulose and sparsely punctate ektexine. As with *Geocarpon*, the pollen morphology of *Lyallia* appears characteristic of the Centrospermae, but inconclusive with regard to status or family affinity

since these types are of wide occurrence in the order. The evidence from plastid structure is more definitive and supports the treatment of *Hectorella* and presumably also *Lyallia* as a separate family, or at least argues for their exclusion from the Caryophyllaceae. *Hectorella* has the P-type plastid but lacks the polygonal central crystalloid that characterizes the Caryophyllaceae (Behnke, 1975).

The pollen types in Figures 15 and 16 are representative of a small group of genera that have been treated as a subtribe, the Illecebrinae, in the Caryophyllaceae (Pax and Hoffman, 1934) or given family status, the Illecebraceae (Hutchinson, 1959). Pax and Hoffman regarded the subtribe as consisting of four genera, *Illecebrum*, *Haya*, *Cardionema*, and *Chaetonychia*, while Hutchinson's concept of the Illecebraceae includes several additional genera, among them, *Herniaria*. Pax and Hoffman placed this particular genus in the first subtribe, Paronychiinae, with the Illecebrinae as the second. Cronquist (1968:185) regards these genera as a transitional group between the Caryophyllaceae and the Polygonaceae. Figure 15 is a single grain of *Herniaria glabra* and is extremely similar to those of *Illecebrum verticillatum* in scanning electron microscopy and light microscopy. *Herniaria glabra* is illustrated because the material of *Illecebrum* was insufficient for examination by TEM. Figure 16 is *Cardionema ramosissima*; material of *Haya* and *Chaetonychia* was not available.

For a detailed discussion of pollen morphology in the order Centrospermae the reader is advised to consult Nowicke (1975) and Skvarla and Nowicke (1976).

PLUMBAGINACEAE

FIGURES 29–81

Twenty species and one variety, representing nine genera (Table 3), were examined by light microscopy and SEM, and eleven of these species were sectioned and examined by TEM. In all taxa, the apertures appeared to be simple, mostly 3-zonocolpate, rarely 4- (or 5-)zonocolpate, and in one collection of *Ceratostigma willmottianum* (Figure 59) the grains were pantocolpate. The ektexine was either reticulate or verrucose, two sharply distinct morphologies with no intermediate forms. These correspond to the two pollen types noted for

the family by Erdtman (1966:325); the *Plumbago* type, which is verrucose, and the *Armeria* type, which is reticulate. The *Plumbago* type (Figures 29–40, 59–64) has a well-defined foot layer, highly irregular *columellae* and a *continuous tectum*. Extending from the latter is another set of *columellae*, designated as *verrucae*, thicker than those below the *tectum*, with the terminal sculpturing appearing as fine bristles in TEM. The *Armeria* type (Figures 41–58) has a foot layer supporting straight, regular *columellae*, which are fused distally into an incomplete *tectum* of the reticulate configuration.

Heterostyly, frequently associated with dimorphic stigmas and dimorphic pollen grains, is a well-documented phenomenon in the *Plumbaginaceae* (Baker, 1948, 1953, 1966; Dulberger, 1975; Philipp, 1974). Although the collections at the U.S. National Herbarium are too limited and valuable to permit a study of heterostyly *per se*, and this is not our intention, the survey of the *Plumbaginaceae* revealed seemingly controversial results. Neither author claims taxonomic expertise in the *Plumbaginaceae*, but the collection sampled in each case was similar to or within the range of variation of the remaining collections of the particular species as identified. Few specimens had sufficient numbers of open flowers to permit a designation of short- or long-styled with any degree of confidence, nor could we follow Baker's (1966) scheme of labeling the two *Armeria* forms "A" or "B" since this too is based on style length. However, the results in two species with the *Plumbago* type reinforce each other, and the pollen forms found in four species with the *Armeria* type reinforce each other. The following discussions apply only to the particular collections listed in Table 3 for each species, and within each major type the different grains are referred to as forms.

What appears to be the two forms in the *Plumbago* type pollen can be illustrated by two collections of *Ceratostigma griffithii* from China (Figures 29–32) and two collections of *Plumbago europaea* (Figures 35–38). In each species there is a form with pointed *verrucae* (Figures 32, 38) and a form with more rounded *verrucae* (Figures 30, 36). Whether these two forms actually represent dimorphic pollen and are associated with heterostyly remains to be answered, but our results agree, for the most part, with those of Erdtman (1970).

Baker (1948, 1966) regarded *Ceratostigma* and *Plumbago* as having monomorphic pollen, but the similarity of the two forms makes them difficult to distinguish using only light microscopy. As a result only those species examined also by SEM have been designated as having pointed *verrucae* or rounded *verrucae* in Table 3. Collections having the pointed *verrucae* were found in *Plumbago rosea* (Figures 33, 34) and in *Ceratostigma willmottianum* (Figures 59–62). A collection identified as *Plumbago auriculata* (Figures 39, 40) had the more rounded *verrucae*.

The above reservation does not apply to the *Armeria* type in which the two forms are strikingly distinct even in light microscopy. The *Armeria* forms can be illustrated by two collections each of *Armeria maritima* (Figures 43–46), *Limonium vulgare* (Figures 51, 52), and *Statice sinuata* (Figures 55–58) and one collection of *Statice tenella* (Figures 47–50) with several unattached branches, presumably from different plants. In each of the above species there is a prominently (or coarsely) reticulate form (Figures 45–48, 51, 55, 56) and a finely reticulate form (Figures 43, 44, 49, 50, 52, 57, 58). While each form exhibits subtle interspecific differences, i.e., the coarsely reticulate grain of *Armeria maritima* may be slightly different from the coarsely reticulate grain in *Statice sinuata*, the classification of grains as to coarsely or finely reticulate could have been made without knowledge of the alternate form. The remaining *Armeria* types illustrated by SEM are *Goniolium collinum* (Figures 53, 54) and *Limonium viciosoi* (Figures 41, 42). In both species the collection sampled had the coarsely reticulate form.

TEM observations corroborate the dimorphism shown by SEM. The verrucose type is represented by *Ceratostigma griffithii* (Figure 69): the fine bristle-like *columellae* heads correspond to the rounded *verrucae* illustrated in Figure 30 by SEM; in Figure 70, the *verrucae* have thicker bristles, and those with perfect longitudinal section illustrate the large blunt protrusion of the pointed *verrucae* shown in Figure 32 by SEM. In *Armeria maritima* (Figures 67, 68) and *Statice sinuata* (Figures 77–80), representative of the reticulate morphology, TEM reinforces the differences in diameter and length of the *columellae* between the finely and coarsely reticulate forms, and also the existence of a fine

network of sporopollenin around the muri of the coarsely reticulate forms (Figure 67), which was not readily apparent in the finely reticulate forms. Our observations of *A. maritima* agree with the TEM investigations of Erdtman and Dunbar (1966). These workers designated the coarsely reticulate exines as "A-line" and the more finely reticulate exines as "B-line." Direct correlations in exine structure between our TEMs (Figures 67, 68) and those of Erdtman and Dunbar (1966, figs. 1, 2) are obvious.

In all samples examined the endexine pollen wall unit that characteristically occurs beneath the foot layer in the majority of angiosperm pollen grains is highly reduced in the Plumbaginaceae. We have noted its presence only in the aperture region, and, therefore, it is depicted in just a few of the transmission electron micrographs included in this report (Figures 65, 66, 68, 71, 73, 74, 80). Internal foramina in the columellae and foot-layer (Figures 65-67, 75) are also found in the Plumbaginaceae. This feature has been described in the large family Compositae by Skvarla and Larson (1965). These holes are of sporadic distribution and are most commonly noted in the *Armeria* pollen type.

In *Ceratostigma willmottianum*, a collection from India had 3-colpate grains (Figures 61, 62), and a collection from China had pantocolpate grains (Figures 59, 60). The pantocolpate grain has larger clusters of verrucae, but at high magnification, $\times 7500$ (Figures 60, 62), the tips of the verrucae in both forms are very similar in the terminal structure. These results do not correlate with those of *Ceratostigma griffithii* and *Plumbago europaea*, but dimorphic pollen grains based on aperture structure are not unknown (Kohler, 1976). Additional samples are needed to confirm the alternate form as 3-colpate.

As stated above, this study was not intended to document or identify the species of Plumbaginaceae with dimorphic pollen. We are aware that a detailed investigation of each of the species listed in Table 3 might well reveal that a majority of these have dimorphic grains. Also, most pollen samples in this family consist of a single flower with the five anthers. This sampling technique limits damage to the specimen, but does not yield large numbers of grains.

If, especially in the *Armeria* types, 15 or 20 an-

thers from each collection had been examined, the larger sample might have produced results more compatible with those of previous workers. In the case of *Limonium vulgare*, examination of four collections (Table 3) revealed three with the coarsely reticulate form (Figure 51) and one with the finely reticulate form (Figure 52). Our coarsely reticulate form corresponds exactly with the "A" grain of Baker (1966, fig. 1), but we did not find the form which he illustrated as the alternate or "B" (1966, fig. 2) and described as bearing a pattern of small spines on the surface of the grain. In fact, the closest similarity to his "B" grain is *Plumbago rosea* (Figures 33, 34). It seems unlikely that both major pollen types, which are morphologically and structurally very different, would be found in one species, but our results do not exclude this possibility.

Another problematical taxon is *Armeria maritima* var. *sibirica* (Turczaninow) Lawrence. This particular variety, sometimes treated as a subspecies or even as a species, has been investigated by a number of workers, with differing, but not necessarily mutually exclusive, results. Both Baker (1966:355-356) and Philipp (1974:41) regard "*sibirica*" as monomorphic, having the papillate stigma and Type A pollen (coarsely reticulate form). However, in a study of collections made between longitudes 30°W and 60°E, Pragłowski and Erdtman (1969) described six pollen forms, and found as many as four in a single anther. These include an "A" and "B" that correspond to our coarsely and finely reticulate forms. Of all the Plumbaginaceae examined in our study, 39 collections representing 20 species, only *Armeria maritima* var. *sibirica* had both forms within a single sample. The holdings of var. *sibirica* at the United States National Herbarium are mostly from Greenland and Canada, with only two from Norway. Pollen was removed from a single inflorescence on each of six collections (Table 3). The SEMs, taken at a range of low magnifications, illustrate mixtures of the finely and coarsely reticulate *Armeria* forms. Unfortunately this variety was examined late in the study and the micrographs could not be included here. However, two observations seem worthy of note: the coarsely reticulate form appears to be predominant, and, secondly, the distinction between the two forms is not as striking as in the other dimorphic *Armeria* taxa. Philipp (1974, fig. 1) illustrates grains from dimorphic

Danish *Armeria maritima* (1974, fig. 1A,B) which agree very well with our Figures 43–46, but more importantly the two SEM's from monomorphic Greenland plants (1974, fig. 1c,d) also show a possible dilution of the distinction: the mesh of what could be the finely reticulate form (fig. 1c) is larger, and the mesh of what could be the coarsely reticulate form (fig. 1d) is slightly smaller.

Philipp (1974:49) also cites the existence of large and small pollen grains in the hybrids between the dimorphic subspecies, *A. maritima* ssp. *maritima* × ssp. *elongata*. The proportion of the grains varies widely; in one cyme the percentage of large grains in open flowers ranged from 45 to 90. In one plant the maximum variation between the cymes was from 24% to 90% large grains. The variation in size is not exactly comparable to the structural variation in the exine, but her results, those of Prąglowski and Erdtman (1969), and ours, indicate that one plant, or even one inflorescence, is capable of producing variable or dimorphic grains.

To summarize the results of pollen analysis in this family—the striking difference in the two types designated as “*Armeria*” and “*Plumbago*,” the distinction of the *Plumbago* type from all other pollen examined to date in these studies, the existence of the two *Armeria* forms within a single inflorescence raise more questions than they answer. The existence of heterostyly and dimorphic pollen grains in the *Plumbaginaceae*, however, in no way detracts from the conclusion of this study: None of the pollen examined in the *Plumbaginaceae* is similar or related to the common type found in the *Centrospermae*.

POLYGONACEAE

FIGURES 82–173

This is a much larger family than either the *Plumbaginaceae* or *Primulaceae*. The possibility of a relationship with the *Centrospermae* is more widely held and thus was examined in greater depth. The 85 species (Table 4) representing 36 genera were examined by light microscopy and SEM; 32 of these species were sectioned and examined by TEM.

The *Polygonaceae* are one of the most palynologically diverse families in the dicotyledons, and

this extensive variation may have great taxonomic potential at all levels, particularly that of generic definition.

The aperture structure is more complex and variable than in the *Primulaceae* and much more so than in the *Centrospermae* or *Plumbaginaceae*. While the most common type in the *Polygonaceae* is 3– (rarely 4–) colporate, the endoaperture, readily delimited in light microscopy, is variable and includes some zonorate types. Also found in the family are taxa with pantoporate (Figures 113, 114, 134) and pantocolpate (Figures 112, 118, 120, 133) apertures. Some collections of 3-colporate taxa had occasional grains that were syncolporate.

The surface of the ektexine varies widely and includes tectate and nontectate (reticulate) forms. The tectate forms can be punctate (Figures 82–85); punctate-striate (Figures 94–99); prominently spinulose (Figures 133, 134); or perforate and small-spinulose (Figures 136, 138); and there are some unique types that are difficult to describe accurately in text (Figures 98, 106, 108, 110). The nontectate forms are finely to coarsely reticulate (Figures 112–123). In some taxa the grains had one type of surface outlining the colpi, and another on the poles and mesocolpial ridges (Figures 130, 140).

The most common surface pattern is punctate. The size and distribution alone of these punctae vary widely, but an additional characteristic is present in many taxa—the punctae are connected by grooves or striae which are also variable in depth, width, and placement (Figures 89, 91, 93, 95, 97, 99). In *Ruprechtia laxiflora* (Figure 106), the tectum between the striae is variously upraised, producing an uneven surface. In *Ruprechtia ramiflora* (Figures 108, 109), the intergroove tectum is more prominently upraised. In *Atraphaxis buxifolia* (Figures 98, 99), the connecting striae are larger, tend to be parallel, and result in, at least superficially, a striate-like surface pattern. These distinctions are not as conspicuous in TEM (*Atraphaxis*, Figure 143; *Ruprechtia laxiflora*, Figure 171; *R. pallida*, Figure 172), but this, of course, is frequently the case when cross-sections are compared with surfaces having irregular variations.

Within the broad category of punctate ektexines, the following six subtypes with some representative species can be recognized:

1. Ektexine finely punctate: *Chorizanthe breweri*,

Eriogonum correllii, and *Nemacaulis denudata* (Figure 82).

2. Ektexine with clustered punctae: *Centrostegia thurberi*, *Chorizanthe fimbriata* (Figure 84), *C. paniculata* (Figure 85), *Eriogonum parishii*, and *E. racemosum*.

3. Ektexine punctate, the punctae connected by small striae: *Eriogonum inflatum*, *E. marifolium* (Figures 90, 91), *E. thomasi*, *Mucronea californica* (Figures 88, 89), *Oxytheca trilobata* (Figure 83).

4. Ektexine more prominently punctate-striate: *Antigonum guatemalense*, *Calligonum comosum* (Figures 94, 95), *Gymnopodium antigonoides* (Figures 92, 93), *Harfordia macroptera* (Figures 96, 97), *Muehlenbeckia chilensis* (Figures 102, 103), *M. polybotryar*, *Neomillspaughia paniculata*, and *Triplaris americana* (Figure 86).

5. Ektexine with prominent sunken punctae: *Fagopyrum esculentum* (Figure 87), *Muehlenbeckia tamnifolia* (Figures 104, 105).

6. Ektexine microreticulate: *Oxygonum dregeanum*, *O. zeyheri*, and *Podopterus mexicanus* (Figure 132).

The subtypes listed above should be treated with reserve since the distinction between consecutive ones is not very great, particularly between subtypes 3 and 4. Also, variation within a sample made classification of some taxa arbitrary or impossible.

Observations of exine wall with TEM indicate that the six subtypes established by SEM have considerable structural diversity as well. Sixteen of these taxa were examined in sections: *Chorizanthe breweri* (Figure 145) and *Nemacaulis denudata* (Figure 157) of subtype 1, *Chorizanthe paniculata* (Figure 146) and *Eriogonum parishii* (Figure 149) of subtype 2, *Eriogonum marifolium* (Figure 148) and *Oxytheca trilobata* (Figure 158) of subtype 3, *Antigonum guatemalense* (Figure 142), *Calligonum comosum* (Figure 144), *Harfordia macroptera* (Figure 152) and *Muehlenbeckia polybotryar* (Figure 156) of subtype 4, and *Muehlenbeckia tamnifolia* (Figure 154) and *Fagopyrum esculentum* (Figure 150) of subtype 5 are all essentially similar in possessing a moderate to thick tectum, long, narrow columellae (*Calligonum comosum*, Figure 144, excepted), a very reduced (absent?) foot-layer, and a distinguishable endexine. The TEM's of some of the above taxa revealed an unusual characteristic that may be of phylogenetic significance: *Chori-*

zanthe spp. (Figures 145, 146), *Eriogonum parishii* (Figure 149), *Nemacaulis* (Figure 157), and *Oxytheca trilobata* (Figure 158) all had a tectum in which the inner face was conspicuously granular.

Two of these 16 taxa examined by TEM, *Muehlenbeckia chilensis* (Figure 153) and *Podopterus mexicanus* (Figure 160), are distinguished from the preceding ones by a prominently developed foot layer and an endexine well developed only in the region of the aperture. *Gymnopodium* (Figure 151) and *Triplaris* (Figure 173), with a thin foot-layer and endexine, appear intermediate between the above groups.

The second most common surface pattern is a reticulum formed by larger and fewer columellae, arranged in a network and distally fused, thus producing incomplete tectum. Differences in the size and placement of the primary columellae and in the surface of the lumina produce wide varieties and some recognizable pollen types. Grains with this ektexine were 3-colpate (colporate?) (Figures 116, 122), pantocolpate (Figures 112, 118, 120), or pantoporate (Figures 113, 114). In *Polygonum capitatum* (Figures 122, 123) and *P. dielsii* (Figures 116, 117) the columellae are massive, and a high, conspicuous reticulum is the result. The lumina are larger in *P. dielsii*, but in both species they are almost free of any columella material. In *Polygonum acuminatum* (Figure 113) and *P. orientale* (Figures 114, 115), both pantoporate, the muri alternate with large lumina filled with smaller, free columellae. In three pantocolpate taxa, *Persicaria coccinea* (Figure 112), *Polygonum amphibium* (Figures 120, 121), and *P. virginianum* (Figures 118, 119), the columellae which form the reticulum are smaller in length and diameter, closely placed, and a finer reticulum results. In all three the lumina are filled with small, free columellae.

Thin-sections of *Polygonum orientale* (Figure 159), *P. dielsii* (Figure 166), *P. amphibium* (Figures 162, 163), and *P. virginianum* (Figure 169) emphasize the SEM observations.

The formation of the reticulum in the above Polygonaceae is unusual: the ridges or muri are formed by distal fusion along the midline of two rows of columellae, which are opposite or sometimes alternate, producing a "staggered" effect best illustrated in a "planar" view (Figures 115, 117).

Four species of *Polygonum*, *P. affine* (Figure 124),

P. bistorta (Figures 128, 129), *P. vacciniifolium* (Figures 126, 127) and *P. viviparum* (Figure 125), which belong, among others, to the *Bistorta* complex (Hedberg, 1947), and an Australian species of *Muehlenbeckia*, *M. cunninghamii* (Figures 100, 101), have an ektexine pattern that could be described as sparsely spinulose and sparsely punctate. Grains of all five taxa were 3-colporate, the endoaperture well defined. In thin-section, *Muehlenbeckia cunninghamii*, (Figure 155) is very similar to the other species of *Muehlenbeckia* examined by TEM (Figures 153, 154, 156).

It is difficult to reconcile the TEM of *P. bistorta* (Figure 164) with the sparsely spinulose and sparsely punctate ektexine depicted in SEM (Figures 128, 129). The lack of a continuous tectum may be due in part to an oblique section and perhaps to the densely packed columellae. The SEM's of *P. vacciniifolium* (Figures 126, 127), with the larger perforations in the tectum, are more compatible with the cross-section illustrated in TEM (Figure 168).

Koenigia islandica, *Polygonum cyanandrium* (Figures 134, 135), and *P. forrestii* (Figure 133) had grains that were either pantoporate or pantocolpate with a prominently spinulose ektexine. Comparison of these grains (Figures 133–135) with the common type in the Centrospermae (Figures 1–12) indicates that the above species could not be related palynologically to that order. *Polygonum forrestii* (Figure 167) was the most distinctive *Polygonum* of those examined by TEM. The exine consists of a thin endexine and an ektexine containing abundant holes or internal foramina. The surface of the tectum was composed of very large, solid spines with numerous, small projections in between.

Hedberg (1947), in a classic study of pollen morphology in the genus *Polygonum*, sensu lato, recognized ten pollen types for which he gave descriptions and listed species. He segregated *Polygonum convolvulus* (Figures 140, 141), *P. cristatum*, and *P. dumetorum* as slightly aberrant forms of his *Tiniaria* type. These three species have almost identical pollen grains: 3-colporate with a zonorate endoaperture, the ektexine echinate near the colpi and psilate at the poles and the mesocolpial regions. The above characteristics make the grains distinct, not only from the more typical *Tiniaria* pollen, but from the remaining species examined in the present study. This particular morphology is

paralleled by that of *Polygonella fimbriata* (Figure 130) and closely related species (Horton, 1963. 181–183): both groups have grains with similar apertures and a dimorphic ektexine in which the two surface patterns have the same distribution. Examination of *P. convolvulus* in TEM (Figure 165) revealed a remarkably uniform tectum (throughout the psilate area of the ektexine) and foot layer, underlain by a prominent endexine. This rare combination of well-developed foot layer and endexine was also found in *Polygonella* (Figure 161), which reinforces the parallel exomorphologies. *Polygonum cilinode*, *P. cuspidatum*, and *P. multiflorum*, which Hedberg lists as typical *Tiniaria*, have 3-colporate grains and a uniform ektexine, punctate-striate or prominently punctate.

Four species of *Rumex* were examined: *R. aquaticus*, *R. acetosa* (Figures 138, 139), *R. acetosella*, and *R. scutatus*, all of which had a perforate and very finely and evenly spinulose ektexine (Figure 139). Two species of *Emex* had an ektexine (Figure 136) similar to that of *Rumex*, but with a distinctive aperture structure. The ectoaperture is very reduced in length, and its polar margins almost coincide with those of the endoaperture. The close similarity of the ektexine in *Emex* and *Rumex* and its restricted occurrence reinforce Dammer's (1893) consecutive placement of the two genera. Comparison of the ektexine of *Rumex* (Figure 139) with the common Centrospermae type (Figures 7–12) indicates that there is not a close relationship between the two groups. The section of *Rumex acetosa* (Figure 170) reveals a thin exine in which the columellae and especially the foot-layer-endexine unit are greatly reduced.

The ektexine of seven species in the large New World genus *Coccoloba* illustrates a continuous variation. All taxa are 3-colporate, and *Coccoloba cordata* (Figures 110, 111) has an ektexine best described as columnar-pyramidal on a base of randomly oriented small rods; *C. barbeyana* has an ektexine similar to *Ruprechtia ramiflora* (Figures 108, 109); *C. diversifolia* is similar to *Calligonum comosum* (Figures 94, 95); *Coccoloba venosa* and *C. obovata* are prominently punctate; and *C. parimensis* has a microreticulate ektexine similar to *Podopterus mexicanus* (Figure 132) and *Polygonella polygama* (Figure 131), but with slightly smaller lumina.

The internal morphology of *Coccoloba cordata* pollen (Figure 147) also appears unique for the family. The ectexine surface consists of prominent irregular protuberances supported by a moderately thick tectum underlain by notably reduced columellae, greatly thickened foot-layer, and an extremely thin endexine, if any.

The genus *Lastarriaea* has been regarded as consisting of two endemic species, *L. chilensis* Remy in Chile, and *L. coriacea* (Goodman) Hoover in Baja and Southern California. The California taxon has been treated as *L. chilensis* ssp. *californica* Gross, or as a species of *Chorizanthe*, *C. coriacea* Goodman, who had to select another specific epithet since "californica" was already applied. The pollen of *Lastarriaea chilensis* (Figure 137), *L. coriacea*, and *Chorizanthe* species (Figures 84, 85) are all very similar, 3-colporate with a punctate ectexine. This is the most common morphology in the family, however, and the similarity does not necessarily indicate that *Lastarriaea* is congeneric with *Chorizanthe* or is closely related. For the same reason, the close similarity of the pollen in the two species of *Lastarriaea* does not, a priori, indicate a single species. Careful observation of the floral morphology when sampling for pollen, however, revealed that the flowers of the plants from Chile and from California are nearly identical in structure. Goodman (1934), in a revision of the North American species of *Chorizanthe* that included the California taxon, described the genus as having nine stamens, rarely six or three. The California and Chilean species of *Lastarriaea* have only three stamens.

Within limits of the taxa investigated (Table 4), a number of pollen types were found in only one species, and such cases are discussed separately here.

Polygonella fimbriata (Figure 130). Grains 3-colporate, the endoaperture zonorate; the tectum variable: finely punctate in the region of the colpus, conspicuously reticulate at the mesocolpial ridges and more so at the poles. The TEM also indicates that *P. fimbriata* is distinctive for the family. This conclusion is based on the presence of a well-developed foot-layer and a thickened endexine (Figure 161), two characteristics that were rarely combined. See also the earlier discussion of *Polygonum convolvulus* and allied species.

Polygonella polygama (Figure 131). Grains 3-colporate, the endoaperture zonorate, the nexine

thickened at the margins; the ectexine \pm microreticulate.

Comparison of the major subdivisions of the Polygonaceae (Dammer, 1893; Roberty and Vautier, 1964; Reveal and Howell, 1976) with pollen morphology reveals little correlation. This lack of correlation is due primarily to two complementary phenomena: the wide distribution of the punctate-striate pollen type, which cuts across subfamily and tribal lines, and the wide array of pollen types within one genus, *Polygonum*. Thus far, the pollen morphology would support Reveal's concept (Reveal and Howell, 1976) of the subfamily Eriogonoideae. Twelve of the 13 genera that he assigned to this subfamily, have been examined by light microscopy and/or SEM, and all are 3-colporate with either punctate or punctate-striate ectexines, the most common pollen type in the Polygonaceae. However, an unusual characteristic illustrated by TEM, a granular inner surface of the tectum, is known thus far to be restricted to the Eriogonoideae: *Chorizanthe* (Figures 145, 146); *Eriogonum* (Figures 148, 149); *Nemacaulis* (Figure 157); *Oxytheca* (Figure 158). Another genus in this subfamily, *Harfordia* (Figure 152), is slightly granular. Examination of additional genera by TEM might well reinforce the value of this characteristic and also the validity of the subfamily.

PRIMULACEAE

FIGURES 174-200

Twenty-nine species (Table 5) representing 22 genera were examined by light microscopy and SEM, and 9 of these were sectioned and examined by TEM.

The structure of the aperture in the Primulaceae is more complex than in the Plumbaginaceae and in the Centrospermae. If the number is three or four, the apertures are generally compound, and the endoaperture is easily seen in light microscopy. A number of taxa with 3-colporate grains had a bridge over the endoaperture formed by the extension of the two lateral margins of the colpus (Figures 175, 180-184). One species, *Lysimachiopsis hillebrandia*, had 4-colporate grains in which each side of an endoaperture frequently terminated in a V-shaped process. Sometimes the V from one endo-

aperture and that of the adjacent one formed the outline of a diamond. Grains with 5–8 apertures, e.g., some *Primula* species, are generally zonocolpate (Figure 186). In some taxa, e.g., *Cortusa matthioli* L. (Figure 188), the colpi fuse at the poles to form a triangular apocolpial field.

Different surface patterns were due largely to variation in the perforation of the tectum. In some grains the surface was finely punctate (*Lysimachia hybrida*, Figure 175; *Douglasia montana*, Figure 182), in others prominently punctate (*Coris monspeliensis*, Figure 174; *Cyclamen neopolitanum*, Figure 184), irregularly perforate (*Naumbergia thrysiflora*, Figure 176), or microreticulate (*Hottonia palustris*, Figure 185; *Primula veris*, Figures 186, 187; *Omphalogramma vinciflorum*, Figure 191). Still others (*Lysimachia terrestris*, Figure 177; *Stimpsonia chamaedryoides*, Figures 178, 179) might be described as finely reticulate. Additionally, in some grains the tectal perforations were most pronounced in the mesocolpial regions (*Coris*, Figure 174; *Naumbergia*, Figure 176; *Lysimachia terrestris*, Figure 177; *Anagallis*, Figure 183).

Transmission electron microscopy indicates a variability of exine structure within the family. Most taxa examined have a well-developed foot-layer and tectum, e.g., *Anagallis* (Figure 192), *Glaux* (Figure 194), *Naumbergia* (Figure 196), *Omphalogramma* (Figure 197), \pm short columellae, e.g., *Glaux* (Figure 194), *Naumbergia* (Figure 196), and an endexine that is massive in the region of the colpus and thinner but still prominent in the mesocolpial regions, e.g., *Anagallis* (Figure 192), *Glaux* (Figure 194), *Naumbergia* (Figure 196), *Omphalogramma* (Figure 197), *Stimpsonia* (Figure 199). In *Lysimachia hybrida* (Figure 195) the irregular tectum, incomplete columellae, and possibly the extensive endexine, are due to oblique section. Two species of *Primula*, *P. officinalis* (Figure 198) and *P. veris* (Figure 200), are exceptional, the foot-layer seemingly absent.

Heterostyly and dimorphic pollen grains are known to occur in the Primulaceae. Punt, et al. (1974) acknowledge this condition in some species of *Primula* and in *Hottonia palustris*, as well as dimorphic pollen grains in *Trientalis europaea*, due apparently to polyploidy. In *Glaux maritima* the collection of *Redfield s.n.* from Maine was distinct enough from that illustrated by Punt, et al.

(1974, pl. 14: figs. 1, 2) that the identification of *Redfield s.n.* was rechecked and verified, but still a second sample, *Haakana s.n.* from Finland, was examined, and these grains were more similar to those illustrated by Punt, et al. (1974). The differences in *Glaux* pollen may be due to heterostyly, not reported in the literature to our knowledge, or the pollen grains of this species may be simply rather variable. There are also some differences between our illustration of *Hottonia palustris* (Figure 185) and that of Punt, et al. (1974, pl. 4: figs. 11, 12; pl. 5: figs. 1–6), but the distinctly prolate shape shown in Figure 185 may be an artifact of preparation, i.e., collapse. We acknowledge the existence of heterostyly in the Primulaceae and dimorphic pollen (as in the Plumbaginaceae) but did not want the present study to be diluted by a detailed examination of this phenomenon. Whether it is the long- or short-styled form that is illustrated for *Hottonia*, *Primula*, and other Primulaceae, both authors feel strongly that the alternate form will not be shown to have the ektexine characteristic of so many of the centrosperous taxa (Figures 1–12). For detailed descriptions and measurements, the reader is advised to consult the article by Punt, et al. (1974).

Discussion and Conclusions

Of the three families examined in this study, the Polygonaceae is the most frequently considered as being related to the Centrospermae. Of the families that comprise this order, the Caryophyllaceae appears to be the most likely family from which the Polygonaceae could be derived or related to, since both have the anthocyanin pigments. The data from plastid structure, however, does not support a relationship between the Polygonaceae and Caryophyllaceae; the Caryophyllaceae not only have the protein or P-type plastid characteristic of the Centrospermae, but the plastids have a central crystalloid with a distinctive polygonal shape Behnke, 1976:42); the Polygonaceae have the more common starch or S-type plastid, but admittedly this characterization is based on a small number of species.

The data presented in this palynological study indicate that the Polygonaceae and Caryophyllaceae are not related. Although the Polygonaceae is a large and palynologically diverse family, examina-

tion of 85 species representing 36 genera (Figures 82–173), revealed no pollen types similar to those in the Caryophyllaceae. (For additional information on Caryophyllaceae, see Nowicke, 1975; Skvarla and Nowicke, 1976). The pollen data do not support a relationship between the subtribe Illecebrinae (Caryophyllaceae) or the larger Illecebraceae and any of the Polygonaceae examined in this study. The grains of *Illecebrum verticillatum* are almost identical to those of *Herniaria glabra* (Figure 15): in both species the pollen has a distinctive tetrahedral shape with a large aperture on each of the three (four?) faces. *Cardionema ramosissima* (Figure 16) has pantoporate grains, roughly cube-shaped and with a spinulose and tubuliferous/punctate ectexine. The unusual grains of *Illecebrum verticillatum* and *Herniaria glabra* have not been found in any other taxa examined to date, including those remaining in the order Centrospermae, as well as the Plumbaginaceae, Polygonaceae, and Primulaceae. These results would support Hutchinson's (1959) inclusion of *Herniaria* in the Illecebraceae, but not necessarily the family status since the remaining species examined, including another species of *Herniaria*, *H. hirsuta*, all have a common pantoporate grain.

An argument could be raised that the pollen of the Bistorta complex in *Polygonum* (Figures 124–129) and that of *Muehlenbeckia cunninghamii* (Figures 100, 101) provide some evidence for a relationship to the Centrospermae. However, we think it much more likely that the occurrence of this ectexine surface in a limited number of species is a reflection of the enormous palynological diversity in the Polygonaceae: ectexines that are \pm psilate, punctate, punctate-striate, conspicuously spinulose, perforate with small spines, microreticulate, finely reticulate to coarsely reticulate; apertures that are porate, pantocolpate or colporate with variable endoapertures; and grains that are probably unique (limited to the Polygonaceae), such as those of *Polygonella fimbriata* (Figure 130) and related species, *Polygonum convolvulus* (Figures 140, 141) and related species, or *Coccoloba cordata* (Figures 110, 111).

It is also clear that a diversity of structural forms exist in the Polygonaceae. These observations parallel the sculpturing pleomorphism illustrated by SEM. The TEM reveals wide variation in the de-

velopment of two layers—the endexine and foot-layer. The endexine can be absent (apparently) as in *Podopterus* (Figure 160), thin but recognizable as in *Chorizanthe paniculata* (Figure 146), well developed as in *Atraphaxis* (Figure 143) and *Nemacaulis* (Figure 157), and greatly enhanced as in *Eriogonum* spp. (Figures 148, 149). The foot-layer has a similar range of variation: from apparently absent in *Chorizanthe breweri* (Figure 145) and *Nemacaulis* (Figure 157) to prominently thickened in *Coccoloba cordata* (Figure 147) and *Podopterus* (Figure 160), with many intermediate stages represented in other taxa.

Another unusual characteristic is the granular inner surface of the tectum found in a number of closely related genera: *Chorizanthe* spp. (Figures 145, 146), *Eriogonum* (Figure 149), *Nemacaulis* (Figure 157), and *Oxytheca* (Figure 158).

While the tectum tends to be thin in the above taxa, in others, *Fagopyrum* (Figure 150) and *Triplaris* (Figure 173), it is much thicker.

The structure of the exine in the Bistorta complex of *Polygonum* (Figures 164, 168), densely packed columellae, is unique in all the taxa examined with TEM in this study or previously (Skvarla and Nowicke, 1976) and thus diminishes the possibility that the Centrospermae and the Polygonaceae could be linked by this group. In fact, it seems quite notable that in spite of the diverse exine structures in this family, there is very little similarity to the Centrospermae.

The spinulose and punctate ectexine surface found in the Polygonaceae or in the Centrospermae, for that matter, is simple enough to have arisen independently in any of these taxa. However, the significance attached to this ectexine in the Centrospermae is that in every betalain family, as well as in the Caryophyllaceae and Molluginaceae, the overwhelming majority of the species examined had pollen grains with a spinulose and tubuliferous/punctate ectexine, which, moreover, were sometimes identical between families. Insofar as pollen structure is concerned, a more defensible relationship could be proposed between the Polygonaceae and any dicot family with a preponderance of punctate ectexines. Pollen grains with a prominently reticulate ectexine are widely (and randomly?) distributed among dictyodendron families, but this may be due to parallel evolution and does

not necessarily mean that these families are related to each other or to the Polygonaceae.

This study reinforces current opinion (Cronquist, 1968; Philipson, 1975:74; Takhtajan, 1969:220) that the Primulaceae are not related to nor derived from the Centrospermae. According to Cronquist (1968:177, 223) the only special feature in common between the Caryophyllales (Centrospermae) and the Primulales is the free-central placentation. The results of pollen analysis indicate that the ancestors and/or relatives of the Primulaceae are not in the centrospermaous families. Although the pollen of the Primulaceae exhibits some variation (Figures 174–200), none of the taxa examined had grains with a counterpart in the Centrospermae.

Unlike the Primulaceae, the Plumbaginaceae are still regarded as being related to the Centrospermae (Takhtajan, 1969:215), although Cronquist (1968:185) refers to the family as “somewhat more isolated but may also be derived from the Caryophyllales” and Philipson (1975:74) considers the Plumbaginaceae-Centrospermae relationship as more debatable (than that of the Polygonaceae-Centrospermae). The pollen of the Plumbaginaceae (Figures 29–81) consists of the two major types, designated previously as *Armeria* and *Plumbago*, each of which can be dimorphic in heterostyled species. This results in four distinctive types, all 3- (or 4-) colpate (*Ceratostigma willmottianum* and *Limoniastrum monopetalum* notwithstanding): finely and coarsely reticulate *Armeria* forms (Figures 41–58), and pointed-verrucae and rounded-verrucae

Plumbago forms (Figures 29–40). Admittedly the two forms of the *Plumbago* type are based on results from only two species, but the *Plumbago* ektexine type has not been found in any other taxon in this study or in earlier related ones (Nowicke, 1975; Skvarla and Nowicke, 1976). The coarsely reticulate form of the *Armeria* type has a superficial resemblance to some reticulate grains in the Polygonaceae, but the formation of the muri in the Polygonaceae is distinctive, alternate dupli-baculate (Figures 112–117, 122, 123), versus simplibaculate in the *Armeria* forms (Figures 41–58). In reticulate grains found in the Centrospermae and in the Polygonaceae (Figures 113–116), the lumina usually have at least some free columellae (or bacula), whereas in both *Armeria* forms (Figures 42, 44, 46, 48, 51, 55, 56), the lumina are consistently free of any columellar material (the data of Praglow-ski and Erdtman, 1969, notwithstanding).

In the Plumbaginaceae the pollen data, plastid structure, and pigmentation (unless the tie is to the Caryophyllaceae and/or Molluginaceae) suggest that this family is not related to the Centrospermae and that its phylogenetic position needs to be reevaluated.

Like the Plumbaginaceae, the Primulaceae has the anthocyanin pigments, and has the starch type plastid structure (Behnke, pers. comm.). However, most authors (Cronquist, 1968; Philipson, 1975; Takhtajan, 1969) do not regard the Primulaceae as related to the Centrospermae and the pollen data presented here reinforces that view.

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TABLE 1.—Results of pollen analysis of taxa examined for ektexine characteristics

Taxa	Species	Genera	Spinulose + Tubuliferous/Punctate	Other
Plumbaginaceae	20	9	0	21
Polygonaceae	85	36	4?	81
Primulaceae	29	22	0	29
Betalain families plus Caryophyllaceae and Molluginaceae	217		184	33

TABLE 2.—Centrospermae specimens examined, arranged alphabetically by family (pollen types I, II, and III are 3-colpate, pantoporate, and pantocolpate respectively, all with a spinulose and tubuliferous or punctate ektexine; Spec. = specialized, any type not included in I-III)

Taxa	Collector	Location	Pollen description	Figure numbers
AIZOCEAE				
<i>Geocarpon minimum</i> Mackenzie.....	Palmer 5517	Missouri	II	9
<i>Mesembryanthemum variabile</i> Haworth.....	Walther s.n.	California	I	1, 8, 19
<i>Tetragonia arbuscula</i> Fenzl.....	Bayliss 2171	S. Africa	I	
AMARANTHACEAE				
<i>Achyranthes aspera</i> L.	Philipson 10510	New Zealand	II	
<i>Chamissoa altissima</i> (Jacquin) H.B.K.	Curtiss 269	Cuba	II	
<i>Dicraurus altermifolius</i> (Watson) Uline & Bray.	Carter et al. 2061	Mexico	II	
<i>Psilotrichum amplum</i> Suessenguth.....	Burger 3248	Ethiopia	II	13, 20
<i>Ptilotus corymbosum</i> Gaudichaud-Beaupre.....	Pritzel 58	Australia	II	
<i>P. obovatum</i> Gaudichaud-Beaupre.....	Lazarides 4333	Australia	II	

TABLE 2--Continued

Taxa	Collector	Location	Pollen description	Figure numbers
BASELLACEAE				
<i>Anredera scandens</i> Moquin.....	Nelson 1666	Mexico	II	3, 21
CACTACEAE				
<i>Borsicactus tenuiserpens</i> (Rauh & Backeberg) Kimmach.....	Hutchison & Wright 4448	Peru	I	11
<i>Hamatocactus setispinus</i> Britton & Rose.....	Pratt 9483	Texas	III	12
<i>Opuntia lindheimeri</i> Engelm.....	Griffiths 9031	Texas	Spec.	17, 22
CARYOPHYLLACEAE				
<i>Achyronychia cooperi</i> A. Gray.....	Parker et al. 7768	Arizona	II	
<i>Cardionema ramosissima</i> A. Nelson & Macbride...	Fosberg 22540	Ecuador	II	16
<i>Gymnocarpus fruticosum</i> Persoon.....	Chevallier 28	Algeria	II	4, 23
<i>Herniaria glabra</i> L.	Staszkiwicz in Plantae Poloniae, 527	Poland	Spec.	15, 24
<i>H. hirsuta</i> L.	Mandaville 139	Saudi Arabia	II	
<i>Illecebrum verticellatum</i> L.	MO 176804	France	Spec.	
<i>Pollichia campestris</i> Aiton.....	Wood 591	S. Africa	II	
<i>Silene armeria</i> L.	Klein 2621	Brazil	II	
<i>Siphonychia americana</i> (Nuttall) Torrey & A. Gray.....	Thorne 15254	Florida	II	14
<i>Tunica stricta</i> (Bunge) Fischer & Meyer.....	Goloskokov s.n.	USSR	II	
CHENOPODIACEAE				
<i>Chenopodium ambrosioides</i> L.	Guinea 112	Spain	II	5, 25
HECTORELLACEAE				
<i>Lyallia kerguelensis</i> Hooker.....	Transit of Venus Expd.	New Zealand	II	
MOLLUGINACEAE				
<i>Limnium viscosum</i> Fenzl.....	Seydel 751	SW Africa	I	2, 7, 26
<i>Mollugo oppositifolius</i> L.	Gandhi 2092	India	I	
NYCTAGINACEAE				
<i>Abronia angustifolia</i> Greene.....	Peebles & Harrison 3949	Arizona	Spec.	18, 27
<i>Bougainvillea peruviana</i> H.B.K.	Hutchison 1415	Peru	Spec.	
<i>Mirabilis alipes</i> Watson.....	Atwood 4550	Utah	II	
<i>Selinocarpus diffusus</i> A. Gray.....	Wootton s.n.	New Mexico	II	
PHYTOLACCACEAE				
<i>Agdestis aematidea</i> Mocino & Sesse.....	Pringle 3276	Mexico	I	
<i>Microtea myypurensis</i> (H.B.K.) G. Don.....	Bang 1589	Bolivia	II	
<i>Stegnosperma cubense</i> A. Richardson.....	Goldsmith 99	Mexico	I	
PORTULACACEAE				
<i>Lesnia chamaepithys</i> Philippi.....	Johnston 6091	Argentina	I	
<i>Lewisia columbiana</i> (Howell) Robinson.....	Jones 214	Idaho	I	
<i>Montia meridensis</i> Friedrich.....	Hammen 1194	Colombia	Spec.	
<i>Naiocrene parvifolia</i> (Moquin) Rydberg.....	Applegate 2556	Oregon	III	6, 10, 28

TABLE 3.—Plumbaginaceae specimens examined (all 3-colpate except as noted; A = *Armeria* type, AC = coarsely reticulate *Armeria* form, AF = finely reticulate *Armeria* form, P = *Plumbago* type, PP = pointed verrucae *Plumbago* form, PR = rounded verrucae *Plumbago* form)

Species	Collector	Location	Pollen description	Figure numbers
<i>Acantholimon glumaceum</i> Boissier.....	Unknown collector	Cultivated Hort. Brussels	AC	
<i>A. olivieri</i> Jaubert & Spach..	Koelz 15794	Iran	AC	65, 66
<i>A. phrygium</i> Boissier.....	Bornmuller 5511	Turkey	AF	
<i>Armeria maritima</i> (Miller) Willdenow.....	Mathiesen & Pedersen s.n. Svenson s.n. Thedenius s.n.	Denmark 'Scandinavia' Sweden	AC AF AC	45, 46, 67 43, 44, 68
<i>A. maritima</i> var. <i>sibirica</i> (Turczaninow) Lawrence.....	Bartlett 147 Calder 2014 Cody 1794 Ekblaw 610 Lindager s.n. Stein 175	Greenland Canada Greenland Greenland Greenland Greenland	A A A A A A	
<i>A. scabra</i> Pallas.....	H. Smith s.n.	Sweden	AC	
<i>Ceratostigma griffithii</i> C. B. Clarke.....	Rock 6577 Rock 11578	China China	PP PR	31, 32, 70 29, 30, 69
<i>C. minus</i> Stapf.....	Schneider 2584	China	P	
<i>C. willmottianum</i> Stapf.....	Kingdon-Ward 12530 MO Wilson 1373	India China	PP PP ¹	61, 62 59, 60, 71
<i>Dyerophytum africanum</i> (Lamarck) O. Kuntze.....	Goldblatt 2250 MO Werdermann & Oberdieck 594 Seyel 4025 MO	S. Africa S. Africa Namibia	PR P P	63, 64, 72
<i>Goniolimon collinum</i> (Grisebach) Boissier.....	Rechinger f. 10375	Greece	AC	53, 54, 73
<i>Limoniastrum guyonianum</i> Durieu de Maisonneuve.....	Chevallier 82	Algeria	AF	74
<i>L. monopetalum</i> Boissier.....	Puech s.n.	France	AC ²	
<i>Limonium viciosi</i> Pau.....	Vicioso s.n.	Spain	AC	41, 42, 75
<i>L. vulgare</i> Miller.....	Holm-Nielsen s.n. MO Hubbard 13206 MO Moss MO Lawalree 3820 MO	Denmark Britain Britain Belgium	AF AC AC AC	52 51
<i>Plumbago auriculata</i> Lamarck.....	Bayliss 1187 GH Bayliss 3106 MO	S. Africa S. Africa	PR P	39, 40
<i>P. europaea</i> L.	Raine s.n. GH Sporiks s.n. GH	'Almunarro' Persia	PP PR	37, 38 35, 36
<i>P. rosea</i> L.	Urban 5490 GH	Puerto Rico	PP	33, 34
<i>P. scandens</i> L.	Woytkowski 5592	Peru	P	76
<i>Statice sinuata</i> L.	Maire & Wilczek 1048 Vaccari 495	Morocco Greece	AF AC	57, 58, 77, 78 55, 56, 79, 80
<i>S. tenella</i> Turczaninow.....	Chaney 517 Chaney 517a	Mongolia Mongolia	AC AF	47, 48, 81 49, 50

¹ Pantocolpate

² 4-5 zonocolpate

TABLE 4.—Polygonaceae specimens examined (3C = 3-colporate, PC = pantocolpate, PP = pantoporate)

Species	Collector	Location	Pollen description	Figure numbers
<i>Afrobrunnichia erecta</i> Hutchison & Dalziel.....	Baldwin 11489	Liberia	3C, punctate	
<i>Antigonon guatemalense</i> Meisner.....	Laughlin 2635	Mexico	3C, punctate-striate	142
<i>Atraphaxis buxifolia</i> Jaubert & Spach.....	Woronow s.n.	USSR	3C, striate-punctate	98, 99, 143
<i>Brunnichia cirrhosa</i> Banks..	Biltmore Herb. 1678 B	Alabama	3C, punctate-striate	
<i>Calligonum comosum</i> L'Heritier.....	Mandaville 69	Saudi Arabia	3C, punctate-striate	94, 95, 144
<i>Centrostegia thurberi</i> A. Gray.....	Hoover 4373	California	3C, clustered punctate	
<i>Chorizanthe breweri</i> S. Watson.....	Hoover 11393	California	3C, finely punctate	145
<i>C. fimbriata</i> Nuttall.....	Wiggins 9908	Mexico	3C, clustered punctate	84
<i>C. membranacea</i> Bentham.....	Bruce 155	California	3C, clustered punctate	
<i>C. paniculata</i> Bentham.....	Bro. Claude Joseph 2997	Chile	3C, punctate	85, 146
<i>Chorizanthe</i> sp.	Simon 289	Chile	3C, punctate	
<i>Coccoloba barbeyana</i> Lindau.	Schunke 76	Peru	3C, deeply punctate-striate	
<i>C. cordata</i> Chamisso.....	Hatschbach et al. 13352	Brazil	3C, columnar-pyramidal	110, 111, 147
<i>C. diversifolia</i> Jacquin....	Bro. Clemente s.n.	Cuba	3C, punctate-striate	
<i>C. obovata</i> H.B.K.	Duke 4988	Panama	3C, prominently punctate	
<i>C. parimensis</i> Bentham.....	Ducke 1289	Brazil	3C, microreticulate	
<i>C. swartzii</i> Meisner.....	Webster et al. 10296	Bahamas	3C, punctate-striate	
<i>C. venosa</i> L.	Harris & Britton 10756	Jamaica	3C, punctate	
<i>Dedeckera eurekaensis</i> Reveal & Howell.....	Reveal et al. 3909	California	3C, punctate	
<i>Emex australis</i> Steinheil...	Scheepers 928 MO	S. Africa	3C, perforate and spinulose	
	Seydel 2975	SW Africa	3C, perforate and spinulose	136
<i>E. spinosa</i> (L.) Campdera...	Koelz 14304	Iran	3C(?), perforate and spinulose	
<i>Eriogonum cornellii</i> Reveal.	Reveal & Davidse 883	Texas	3C, finely punctate	
<i>E. inflatum</i> Torrey & Fremont.....	Gentry 14437	Mexico	3C, clustered punctate	
<i>E. marifolium</i> Torrey & A. Gray.....	Holmgren & Reveal 2706	Oregon	3C, finely punctate-striate	90, 91, 148
<i>E. parishii</i> S. Watson.....	Wiggins & Demaree 4913	Mexico	3C, clustered punctate	149
<i>E. racemosum</i> Nuttall.....	Eggleston 5847	Colorado	3C, clustered punctate	
<i>E. thomasi</i> Torrey.....	Jones s.n.	California	3C, punctate-striate	
<i>Fagopyrum esculentum</i> Moench.....	Braun s.n.	Ohio	3C, deeply punctate	87, 150
<i>Gilmania luteolum</i> (Coville) Coville.....	Gilman 1520	California	3C, punctate	
<i>Gymnopodium antigonoides</i> (Robinson?) Blake.....	Gaumer & Sons 23207 Goldman 743	Mexico Mexico	3C, punctate-striate 3C, punctate-striate	92, 93, 151
<i>Harfordia macroptera</i> (Bentham) Greene & Parry.	Wiggins 7601	Mexico	3C, punctate-striate	96, 97, 152
<i>Hollisteria lanata</i> S. Watson.....	Hoover 3496	California	3C, punctate	
<i>Koenigia islandica</i> L.	Koelz 6424	India	PP, spinulose	
<i>Lastarriaea chilensis</i> Remy.	Worth & Morrison 16270 UC	Chile	3C, punctate	
	Worth & Morrison 16338 UC	Chile	3C, punctate	137
<i>L. coriacea</i> (Goodman) Hoover.....	Leiberg 3260 Howell 32083	California California	3C, punctate 3C, punctate	
<i>Mucrona californica</i> Bentham.....	Grinnell s.n.	California	3C, finely punctate-striate	88, 89
<i>Muehlenbeckia chilensis</i> Meisner.....	E. & M. Holway 199	Chile	3C, punctate-striate	102, 103, 153
<i>M. cunninghamii</i> Mueller....	Aston 984	Australia	3C, sparsely spinulose and punctate	100, 101, 155
	Constable 18440	Australia	3C, sparsely spinulose and punctate	
	Lazarides 5745	Australia	3C, sparsely spinulose and punctate	

TABLE 4—Continued

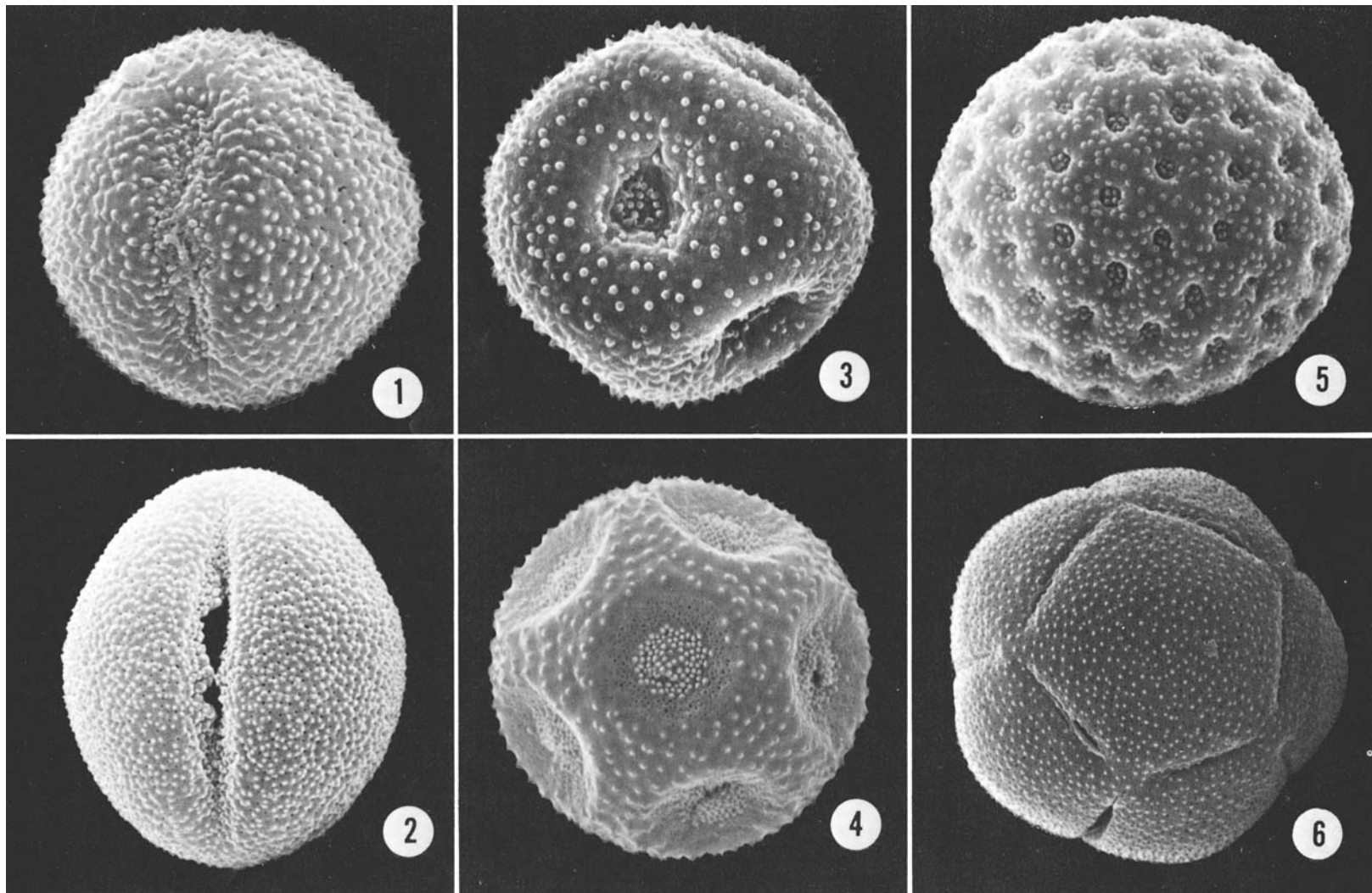
Species	Collector	Location	Pollen description	Figure numbers
<i>M. polybotryar</i> Meisner....	Pritzel 399	Australia	3C, punctate-striate	156
<i>M. tamnifolia</i> (HBK) Meisner.	Balls 5804	Ecuador	3C, punctate-striate	104, 105, 154
<i>Neomillspaughia paniculata</i> (Donnell-Smith) Blake....	Edwards P 675	Honduras	3C, punctate-striate	
<i>Nemacaulis denudata</i> Nuttall.....	Cleveland s.n.	California	3C, finely punctate	82, 157
<i>Oxygonum atriplicifolium</i> Martelli.....	Piemeisel & Kephart 56	Kenya	3C, punctate and microreticulate	
<i>O. dregeanum</i> Meisner.....	Bayliss 4515	S. Africa	3C, microreticulate	
<i>O. zeyheri</i> Sonder.....	Galpin 13075	S. Africa	3C, microreticulate	
<i>Oxyria digynia</i> (L.) Hill...	Neilson 902	Canada	3 colpate-very thin walled	
<i>Oxytheca dendroidea</i> Nuttall.....	Eastwood & Howell 7353	Nevada	3C, finely punctate- striate	
	Wagenknecht 18118	Chile	3C, finely punctate- striate	
<i>O. luteola</i> Parry.....	Pringle s.n.	California	3C, finely punctate- striate	
	Walther 14379	California	3C, finely punctate- striate	
<i>O. parishii</i> Parry.....	S. & W. Parish 993	California	3C, punctate	
<i>O. trilobata</i> A. Gray.....	Abrams 3807	California	3C, finely punctate- striate	83, 158
<i>Pericaria coccinea</i> Greene.	Eastwood 1427	California	PC, finely reticulate	112
<i>Podopterus mexicanus</i> Kunth.	Langlassi 922	Mexico	3C, microreticulate	132, 160
<i>Polygonella fimbriata</i> (Elliot) Horton.....	Ward & Smith 2236	Florida	3C, finely punctate and reticulate	130, 161
<i>P. polygama</i> (Ventenat) Engelmann & A. Gray.....	Bright 6309	S. Carolina	3C, microreticulate	131
<i>Polygonum acuminatum</i> Kunth.	Irwin & Souza 9565	Brazil	PP, reticulate	113
<i>P. affine</i> D. Don.....	Staunton et al. 1328	Nepal	3C, finely punctate and spinulose	124
<i>P. amphibium</i> L.	Braun 29	Indiana	PC, finely reticulate	120, 121, 162, 163
<i>P. bistorta</i> L.	Cantlon & Gillis 57-439	Alaska	3C, finely punctate and spinulose	
	Cantlon & Malcolm 580085	Alaska	3C, finely punctate and spinulose	128, 129, 164
	Calder & Billard 3833	Canada	3C, finely punctate and spinulose	
<i>P. capitatum</i> D. Don.....	Tsiang 4503	China	3C, reticulate	122, 123
<i>P. cilinode</i> Michaux.....	Hardin 722	N. Carolina	3C, finely punctate- striate	
<i>P. convolvulus</i> L.	Horr & McGregor E495	Kansas	3C, psilate and spinulose	140, 141, 165
<i>P. cristatum</i> Engelmann & Gray.....	Graham 25	Texas	3C, psilate and spinulose	
<i>P. cuspidatum</i> Siebold & Zuccarini.....	Makino 13368	Japan	3C, deeply punctate	
<i>P. cyanandrium</i> Diels.....	Rock 5935	China	PP, spinulose	134, 135
<i>P. dielsii</i> Leville (?).....	Henry 9379	China	3C, coarsely reticulate	116, 117, 166
<i>P. dumetorum</i> L.	Makino 13491	Japan	3C, psilate and spinulose	
<i>P. forrestii</i> Diels.....	Rock 9697	China	PC, spinulose	133, 167
<i>P. multiflorum</i> Thunberg....	Makino 15020	Japan	3C, deeply punctate	
<i>P. orientale</i> L.	Johnson s.n.	New York	PP, reticulate	114, 115, 159
<i>P. vacciniifolium</i> Wallich...	Koelz 976	India	3C, punctate	126, 127, 168
<i>P. virginianum</i> L.	Standley 8342	Missouri	PC, finely reticulate	118, 119, 169
<i>P. viviparum</i> L.	Alm s.n.	Sweden	3-4C, very finely spinulose	125
<i>Pteropyrum aucheri</i> Jaubert & Spach.....	Rechinger 27660	Pakistan	3C, punctate-striate	
<i>Pterostegia drymaroides</i> Fischer & Meyer.....	Gillespie 5495	Arizona	3C, punctate-striate	
<i>Rheum delavayi</i> Franchet....	Rock 16256	China	3C, punctate	
<i>Rumex acetosa</i> L.	Greuter & Hainard 567	Switzerland	3(-4)C, perforate and spinulose	138, 139, 170
<i>R. acetosella</i> L.	Rouleau 67	Canada	3(-4)C, perforate and spinulose	

TABLE 4—Continued

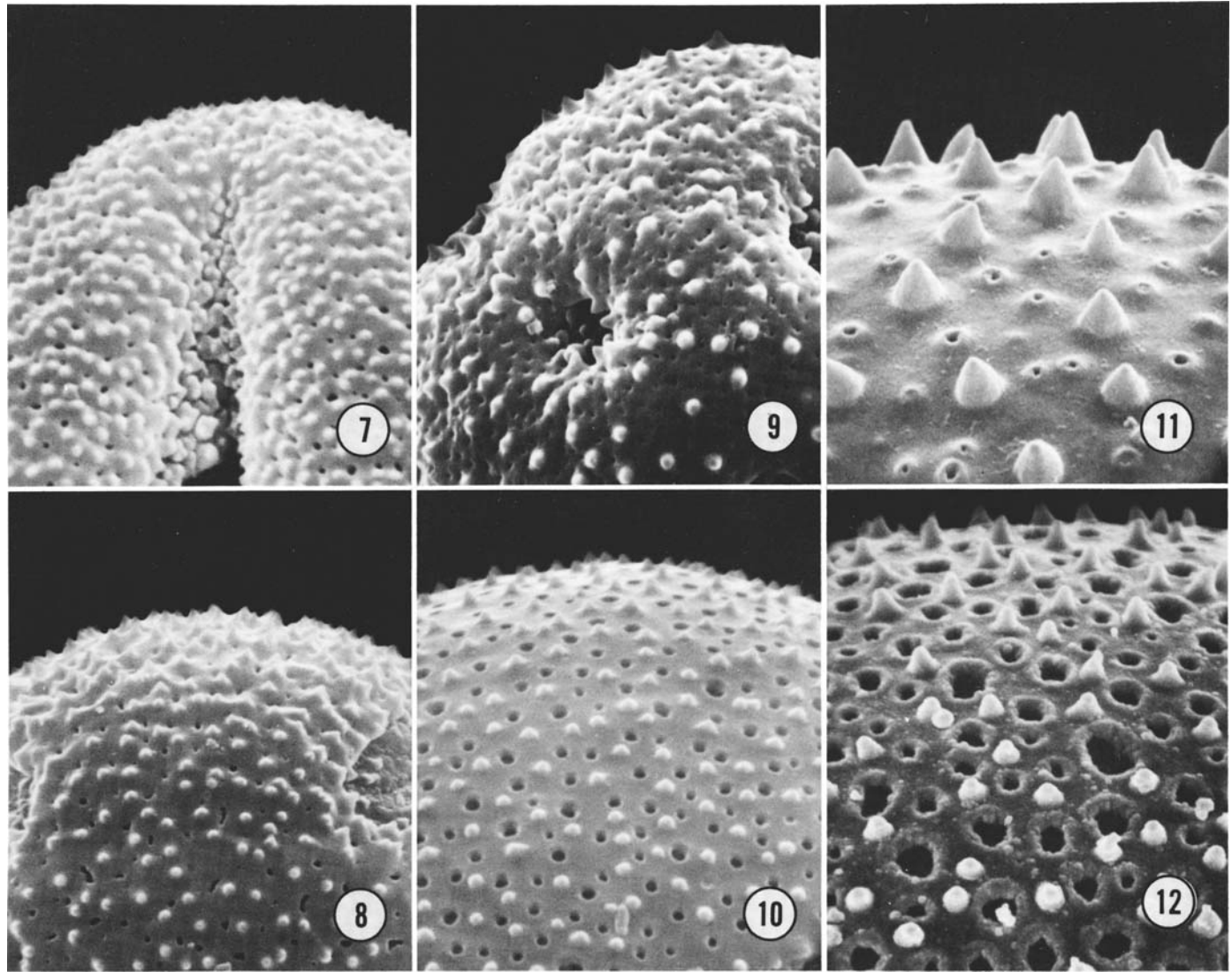
Species	Collector	Location	Pollen description	Figure numbers
<i>R. aquaticus</i> L.	Heikkinen s.n.	Finland	3(-4)C, perforate and spinulose	
<i>R. crispus</i> L.	Standley 18083	Montana	3C, perforate and spinulose	
<i>R. scutatus</i> L.	Pfister 1158/2	France	3C, perforate and spinulose	
<i>Ruprechtia laxiflora</i> Meisner.....	Hatschbach 13161	Brazil	3C, deeply punctate-striate	106, 171
<i>R. pallida</i> Standley.....	Newman 17	Mexico	3C, perforate-rugulose	107, 172
<i>R. ramiflora</i> (Jacquin) Meyer.....	Haught 3914	Colombia	3C, deeply punctate-striate	108, 109
<i>Symmeria paniculata</i> Bentham.....	Ducke 650 MO	Brazil	3C, † psilate	
<i>Triplaris americana</i> L.	Pittier 12204	Venezuela	3C, punctate-striate	86, 173

TABLE 5.—Primulaceae specimens examined (3C = 3-colporate, 4C = 4-colporate)

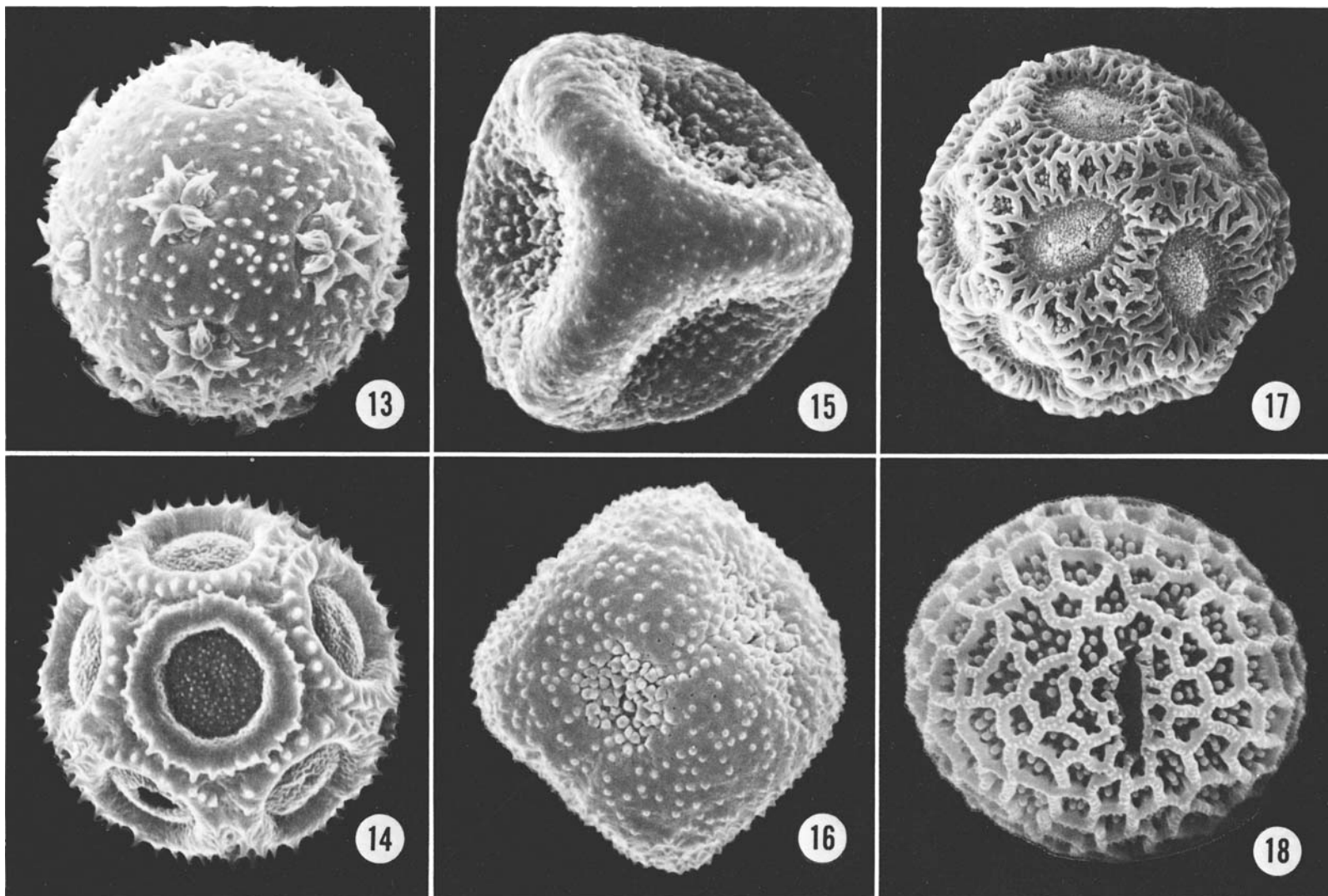
Species	Collector	Location	Pollen description	Figure numbers
<i>Anagallis linifolia</i> L.	Reverchon 388	Spain	3C, prominently punctate	183, 192
<i>Androsace septentrionalis</i> L.	Tarleton 8	Alaska	3C, punctate	
<i>Apochoris pentapetala</i> Duby..	Zimmermann 257	China	3C, microreticulate	
<i>Ardisandra wittsteinii</i> R. Wagner.....	Greenway & Kanuri 15044 MO	Kenya	3C, punctate	
<i>Centunculus pentandrus</i> R. Brown.....	Standley 12941	Florida	3C, microreticulate	
<i>Coris monspeliensis</i> L.	Tidestrom 13554	France	3C, sculptured & psilate	174, 193
<i>Cortusa matthioli</i> L.	Koelz 4994	India	3-syncolporate, granular	
<i>Cyclamen neapolitanum</i> Tenore.....	Stefani s.n.	Corsica	3C, punctate	184
<i>Dionysia mira</i> Wendelbo.....	Mandaville 3600	Oman	6-8 zonocolpate, deeply punctate	
<i>Dodecatheon alpinum</i> (A. Gray) Greene.....	Maguire & Holmgren 26449	Oregon	3C, punctate-granular	180, 181
<i>Douglasia montana</i> A. Gray...	Thompson 13766	Idaho	3C, punctate	
<i>Glaux maritima</i> L.	Haakana s.n.	Finland	3C, punctate-striate	190, 194
	Redfield s.n.	Maine	3C, irregularly punctate-striate	
<i>Hottonia palustris</i> L.	Cernohorsky & Krajina 286	Czechoslovakia	3C, microreticulate	185
<i>Lysimachia ciliata</i> L.	Cronquist & Jones 5956	Idaho	3C, psilate-finely punctate	
<i>L. hybrida</i> Michaux.....	Leonard & Killip 871	Maryland	3C, finely punctate	175, 195
<i>L. terrestris</i> (L.) Britton, Stern & Poggenberg.....	Mac Kenzie 2720	New Jersey	3C, microreticulate	
<i>Lysimachiopsis hillebrandii</i> Heller.....	Degener 21278 MO	Hawaii	4C, punctate-psilate	
<i>Naumburgia thyrsiflora</i> (L.) Reichenbach.....	Andersen s.n.	Norway	3C, irregularly microreticulate	176, 196
<i>Omphalogramma vincaeflora</i> Franchet.....	Rock 3573	China	3C, microreticulate	191, 197
<i>Primula farinosa</i> L.	St. John 90675	Quebec	4-syncolporate, microreticulate	
<i>P. incisa</i> Franchet.....	Rock 17474	China	3C, microreticulate	198
<i>P. officinalis</i> (L.) Jacquin.	Ludera s.n.	Poland	6-8 zonocolpate, microreticulate	
<i>P. veris</i> L.	Charpin et al. s.n.	France	6-10 zonocolpate, microreticulate	186, 187
	Skvortsoo s.n.	USSR	6-8 zonocolpate, microreticulate	
<i>P. vulgaris</i> Hudson.....	Pfister s.n.	Switzerland	6-8 zonocolpate, microreticulate (many abnormal grains)	200
<i>Samolus ebracteatus</i> Kunth...	Francis 8a	Florida	3C, punctate	189
<i>Soldanella alpina</i> L.	Treffer, 1362 in Flora Exsiccata Austro-Hungarica	Austria	3-colpate (syncolpate?), scabrate-spinulose	
<i>S. austriaca</i> Vierhapper....	Keller s.n.	Austria	3-colpate (syncolpate?), scabrate-spinulose	
<i>Stimpsonia chamaedryoides</i> C. Wright.....	Ying Hu 10001	Hong Kong	3C, finely reticulate	178, 179, 199
<i>Trientalis americana</i> (Persoon) Pursh.....	Palmer 1370	Canada	3C, punctate	



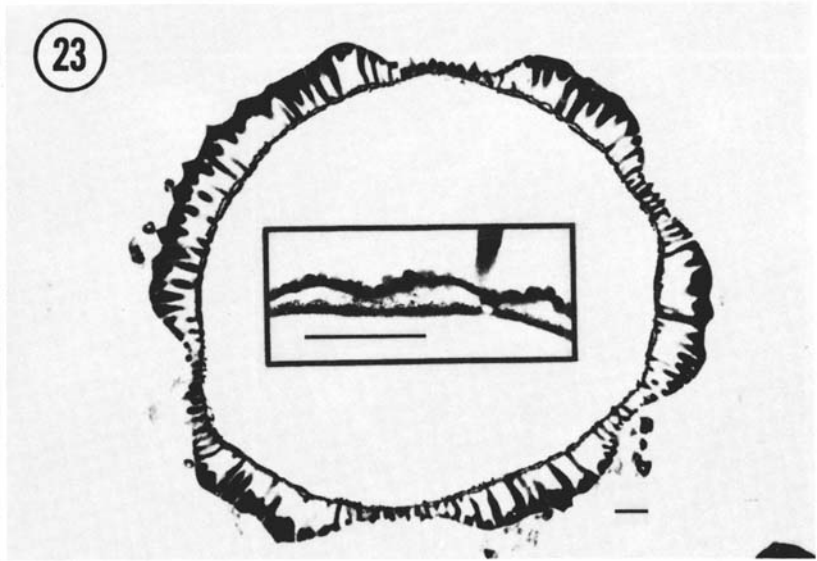
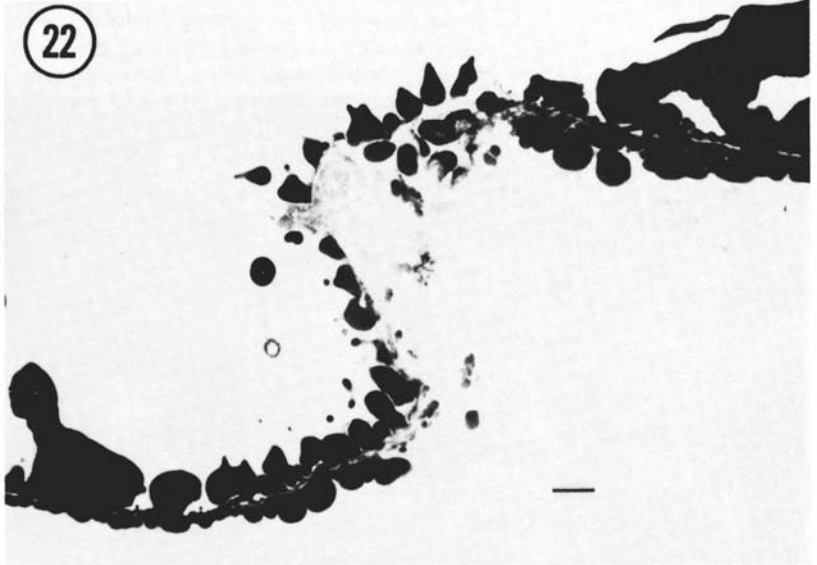
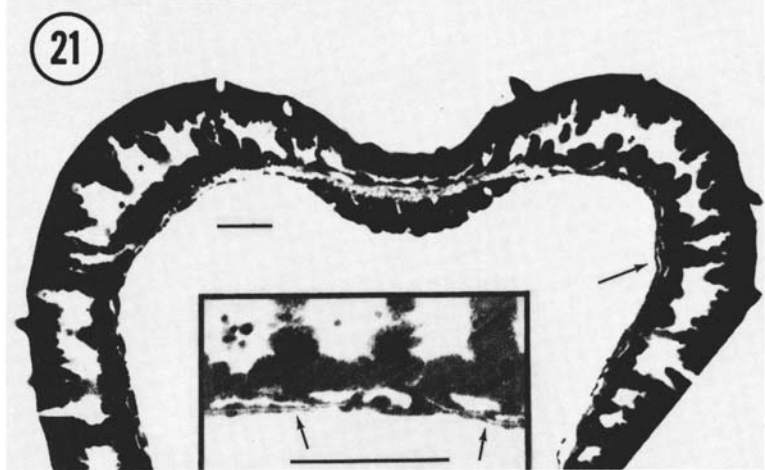
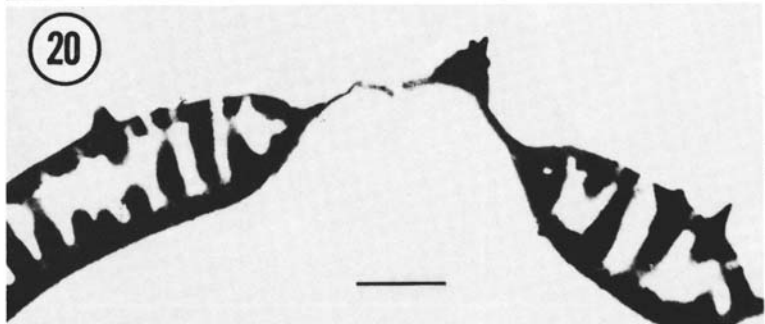
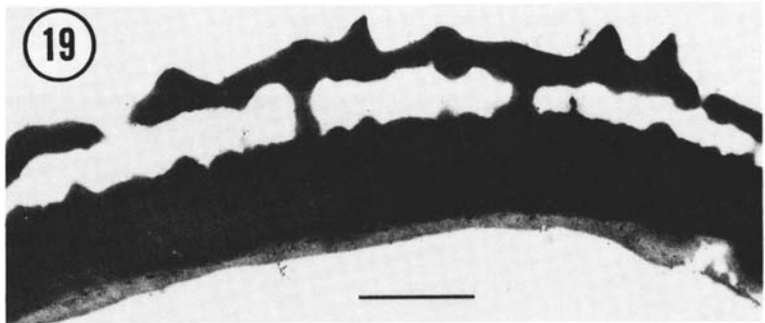
FIGURES 1-6.—Centrospermae pollen, SEM: 1, Aizoaceae, *Mesembryanthemum variabile* Haworth, equatorial view, $\times 4100$; 2, Molluginaceae, *Limeum viscosum* Fenzl, equatorial view, $\times 3900$; 3, Basellaceae, *Anredera scandens* Moquin, $\times 3550$; 4, Caryophyllaceae, *Gymnocarpus fruticosum* Persoon, $\times 3350$; 5, Chenopodiaceae, *Chenopodium ambrosioides* L., $\times 3600$; 6, Portulacaceae, *Naiocrene parvifolia* (Moquin) Rydberg, $\times 1900$. (Photo reduced to 81½ percent.)



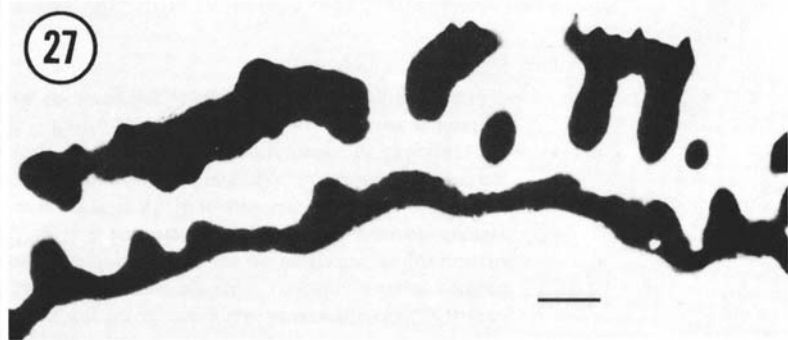
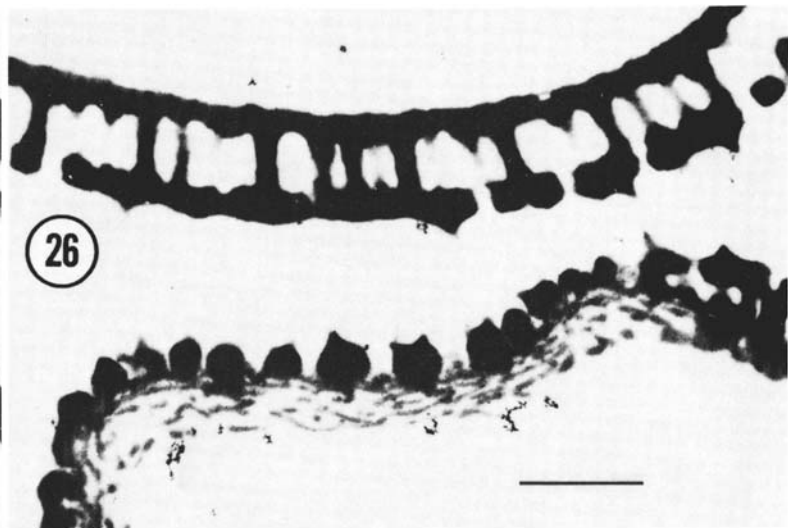
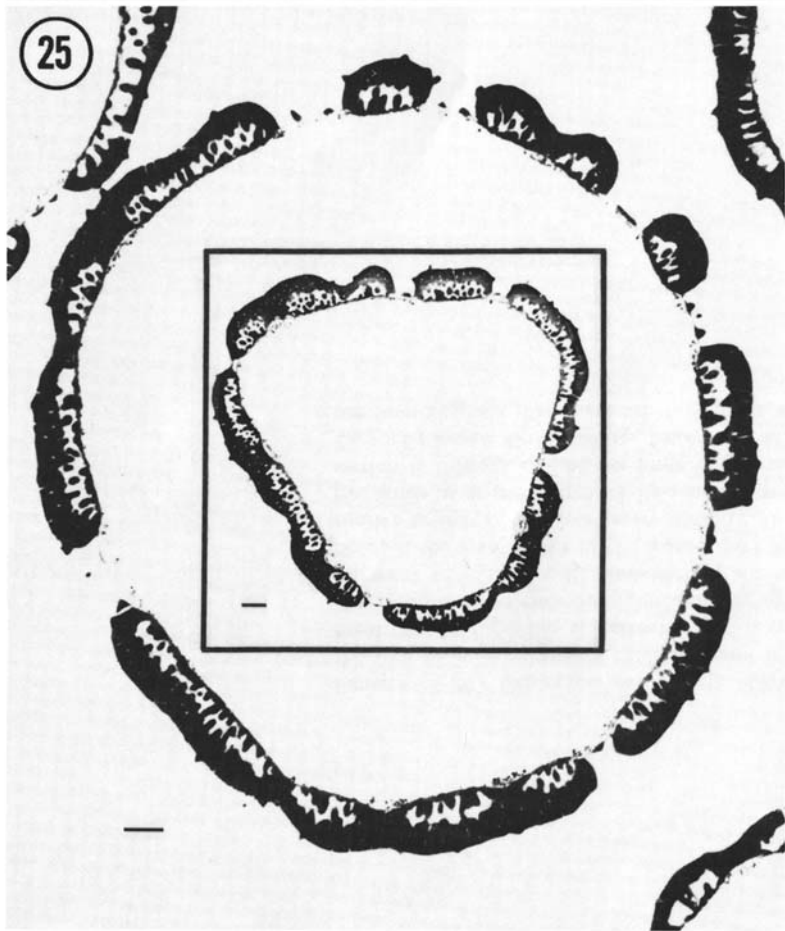
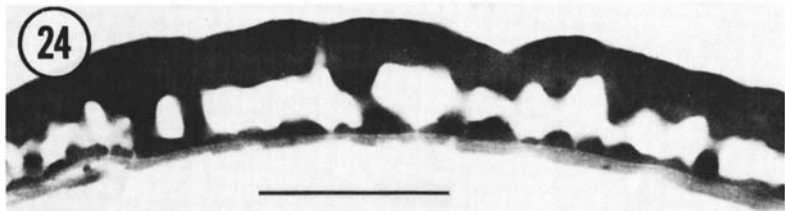
FIGURES 7-12.—Centrospermae pollen, SEM: 7, Molluginaceae, *Limeum viscosum*, ektexine surface, $\times 7500$; 8, Aizoaceae, *Mesembryanthemum variabile*, ektexine surface, $\times 7500$; 9, Aizoaceae, *Geocarpon minimum* Mackenzie, ektexine surface, $\times 7500$; 10, Portulacaceae, *Naiocrene parvifolia*, $\times 7500$; 11, Cactaceae, *Borzicactus tenuiserpens* (Rauh & Backeberg) Kimmach, ektexine surface, $\times 7500$; 12, Cactaceae, *Hamatocactus setispinus* Britton & Rose, ektexine surface, $\times 7500$. (Photo reduced to 76½ percent.)



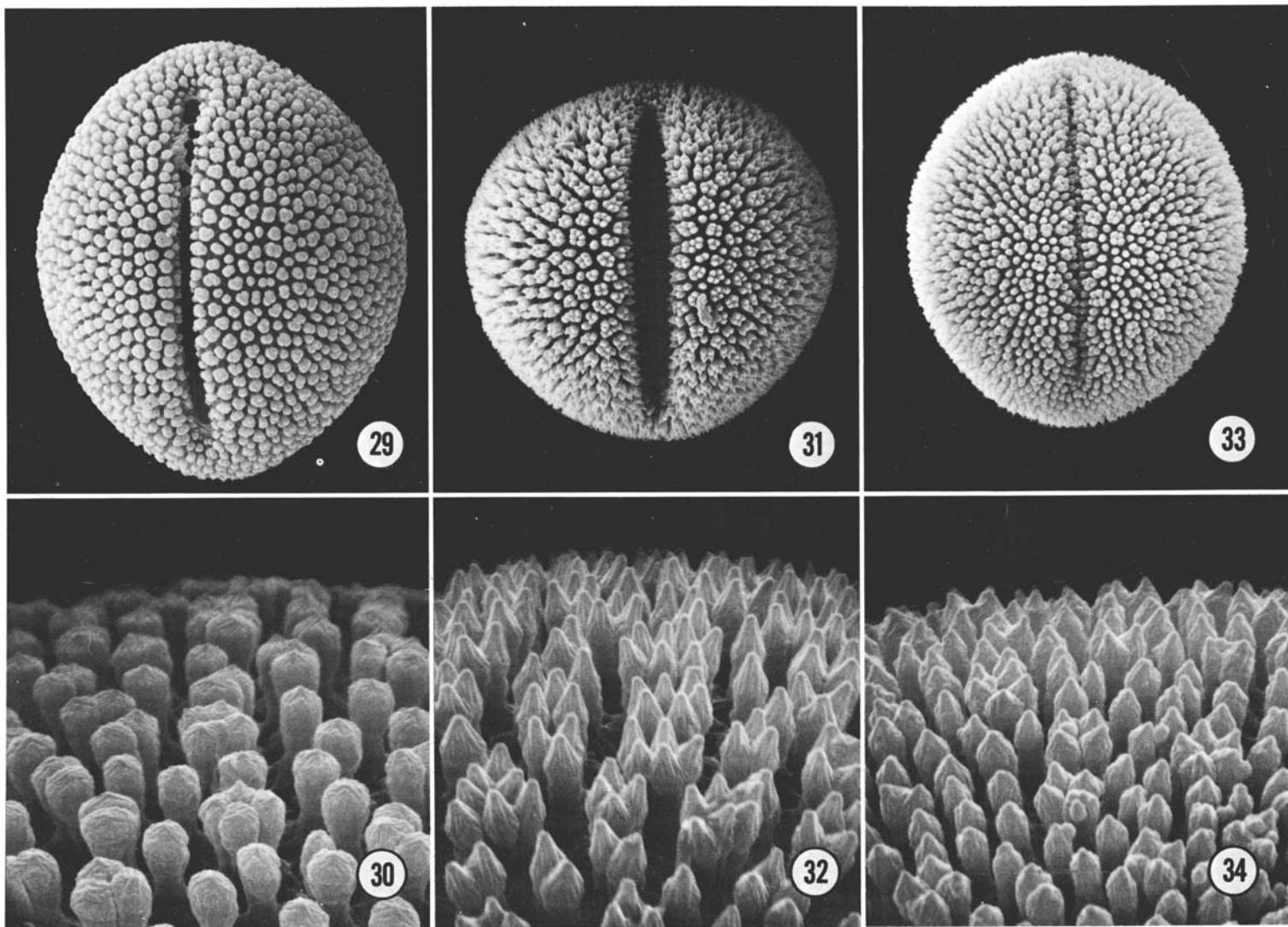
FIGURES 13-18.—Centrospermae pollen, SEM: 13, Amaranthaceae, *Psilotrichum amplum* Sussenguth, $\times 4000$; 14, Caryophyllaceae, *Siphonychia americana* (Nuttall) Torrey & A. Gray, $\times 4600$; 15, Caryophyllaceae, *Herniaria glabra* L., $\times 6000$; 16, Caryophyllaceae, *Cardionema ramosissima* A. Nelson & Macbride, $\times 5500$; 17, Cactaceae, *Opuntia lindheimeri* Engelm., $\times 840$; 18, Nyctaginaceae, *Abronia angustifolia* Greene, equatorial view, $\times 2870$. (Photo reduced to 81 percent.)



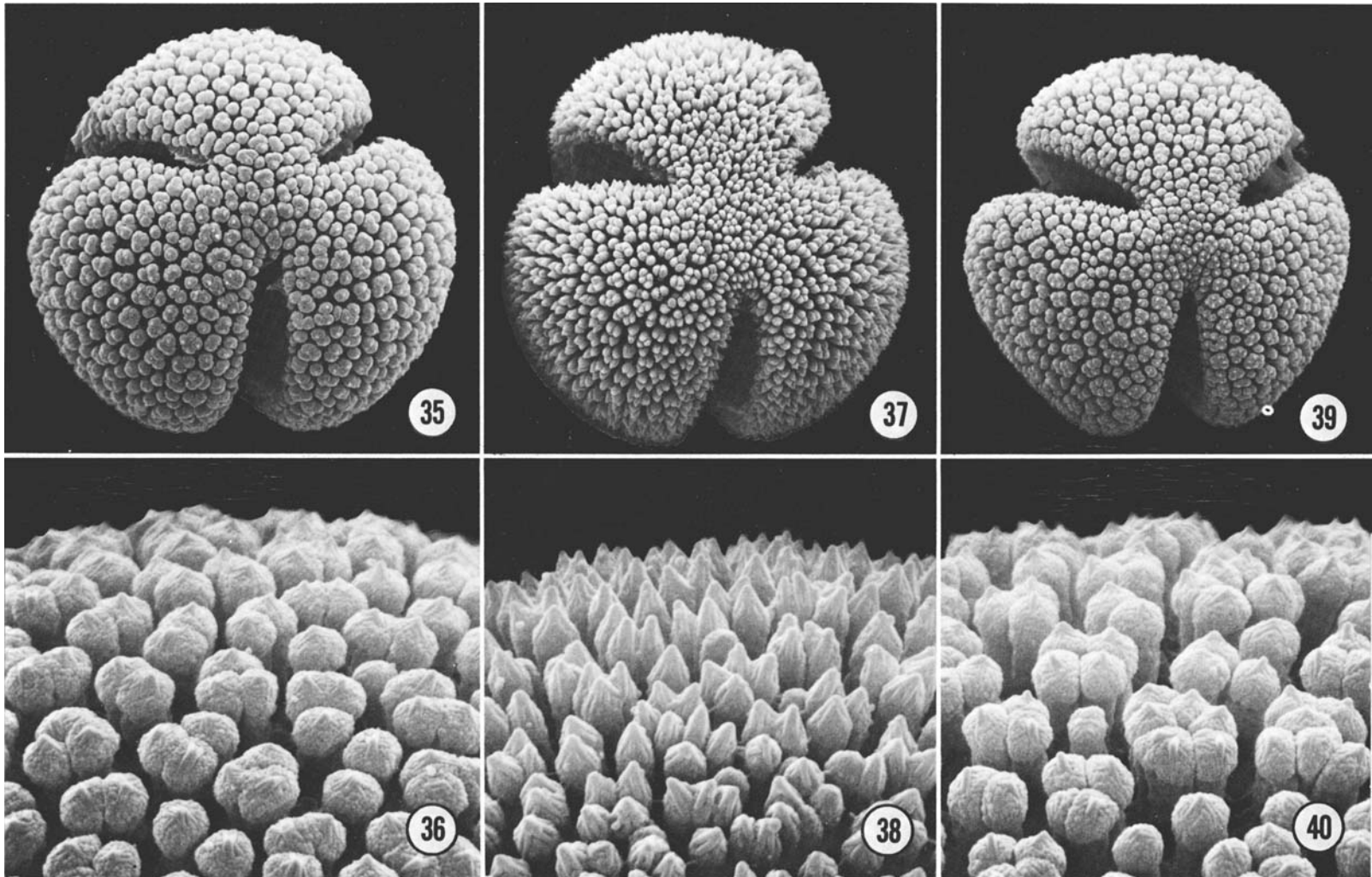
FIGURES 19–23.—Centrospermae pollen, TEM: 19, Aizocaceae, *Mesembryanthemum variabile*, the foot layer is extremely thickened and is underlain by a thin but consistent endexine; the break in the endexine at extreme right may be a ruptured area; 20, Amaranthaceae, *Psilotrichum amplum*, an endexine is entirely absent; the thin-layered aperture contains a large pointed fragment of ectexine; 21, Basellaceae, *Anredera scandens*, a wedge of endexine is prominent beneath the colpus, but in the mesocolpial regions it is less distinct and has an electron density similar to that of the foot layer; however, the endexine is fibrillar and the inset (arrows) shows the fibrils to at least superficially resemble unit membranes; 22, Cactaceae, *Opuntia lindheimeri*, section is through one of the large apertures (Figure 17) with numerous flecks of ectexine; 23, Caryophyllaceae, *Gymnocarpus fruticosum*, it is difficult to distinguish a foot layer or endexine; the inset suggests that there are two layers with an irregular separation. (Scales equal 1 μm .)



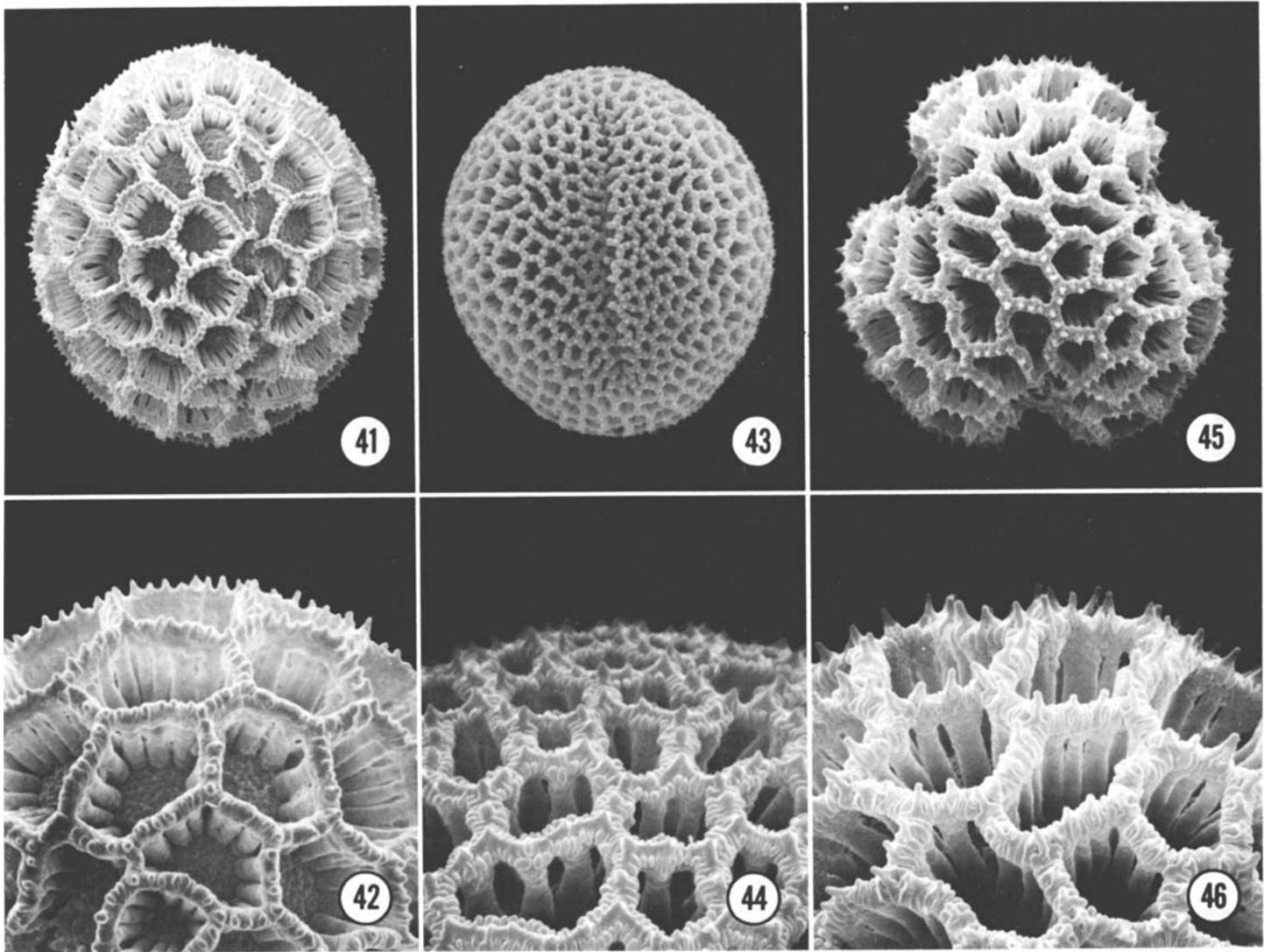
FIGURES 24–28.—Centrospermae pollen, TEM: 24, Caryophyllaceae, *Herniaria glabra*, an irregular but notable endexine is characteristic of this taxon; the absence of spines or perforations in a section is consistent with the surface depicted by SEM (Figure 15); 25, Chenopodiaceae, *Chenopodium ambrosioides*, the equatorial section and that contained in the inset (polar section) indicate a thin foot-layer, a highly irregular and granular endexine, and “internal foramina-like” openings in the thickened tectum; 26, Molluginaceae, *Limeum viscosum*, micrograph includes sections through mesocolpial (upper) and apertural (lower) regions; aperture has numerous flecks of ectexine; 27, Nyctaginaceae, *Abronia angustifolia*, the irregular structures are due to an oblique section through a coarsely reticulate ectexine; an endexine is not evident in this taxon; 28, Portulacaceae, *Naiocrene parvifolia*, the endexine is evident in the aperture region while in the mesocolpial regions it is either reduced or absent. (Scales equal 1 μm .)



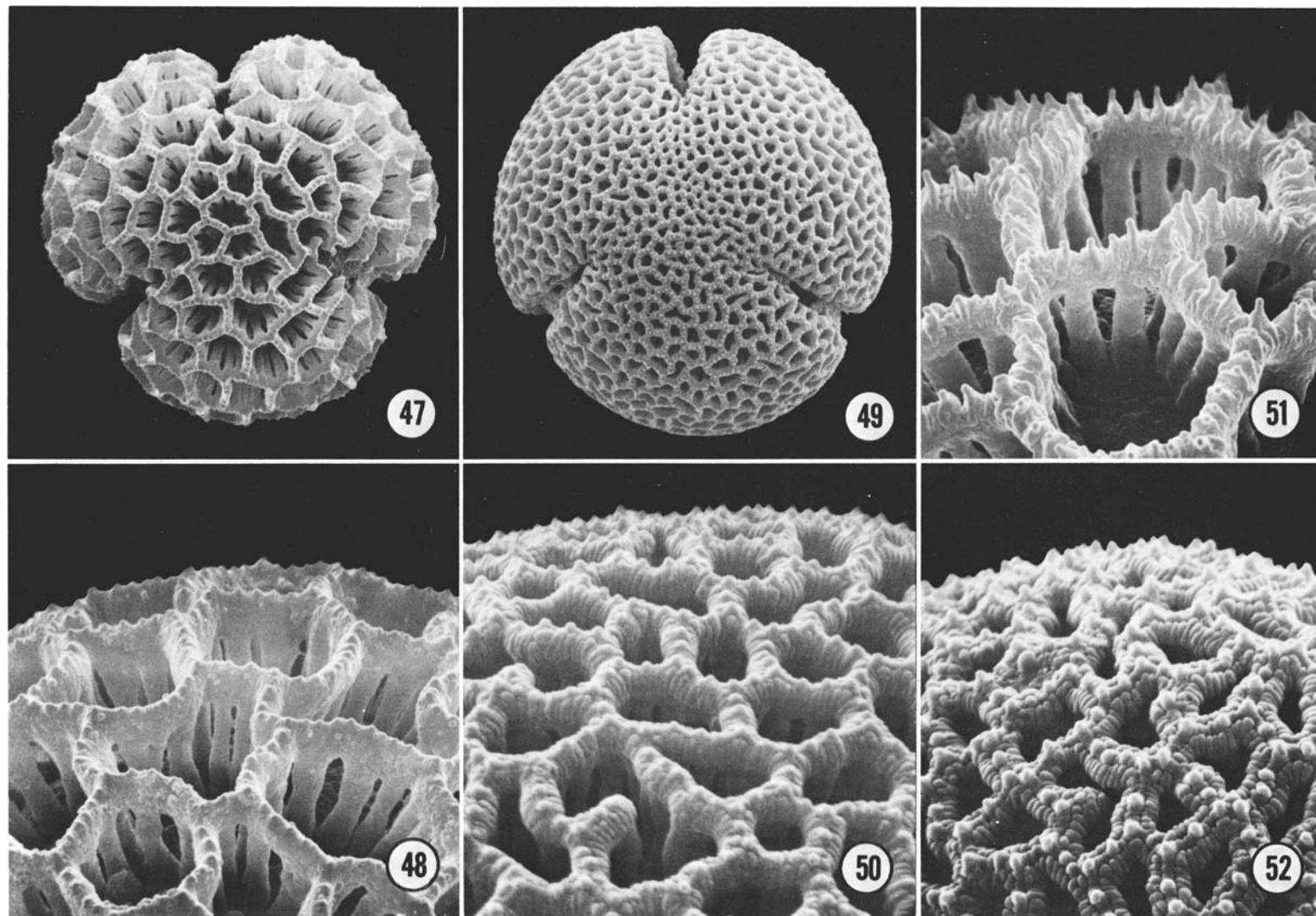
FIGURES 29-34.—Plumbaginaceae pollen, SEM. *Ceratostigma griffithii* C. B. Clarke: 29, equatorial view, $\times 1250$; 30, ektexine surface, $\times 7500$ (29, 30, *Rock 11578*, rounded verrucae *Plumbago* form); 31, equatorial view, $\times 1450$; 32, ektexine surface, $\times 7500$ (31, 32, *Rock 6577*, pointed verrucae *Plumbago* form). *Plumbago rosea* L.: 33, equatorial view, $\times 1500$; 34, ektexine surface, $\times 7500$ (33, 34, pointed verrucae *Plumbago* form). Photo reduced to 74 percent.)



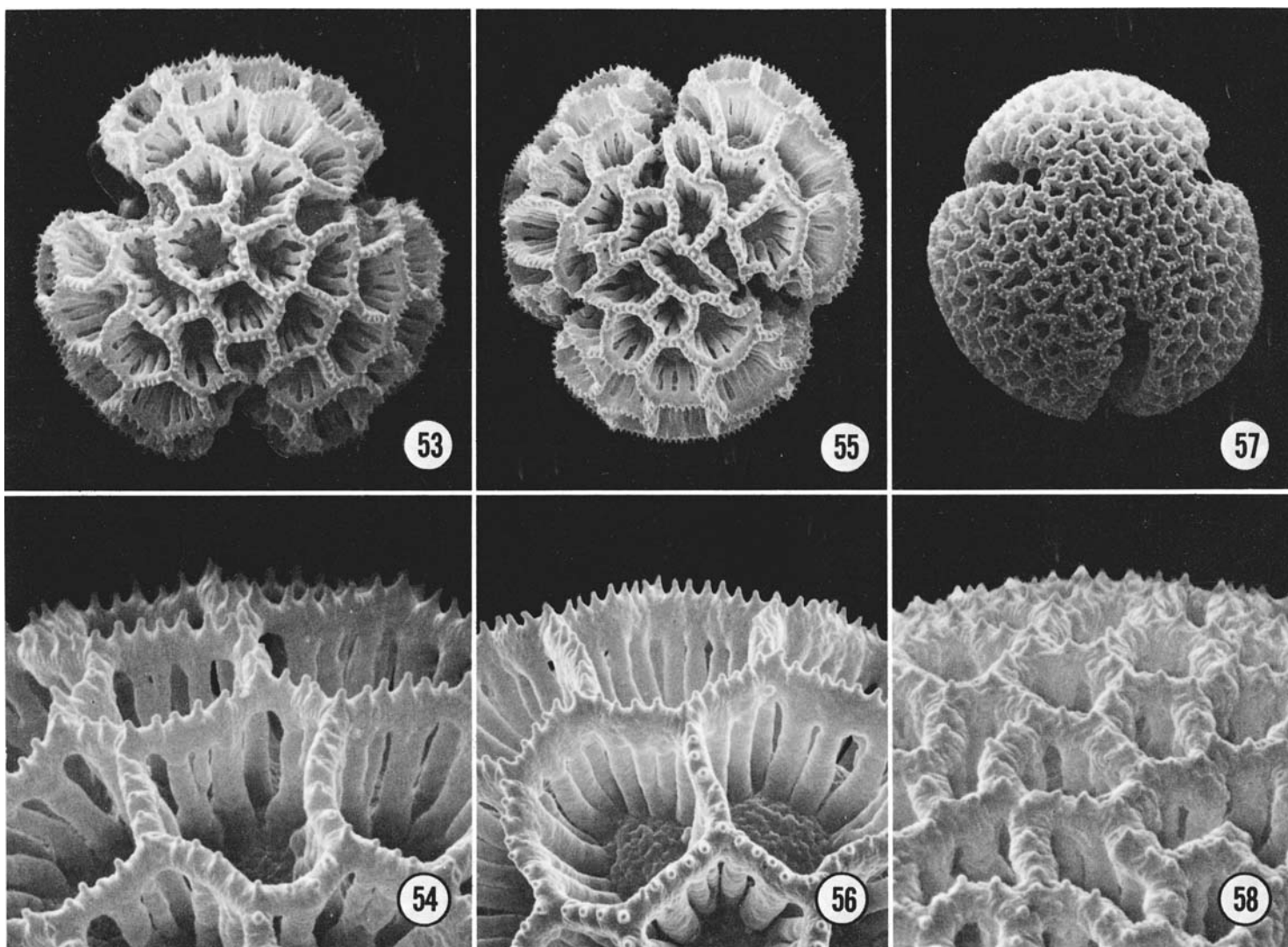
FIGURES 35-40.—Plumbaginaceae pollen, SEM. *Plumbago europaea* L.: 35, polar view, $\times 1700$; 36, ektexine surface, $\times 7500$ (35, 36, *Sporiks s.n.* GH, rounded verrucae *Plumbago* form); 37, polar view, $\times 1700$; 38, ektexine surface, $\times 7500$ (37, 38, *Raine s.n.* GH, pointed verrucae *Plumbago* form). *Plumbago auriculata* Lamarck: 39, polar view, $\times 1250$; 40, ektexine surface, $\times 7500$ (39, 40, *Bayliss 1187* GH, rounded verrucae *Plumbago* form). (Photo reduced to 76½ percent.)



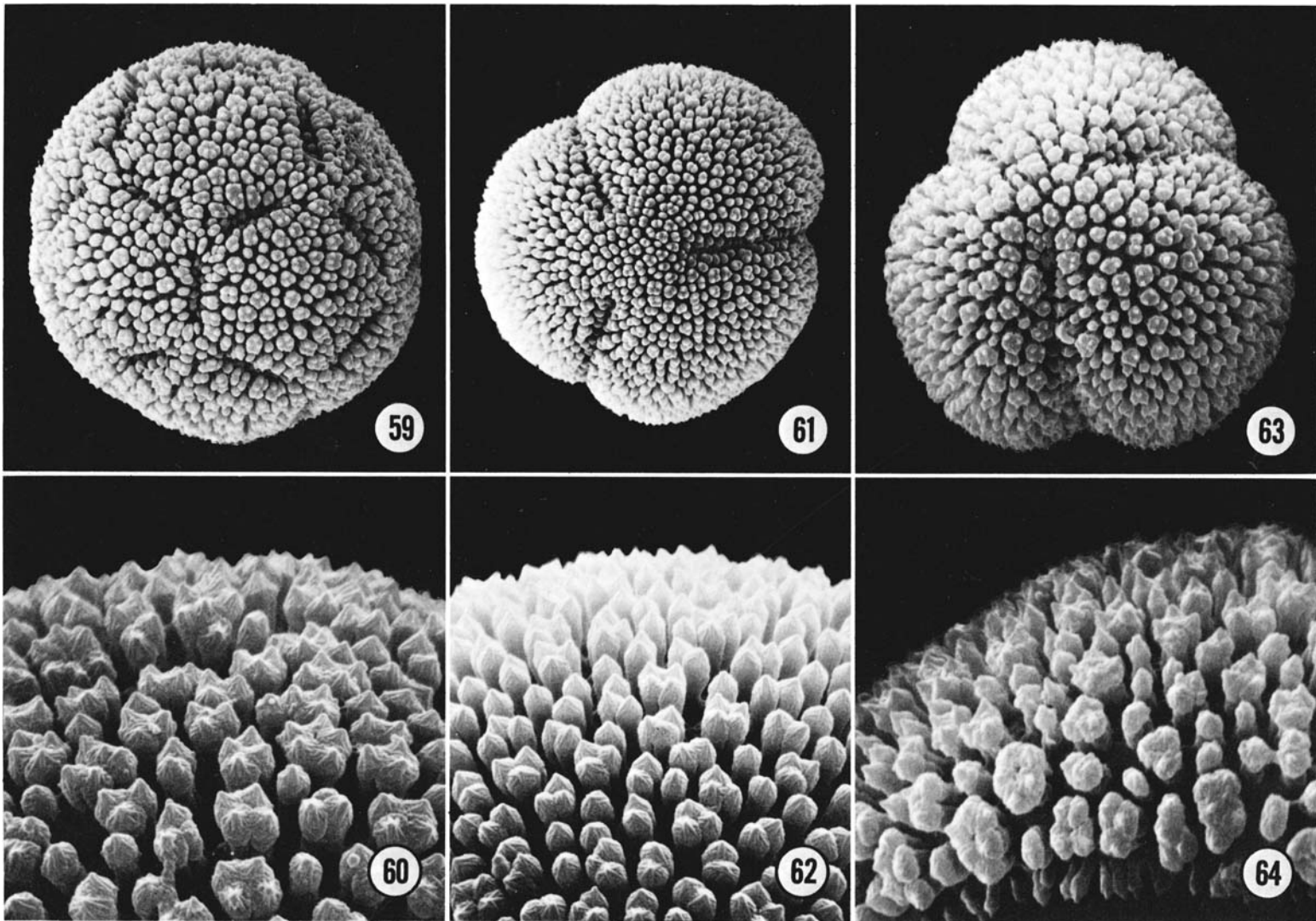
FIGURES 41–46.—Plumbaginaceae pollen, SEM. *Limonium viciosi* Pau: 41, equatorial view, $\times 1250$; 42, ectexine surface, $\times 3000$ (coarsely reticulate *Armeria* form). *Armeria maritima* (Miller) Willdenow: 43, equatorial view, $\times 1150$; 44, ectexine surface, $\times 5000$ (43, 44, *Svenson s.n.*, finely reticulate *Armeria* form); 45, polar view, $\times 1250$; 46, ectexine surface, $\times 3000$ (45, 46, *Mathiesen & Pedersen s.n.*, coarsely reticulate *Armeria* form). (Photo reduced to 77 percent.)



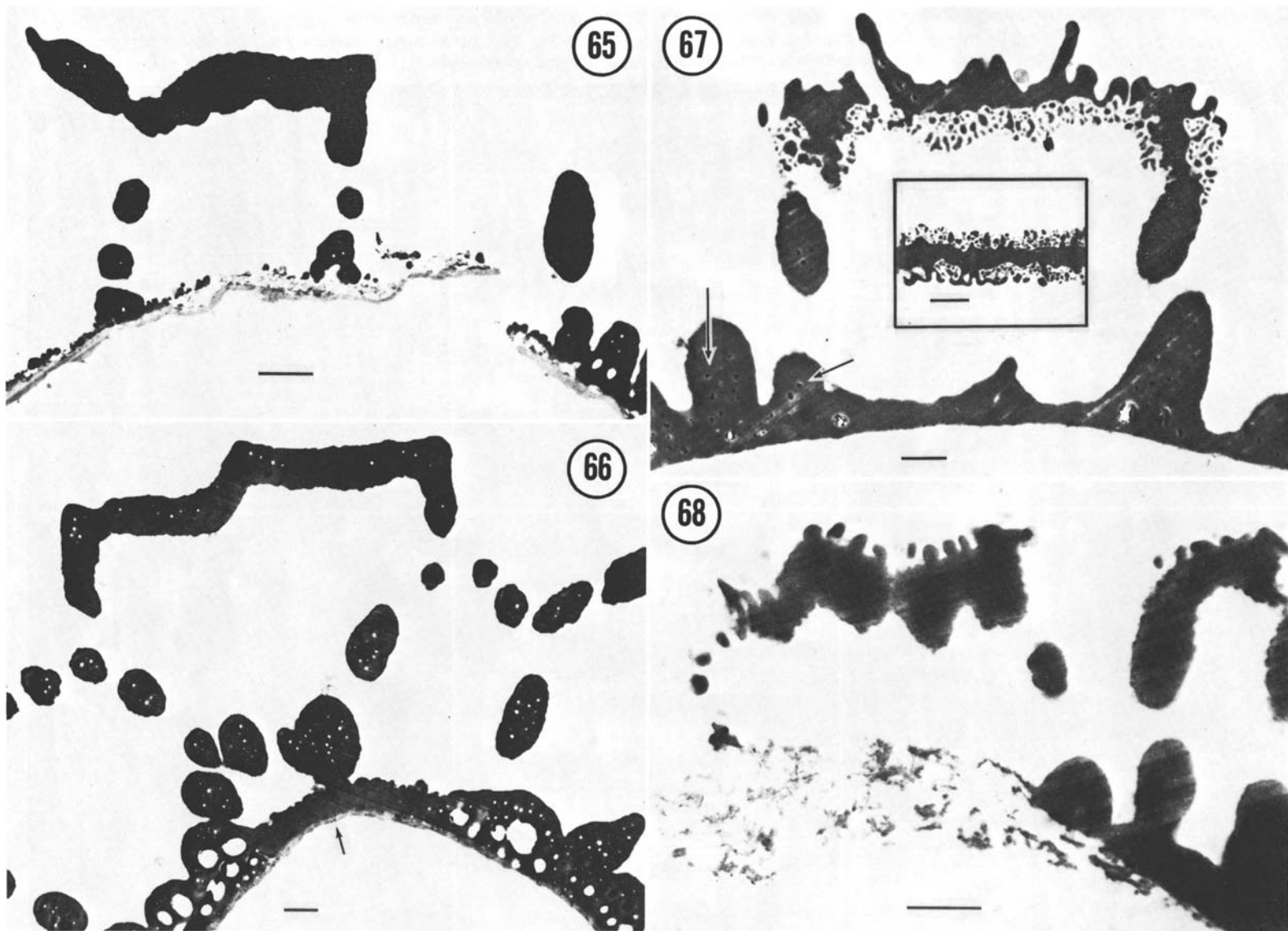
FIGURES 47-52.—Plumbaginaceae pollen, SEM. *Statice tenella* Turczaninow: 47, polar view, $\times 1500$; 48, ektexine surface, $\times 5000$ (47, 48, Chaney 517, coarsely reticulate Armeria form); 49, polar view, $\times 1500$; 50, ektexine surface, $\times 7500$ (49, 50, Chaney 517a, finely reticulate Armeria form). *Limonium vulgare* Miller: 51, ektexine surface, $\times 5000$ (Lawalree 3820 MO, coarsely reticulate Armeria form); 52, ektexine surface, $\times 7500$ (Holm-Nielsen s.n. MO, finely reticulate Armeria form). (Photo reduced to 79 percent.)



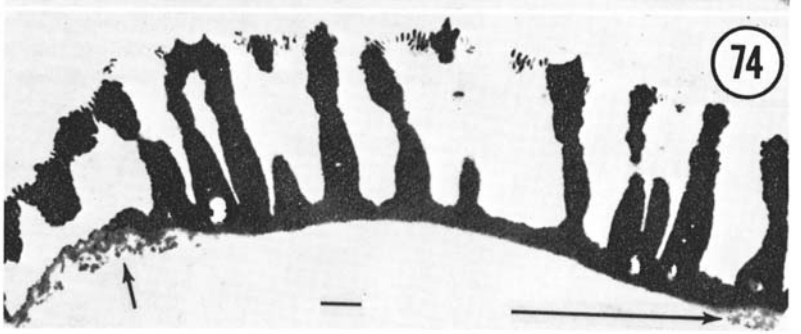
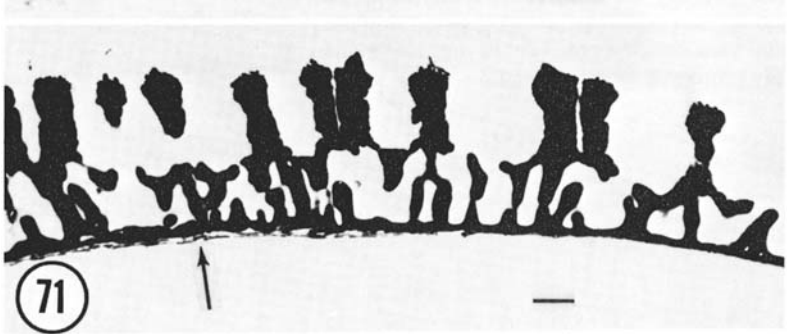
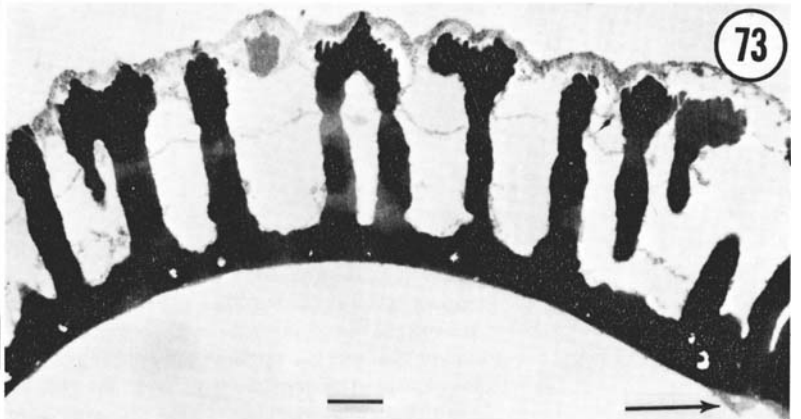
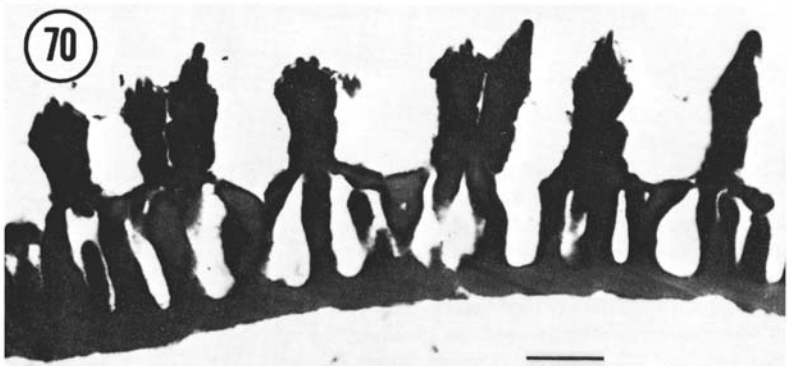
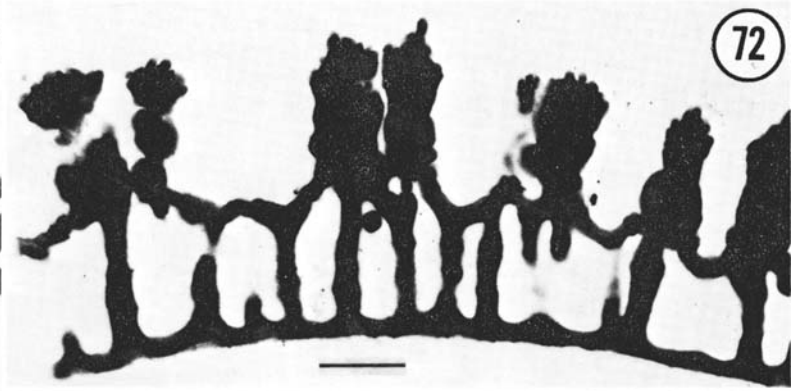
FIGURES 53-58.—Plumbaginaceae pollen, SEM. *Goniolimon collinum* (Grisebach) Boissier: 53, polar view, $\times 1600$; 54, ektexine surface, $\times 5000$ (coarsely reticulate *Armeria* form). *Statice sinuata* L.: 55, polar view, $\times 1500$; 56, ektexine surface, $\times 4000$ (55, 56, *Vaccari 495*, coarsely reticulate *Armeria* form); 57, polar view, $\times 1550$; 58, ektexine surface, $\times 7500$ (57, 58, *Maire & Wilczek 1048*, finely reticulate *Armeria* form). (Photo reduced to 76 percent.)



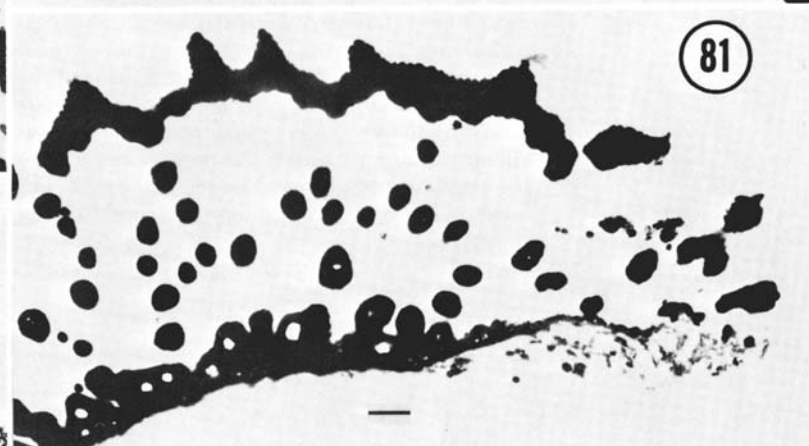
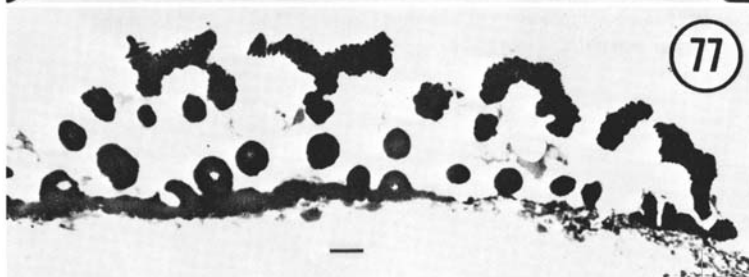
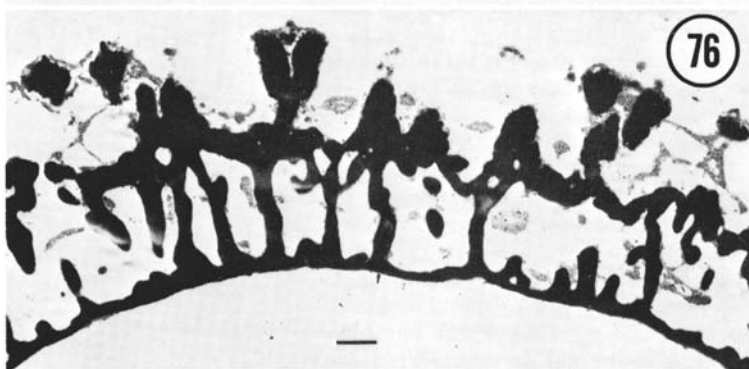
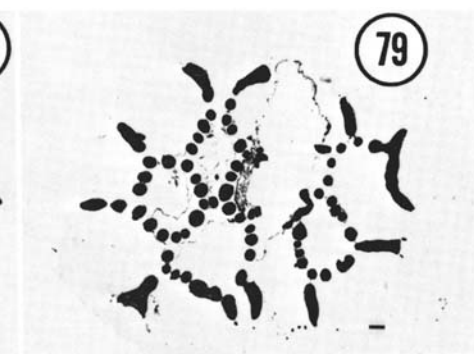
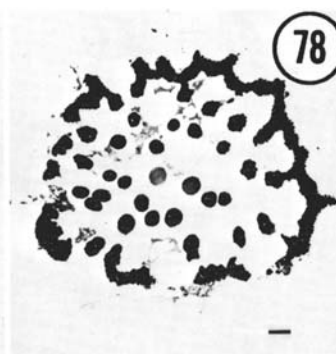
FIGURES 59-64.—Plumbaginaceae pollen, SEM. *Ceratostigma willmottianum* Stapf: 59, $\times 1150$; 60, ectexine surface, $\times 5000$ (59, 60, *Wilson 1373*, pantocolpate *Plumbago* form); 61, polar view, $\times 1300$; 62, ectexine surface, $\times 5000$ (61, 62, *Kingdon-Ward 12530 MO*, 3-colpate *Plumbago* form). *Dyerophytum africanum* (Lamarck) O. Kuntze: 63, polar view, $\times 2000$; 64, ectexine surface, $\times 5000$ (*Werdermann & Oberdieck 594*, pointed? verrucae *Plumbago* form). (Photo reduced to 79½ percent.)



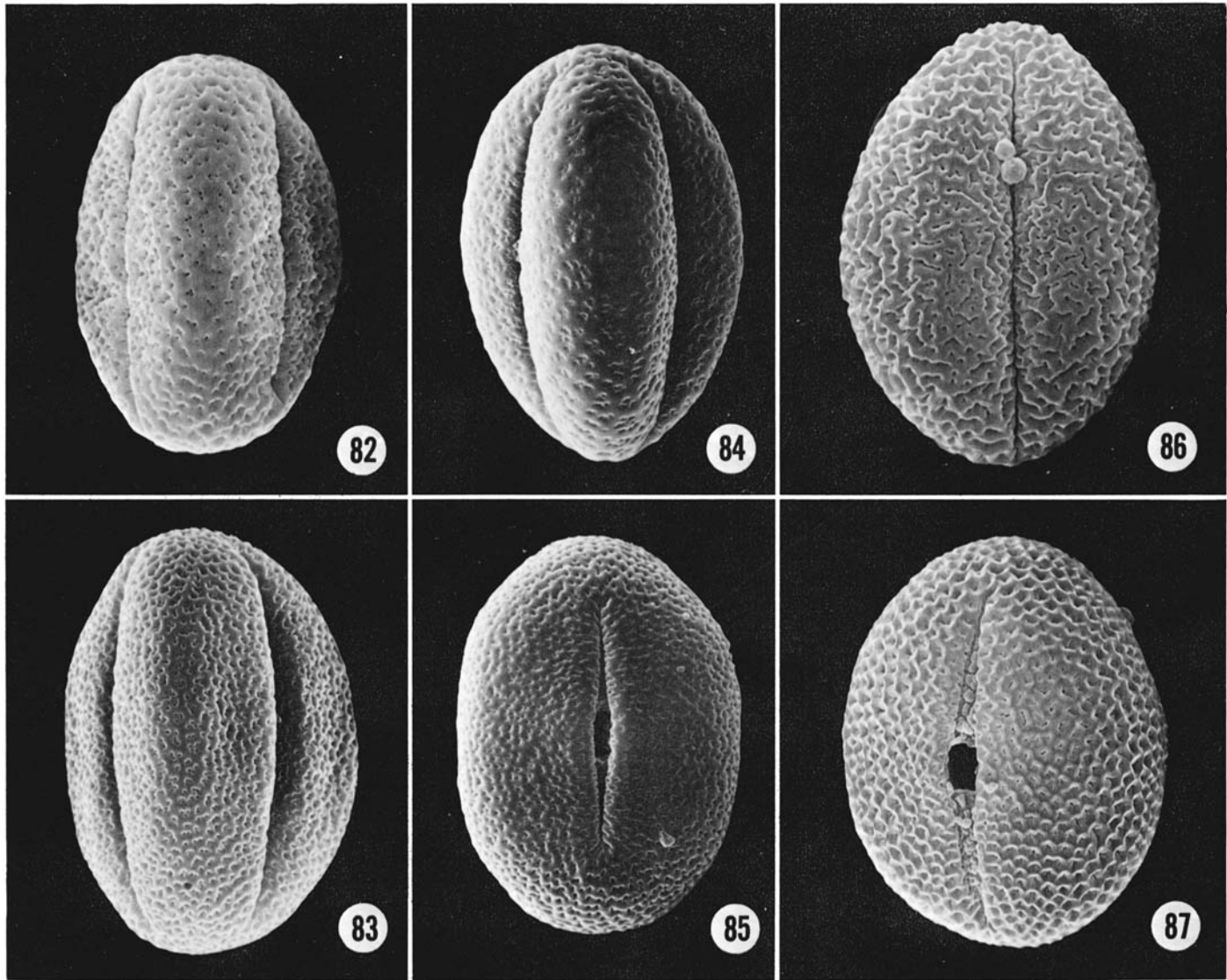
FIGURES 65-68.—Plumbaginaceae pollen, TEM. *Acantholimon olivieri* Jaubert & Spach: 65, oblique section in aperture region; note thin but distinct endexine and random internal foramina (small holes) in the ectexine; 66, oblique section emphasizing thin endexine (arrow) and numerous internal foramina (coarsely reticulate *Armeria* form). *Armeria maritima*: 67, a fine network of sporopollenin surrounds the muri and the inset, a tangential section, clarified this interpretation and correlates with images obtained from SEM (Figures 44 and 46); arrows point to internal foramina partially filled with electron dense material (*Mathiesen & Pedersen s.n.*, coarsely reticulate *Armeria* form); 68, in this section of an aperture the endexine is evident although highly fragmented; note that the outer surface of the muri appears somewhat ridged due to an off-center cut through the smaller spines (*Svenson s.n.*, finely reticulate *Armeria* form). (Scales equal 1 μm .)



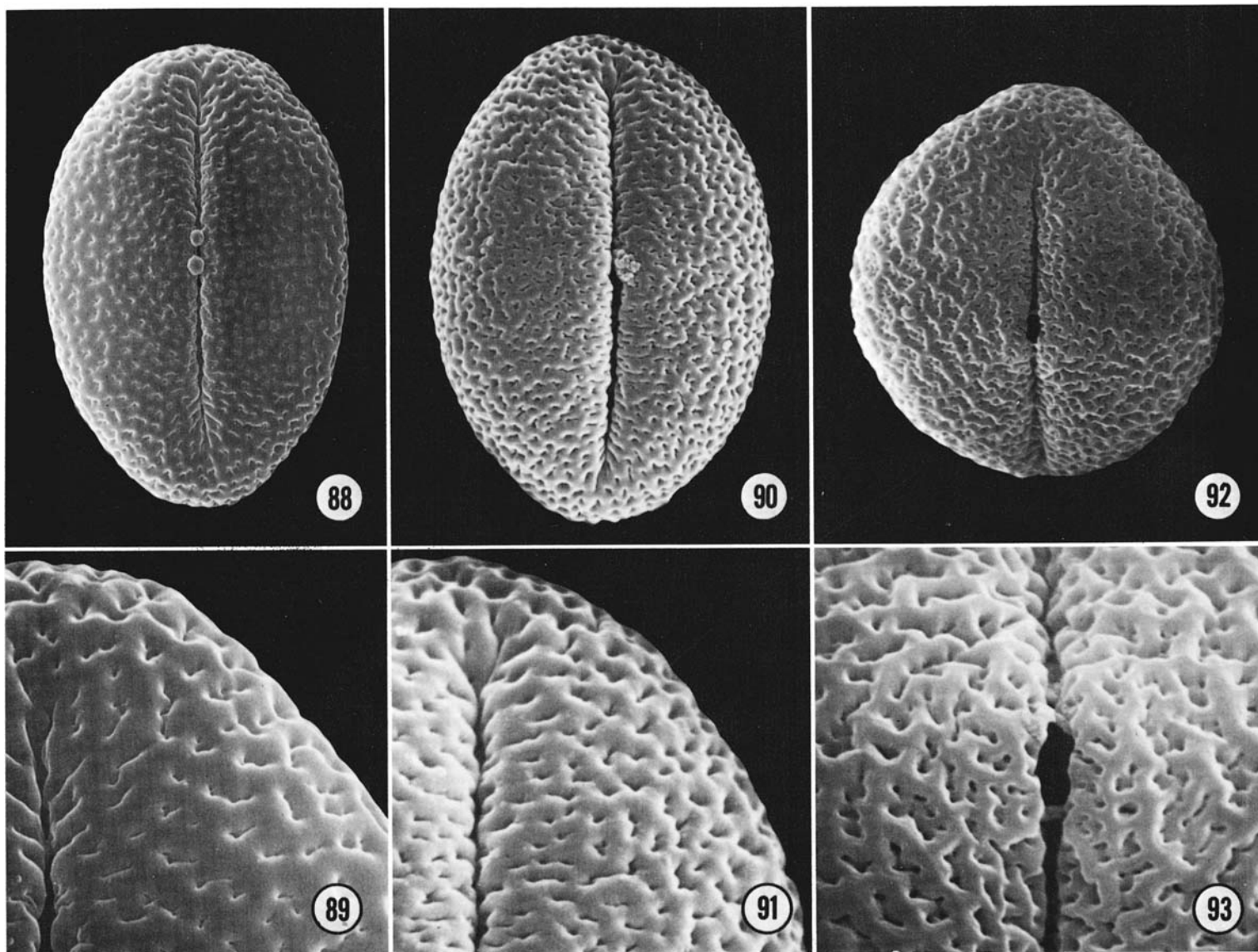
FIGURES 69-74.—Plumbaginaceae pollen, TEM. *Ceratostigma griffithii*: 69, the section is somewhat oblique and therefore the two levels of columellae appear incomplete; note that the terminal portions of the incompletely depicted outer collumellae consist of fine bristle-like structures; the endexine is absent in the mesocolpial areas (*Rock 11578*, rounded verrucae *Plumbago* form); 70, morphology similar to Figure 69 except that the terminal portion of outer columellae appears more massive (*Rock 6577*, pointed verrucae *Plumbago* form). *C. wilmottianum*: 71, note thin, plate-like endexine (arrow) in aperture region (*Wilson 1373*, pantocolpate *Plumbago* form). *Dyerophytum africanum*: 72, radial section illustrates characteristics of inner columellae, smaller in diameter but almost equal in length to the outer columellae (*Werdermann & Oberdieck 594*, pointed? verrucae *Plumbago* form). *Goniolimon collinum*: 73, in contrast to Figures 69-72, all one form or the other of the *Plumbago* type, this section illustrates the single layer of columellae characteristic of the *Armeria* type; the foot layer has perforations but at the present time they are not considered to be internal foramina; arrow points to endexine in the region of the aperture; the granular material surrounding the outer part of the exine appears to be acetolysis resistant and is thought to be a component of the anther rather than the pollen wall (coarsely reticulate *Armeria* form). *Limoniastrum guyonianum* Durieu de Maisonneuve: 74, arrows point to endexine in regions of apertures (finely reticulate *Armeria* form). (Scales equal 1 μm .)



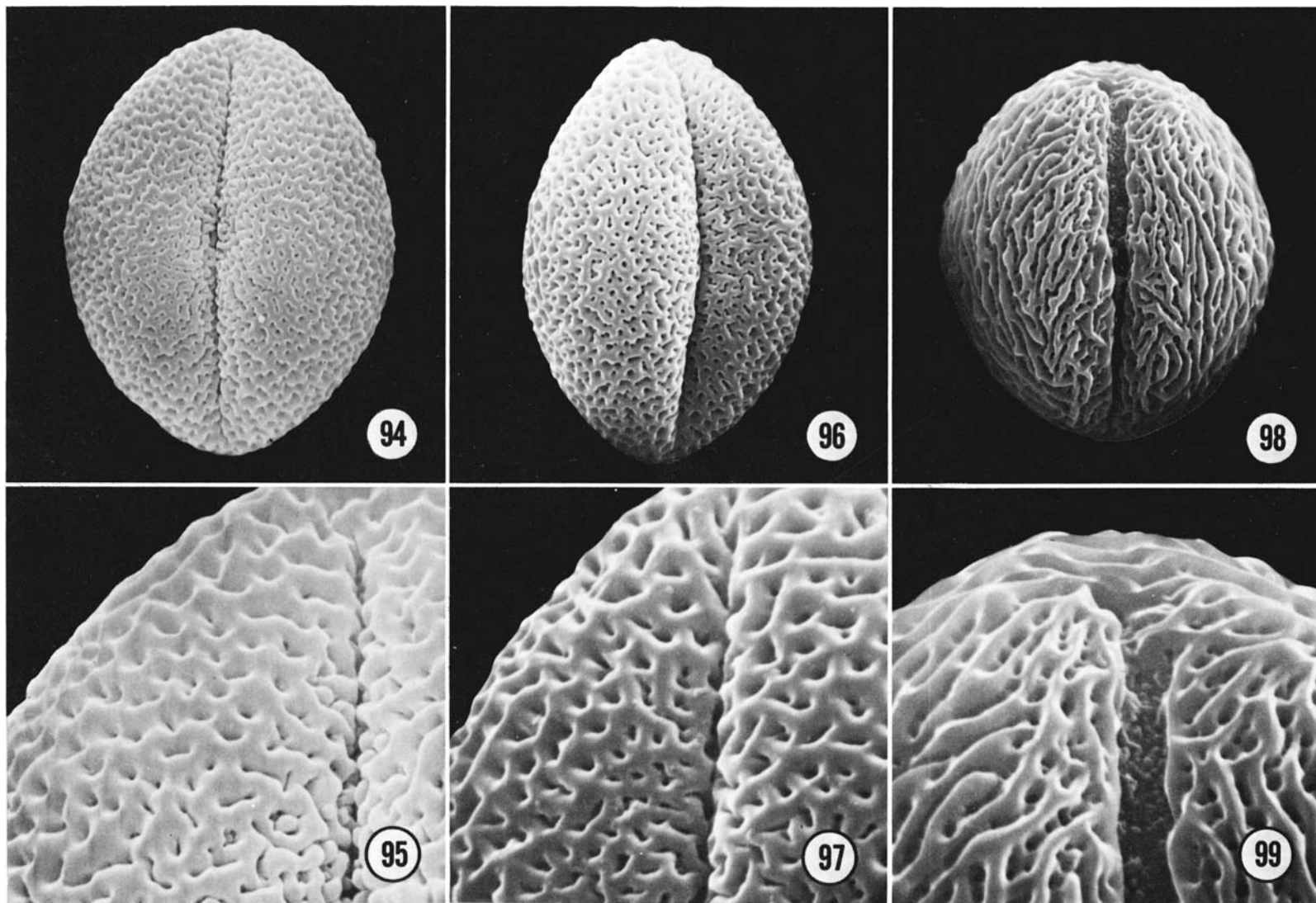
FIGURES 75-81.—Plumbaginaceae pollen, TEM. *Limonium viciosoi*: 75, arrows indicate internal foramina in ectexine; the lower part of the foot layer is somewhat lamellar and may be a thin endexine (coarsely reticulate *Armeria* form). *Plumbago scandens* L.: 76, oblique section (rounded? verrucae *Plumbago* form). *Statice sinuata*: 77, very oblique section; 78, section \pm tangential (77, 78, *Maire & Wilczek 1048*, finely reticulate *Armeria* form); 79, section \pm tangential; 80, note fragmented but visible endexine (79, 80, *Vaccari 495*, coarsely reticulate *Armeria* form). *Statice tenella*: 81, oblique section, fragmented area on right indicates aperture region (*Chaney 517*, coarsely reticulate *Armeria* form). (Scales equal 1 μ m.)



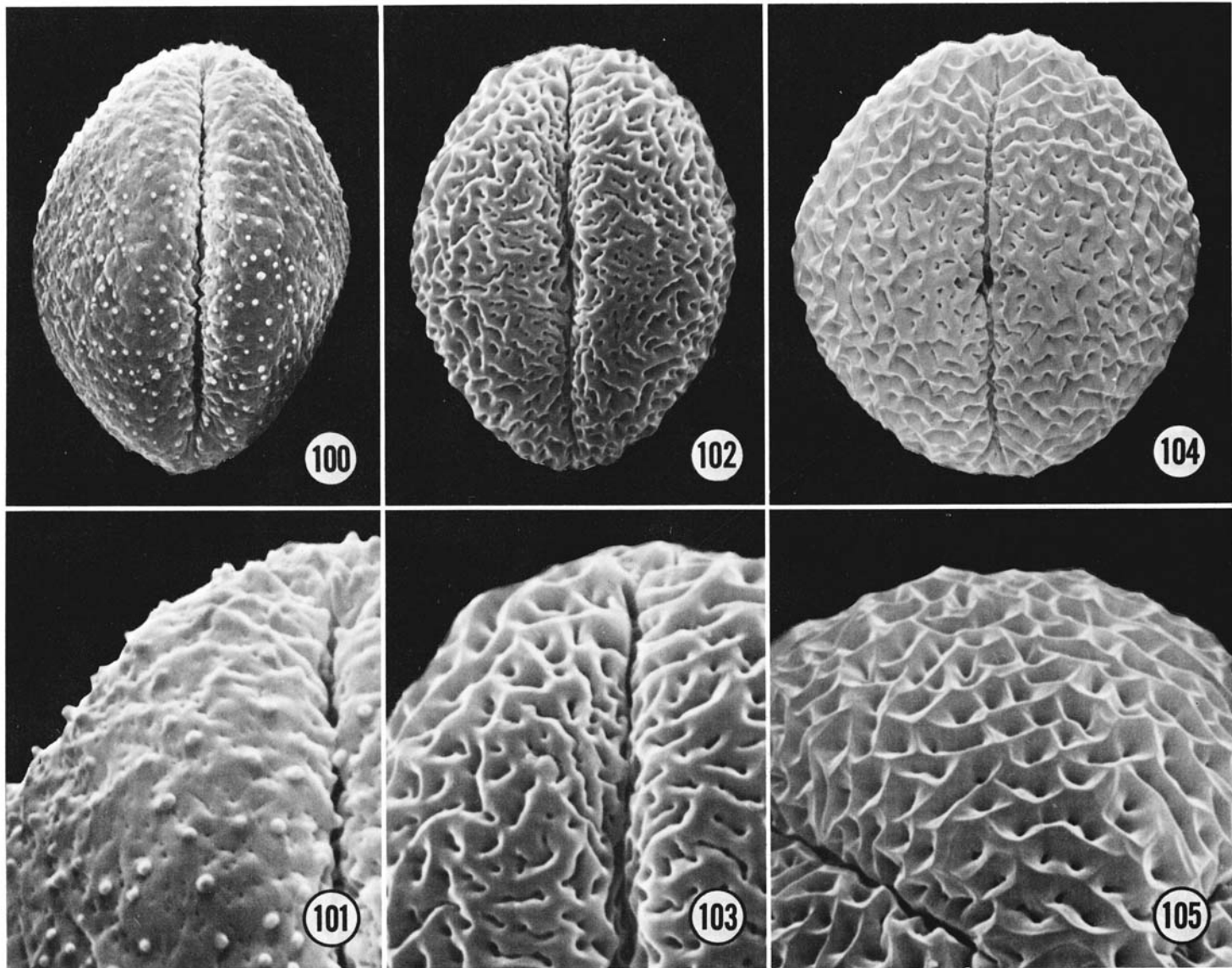
FIGURES 82-87.—Polygonaceae pollen, SEM: 82, *Nemacaulis denudata* Nuttall, mesocolpial view, $\times 3100$; 83, *Oxytheca trilobata* A. Gray, mesocolpial view, $\times 1850$; 84, *Chorizanthe fimbriata* Nuttall, mesocolpial view, $\times 1950$; 85, *C. paniculata* Benthham, equatorial view, $\times 2750$; 86, *Triplaris americana* L., equatorial view, $\times 2650$; 87, *Fagopyrum esculentum* Moench, equatorial view, $\times 1600$ (Photo reduced to 77½ percent.)



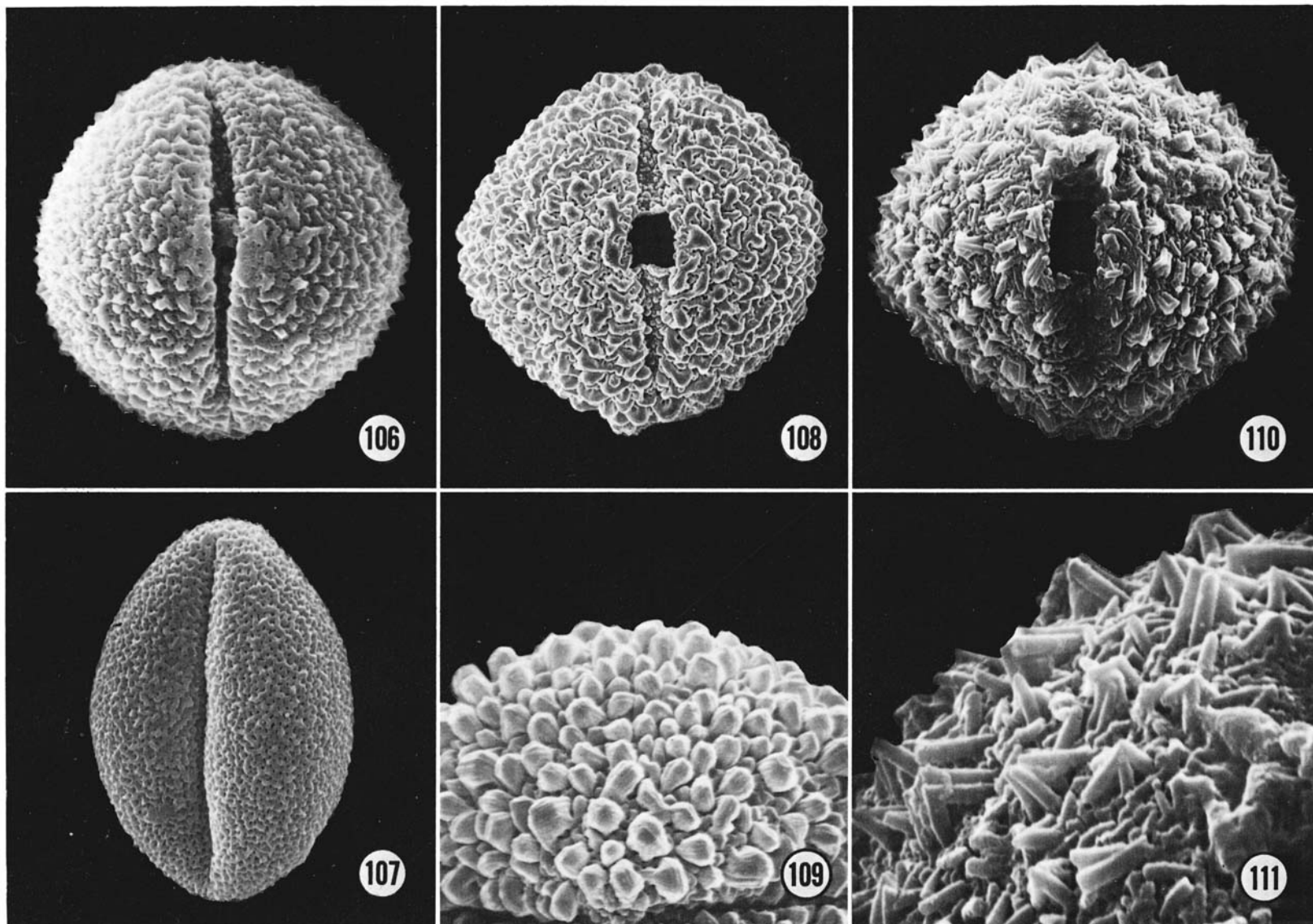
FIGURES 88-93.—Polygonaceae pollen, SEM: 88, *Mucronea californica* Bentham, equatorial view, $\times 2525$; 89, ectexine surface, $\times 7500$; 90, *Eriogonum marifolium* Torrey & A. Gray, equatorial view, $\times 3250$; 91, ectexine surface, $\times 7500$; 92, *Gymnopodium antigonoides* (Robinson?) Blake, equatorial view, $\times 2425$ (Goldman 743); 93, ectexine surface, $\times 7500$ (Goldman 743). (Photo reduced to 76 percent.)



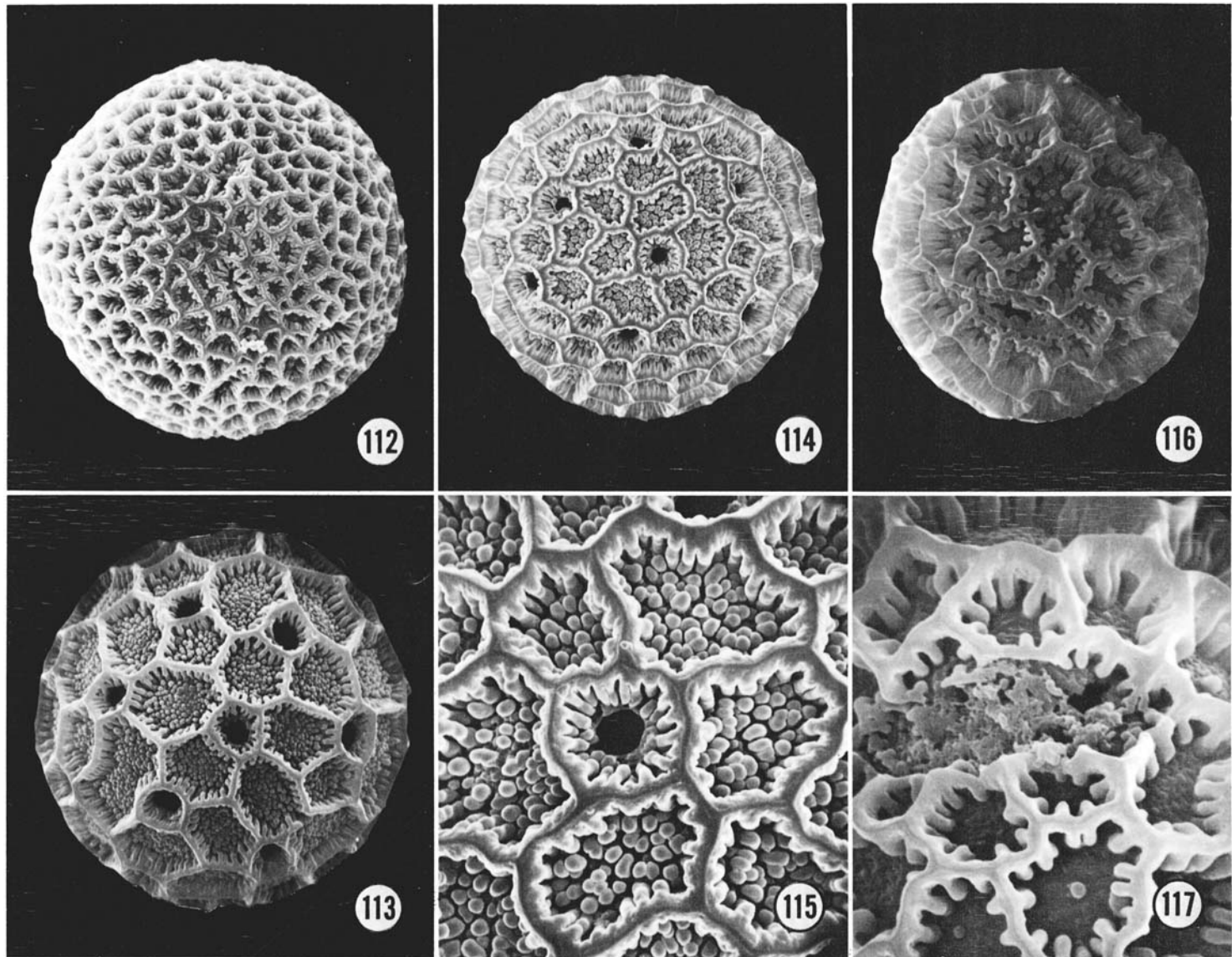
FIGURES 94–99.—Polygonaceae pollen, SEM: 94, *Calligonum comosum* L'Heritier, equatorial view, $\times 2500$; 95, ectexine surface, $\times 7500$; 96, *Harfordia macroptera* (Bentham) Greenc & Parry, equatorial view, $\times 3050$; 97, ectexine surface, $\times 7500$; 98, *Atraphaxis buxifolia* Jaubert & Spach, equatorial view, $\times 2800$; 99, ectexine surface, $\times 7500$. (Photo reduced to 84 percent.)



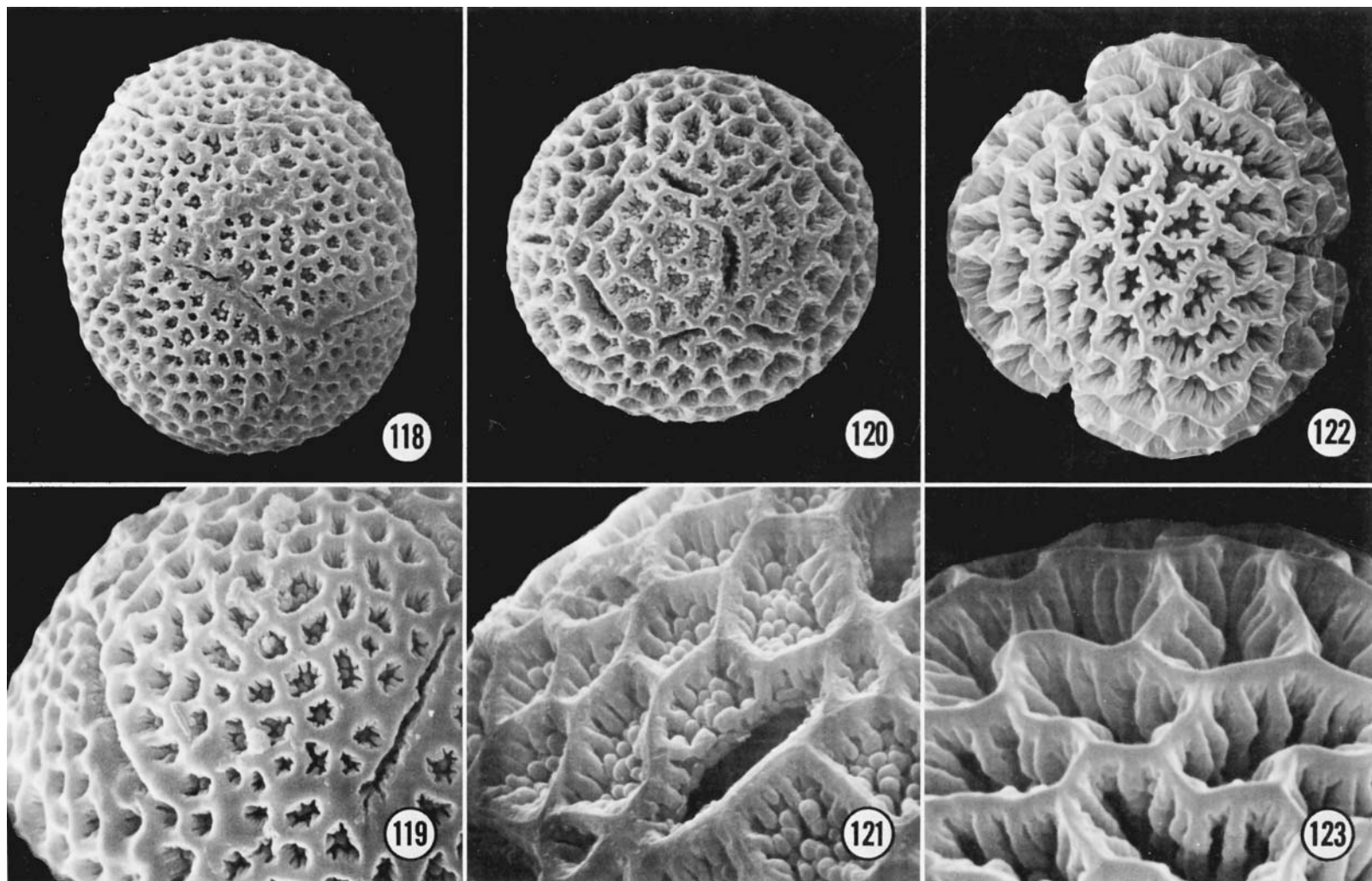
FIGURES 100-105.—Polygonaceae pollen, SEM: 100, *Muehlenbeckia cunninghamii* Mueller, equatorial view, $\times 2730$ (Aston 984); 101, ectexine surface, $\times 7500$ (Aston 984); 102, *M. chilensis* Meisner, equatorial view, $\times 3570$; 103, ectexine surface, $\times 7500$; 104, *M. tamnifolia* (H.B.K.) Meisner, equatorial view, $\times 3600$; 105, ectexine surface, $\times 7500$. (Photo reduced to 83½ percent.)



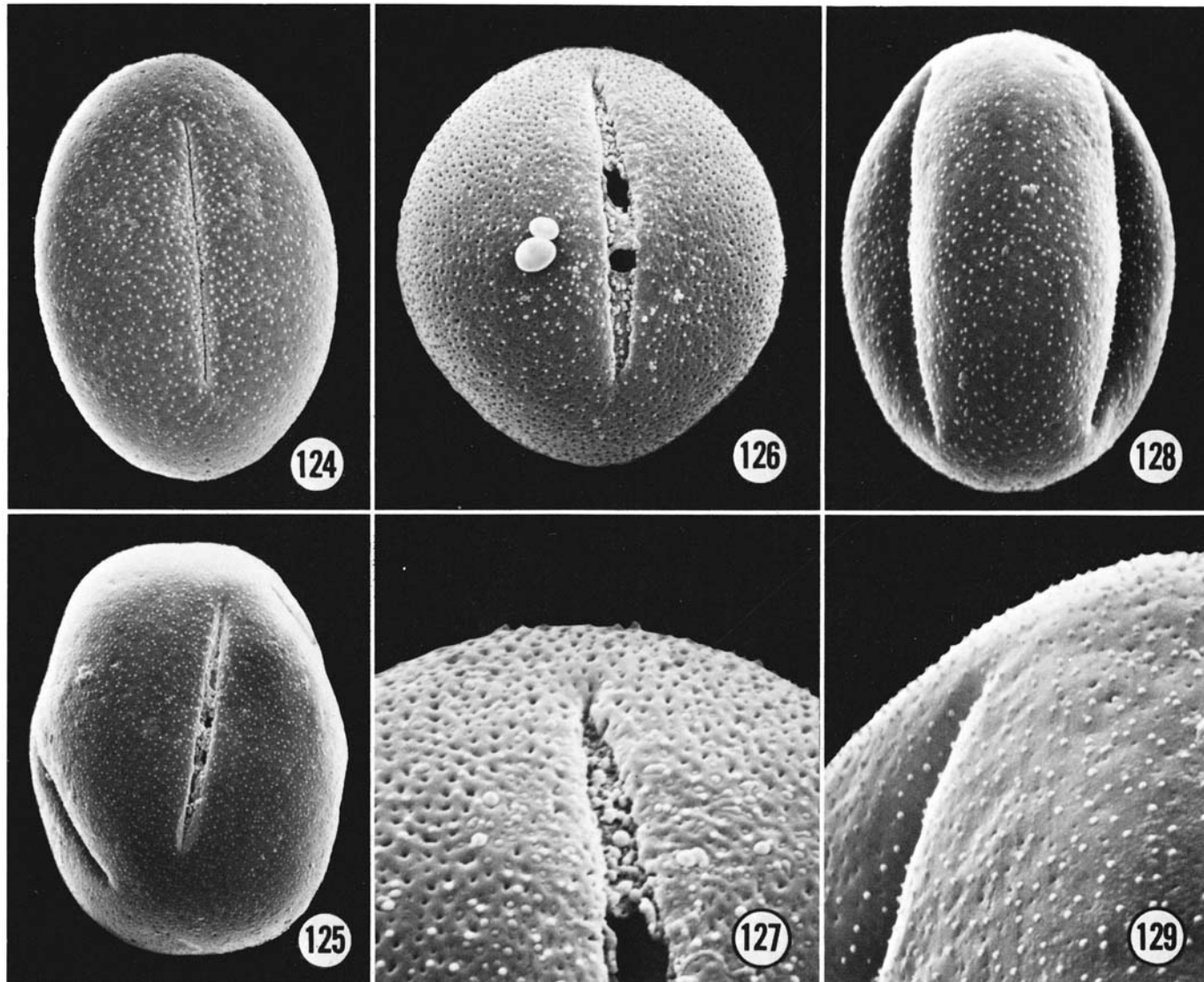
FIGURES 106–111.—Polygonaceae pollen, SEM: 106, *Ruprechtia laxiflora* Meisner, equatorial view, $\times 3400$; 107, *R. pallida* Standlcy, equatorial view, $\times 2500$; 108, *R. ramiflora* (Jacquin) Meyer, equatorial view, $\times 2700$; 109, ectexine surface, $\times 5000$; 110, *Coccoloba cordata* Chamisso, equatorial view, $\times 2520$; 111, ectexine surface, $\times 7500$. (Photo reduced to 79 percent.)



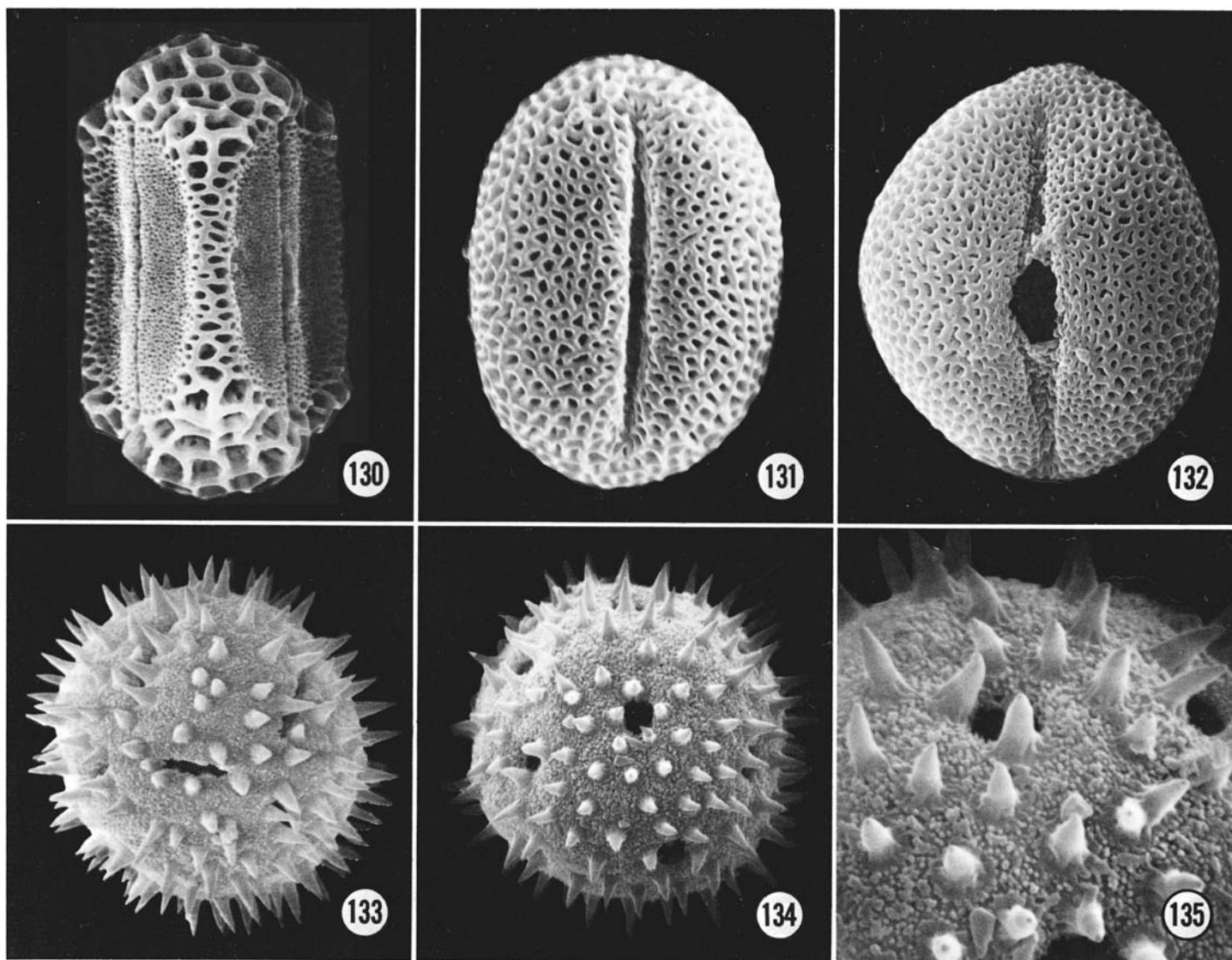
FIGURES 112-117.—Polygonaceae pollen, SEM: 112, *Persicaria coccinea* Greene, $\times 1575$; 113, *Polygonum acuminatum* Kunth, $\times 1575$; 114, *P. orientale* L., $\times 1600$; 115, ectexine surface, $\times 7500$; 116, *P. dielsii* Leville(?), oblique view, colpus horizontal in lower half, $\times 2200$; 117, ectexine surface, colpus in center, $\times 5000$. (Photo reduced to 76 percent.)



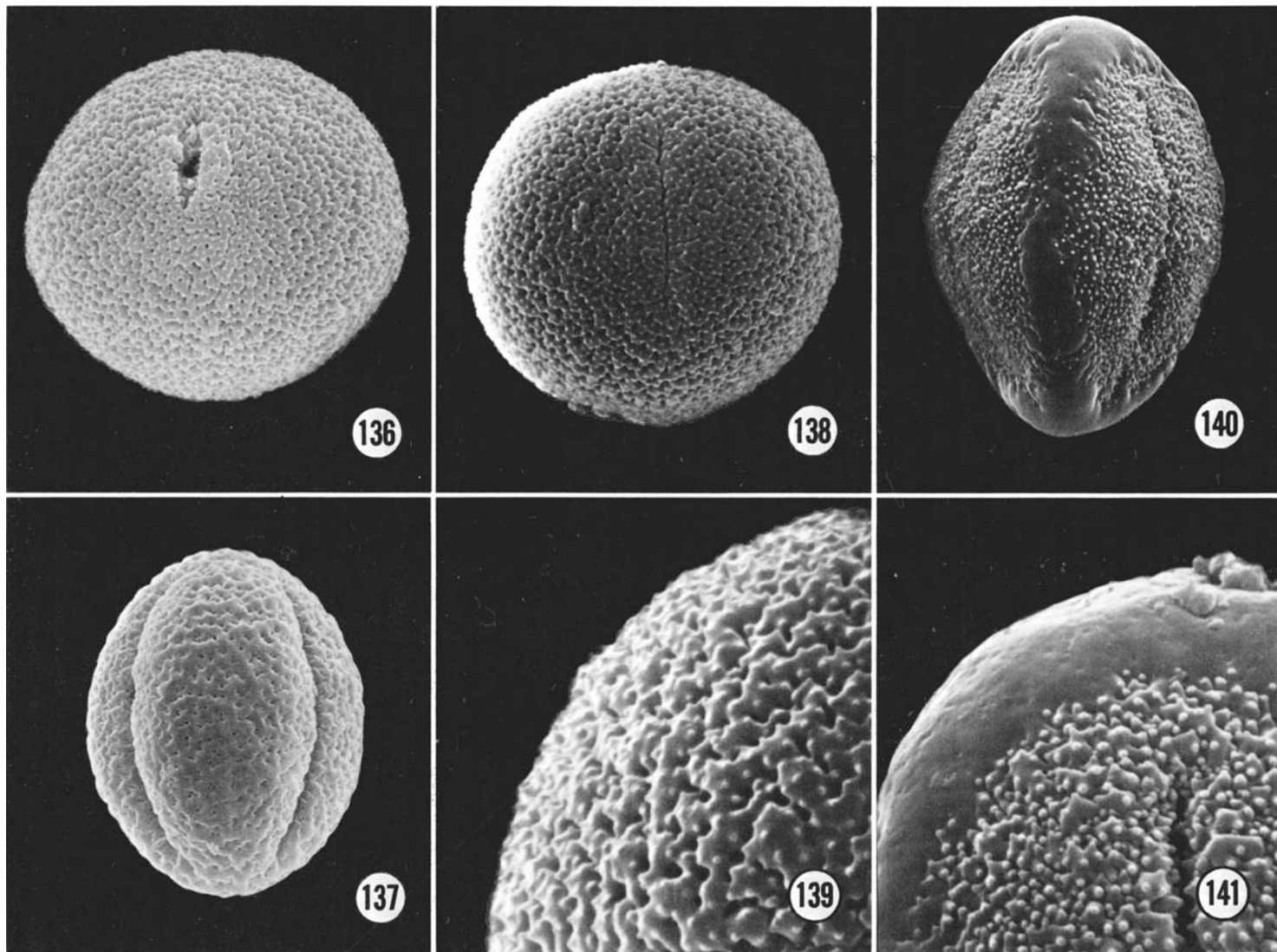
FIGURES 118-123.—Polygonaceae pollen, SEM: 118, *Polygonum virginianum* L., $\times 2000$; 119, ectexine surface, $\times 5000$; 120, *P. amphibium* L., $\times 1400$; 121, ectexine surface, colpus lower right, $\times 5000$; 122, *P. capitatum* D. Don, polar view, $\times 2500$; 123, ectexine surface, $\times 7500$. (Photo reduced to 77½ percent.)



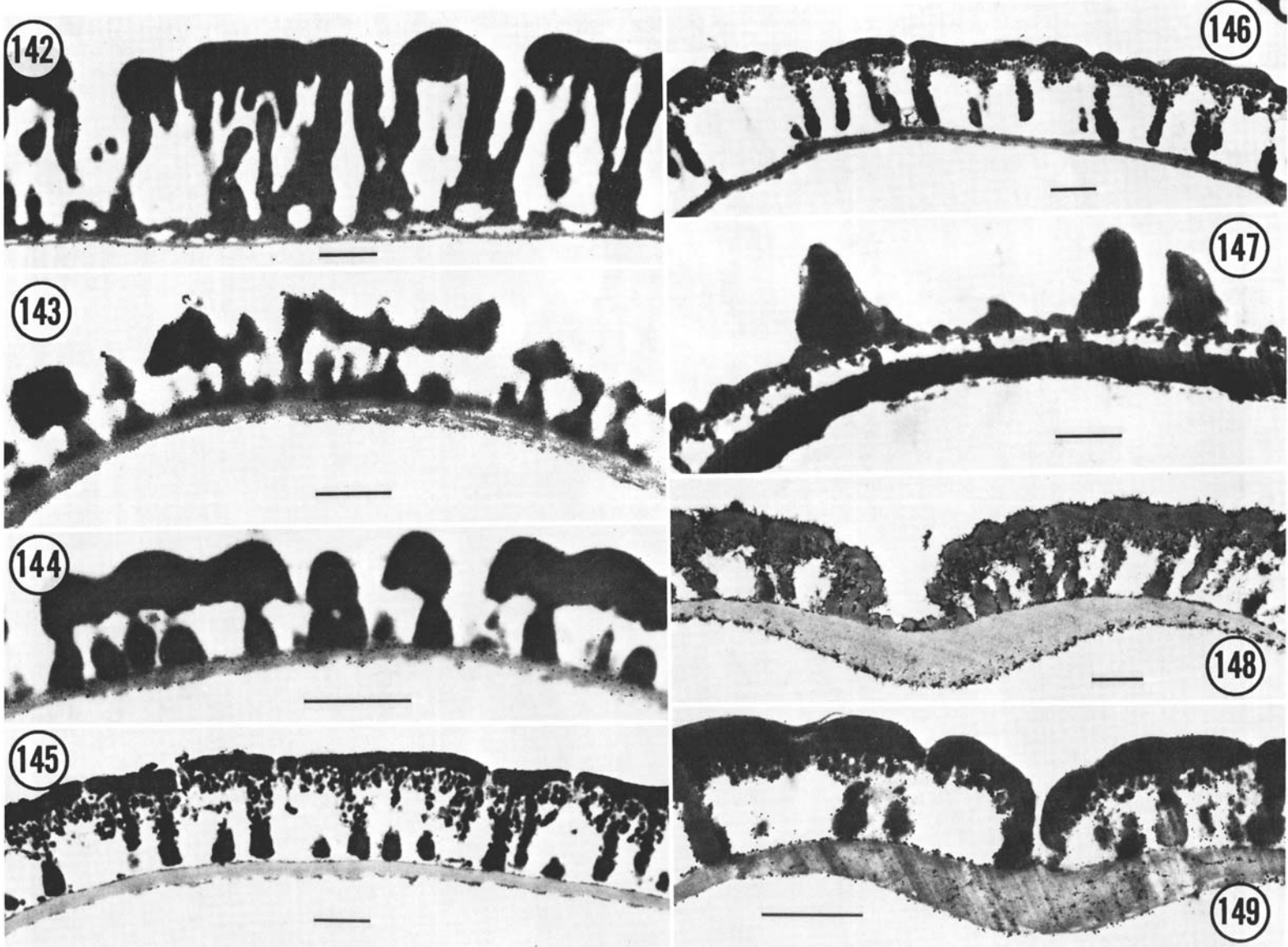
FIGURES 124-129.—Polygonaceae pollen, SEM. *Polygonum affine* D. Don: 124, equatorial view, $\times 2200$. *P. viviparum* L.: 125, slightly oblique equatorial view, $\times 1700$. *P. vacciniifolium* Wallich: 126, equatorial view, $\times 1900$; 127, ektexine surface $\times 5000$. *P. bistorta* L.: 128, mesocolpial view, $\times 2300$; 129, ektexine surface, $\times 5000$ (128, 129, *Cantlon & Malcolm 580085*). (Photo reduced to 83 percent.)



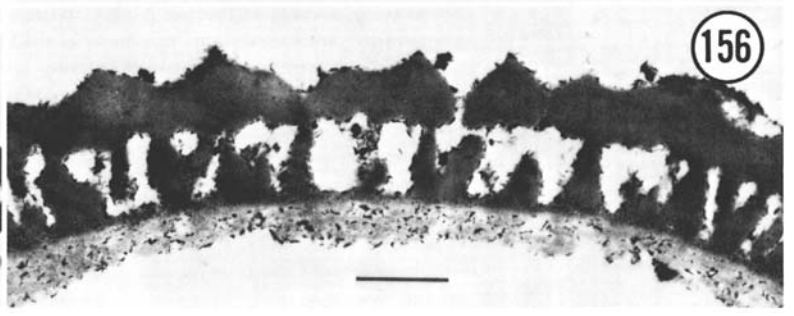
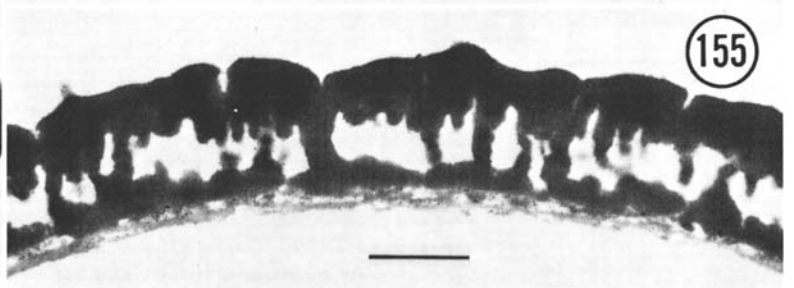
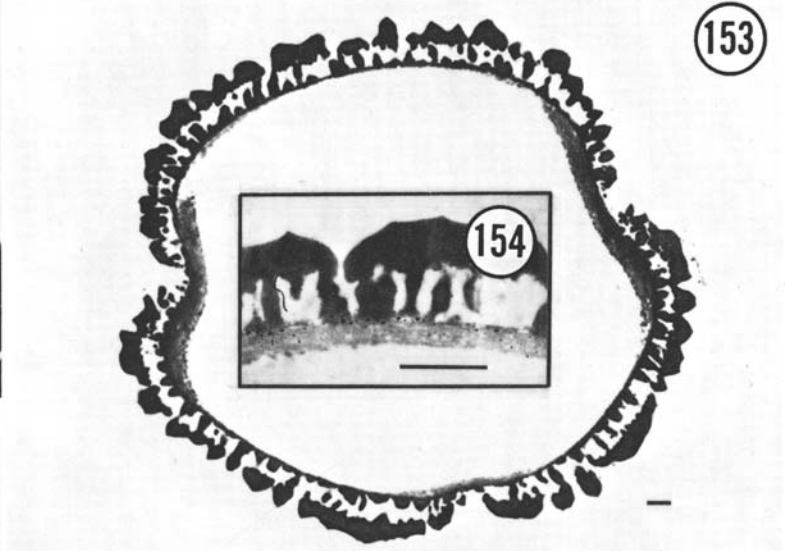
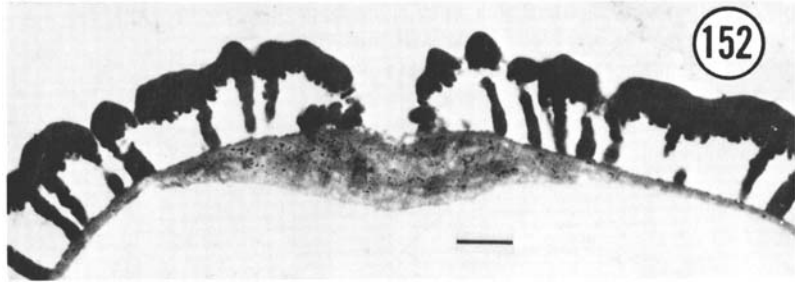
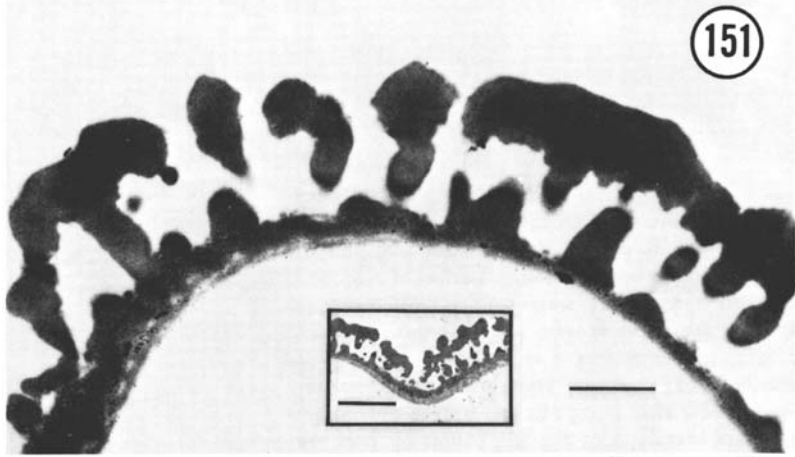
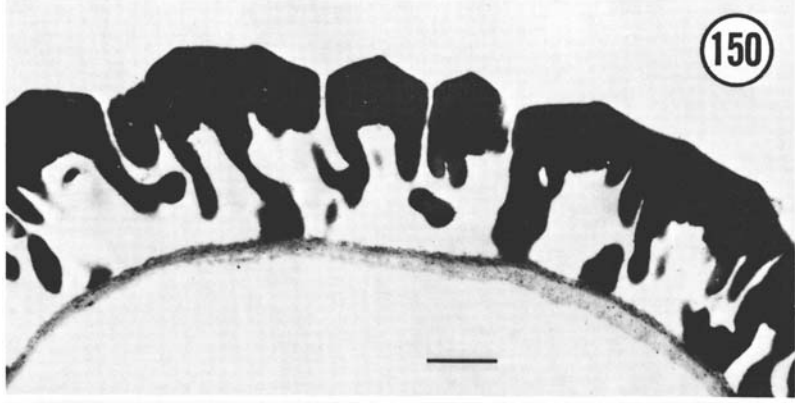
FIGURES 130-135.—Polygonaceae pollen, SEM: 130, *Polygonella fimbriata* (Elliot) Horton, mesocolpial view, $\times 3400$; 131, *P. polygama* (Ventenat) Engelmann & A. Gray, equatorial view, $\times 5750$; 132, *Podopterus mexicanus* Kunth, equatorial view, $\times 2970$; 133, *Polygonum forrestii* Diels, $\times 2900$; 134, *P. cyanandrium* Diels, $\times 3600$; 135, ectexine surface, $\times 8500$. (Photo reduced to 74 percent.)



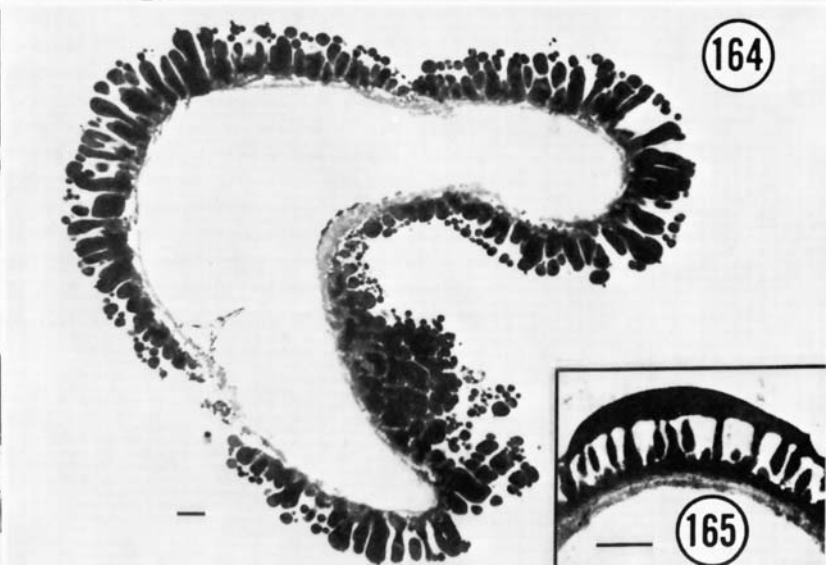
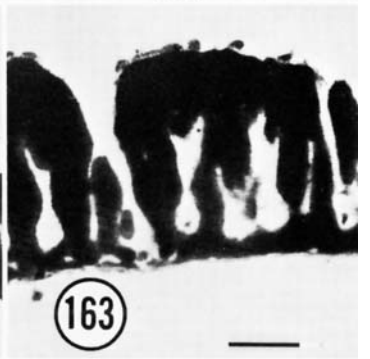
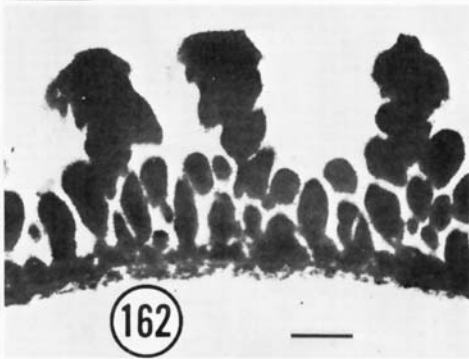
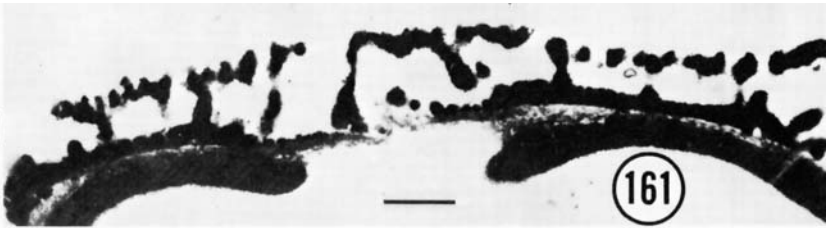
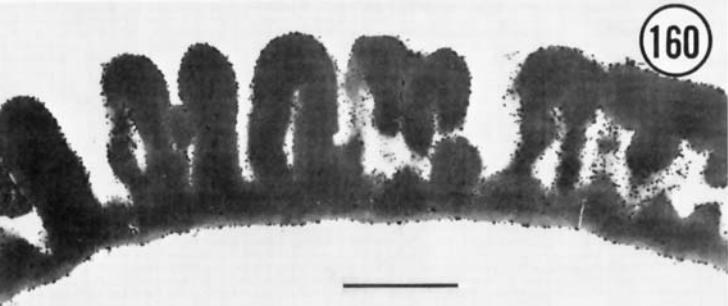
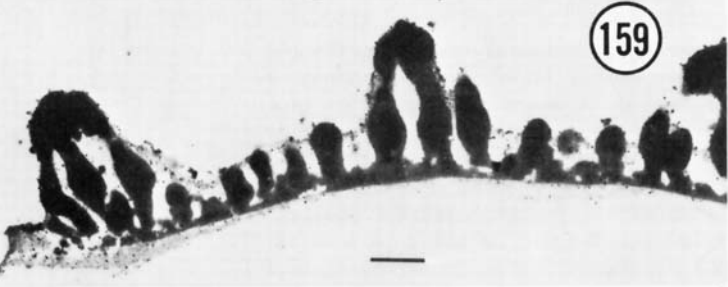
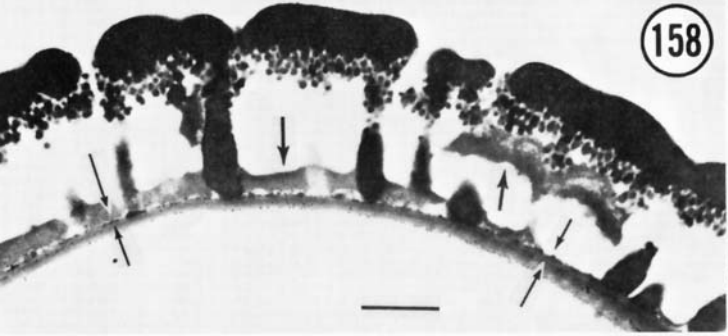
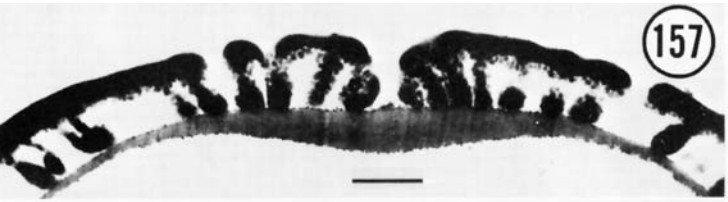
FIGURES 136–141.—Polygonaceae pollen, SEM: 136, *Emex australis* Steinheil, equatorial view, $\times 2990$ (Seydel 2975); 137, *Lastarriaea chilensis* Remy, mesocolpial view, $\times 3400$ (Worth & Morrison 16338 UC); 138, *Rumex acetosa* L., equatorial view, $\times 4400$; 139, ectexine surface, $\times 10,000$; 140, *Polygonum convolvulus* L., mesocolpial view, $\times 3050$; 141, ectexine surface, $\times 7500$. (Photo reduced to 78½ percent.)



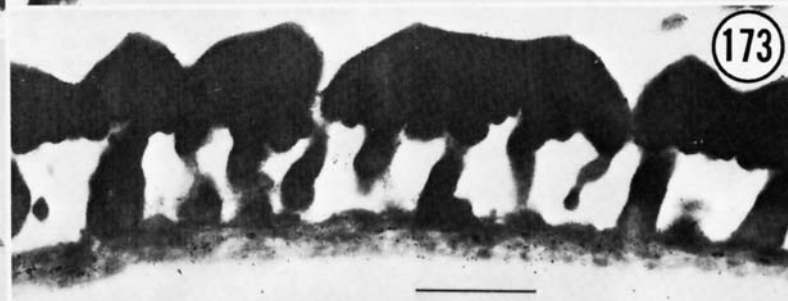
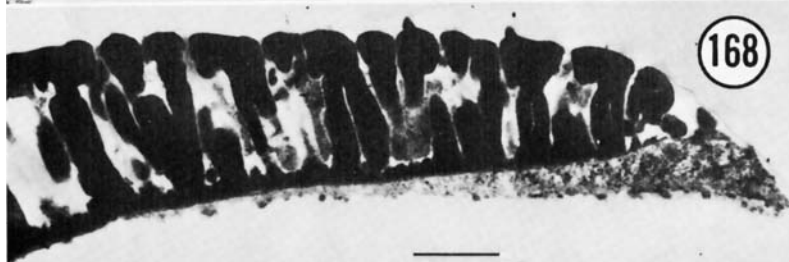
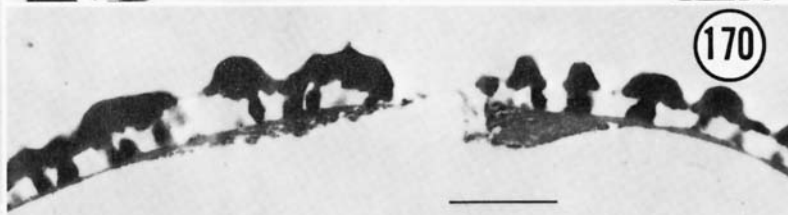
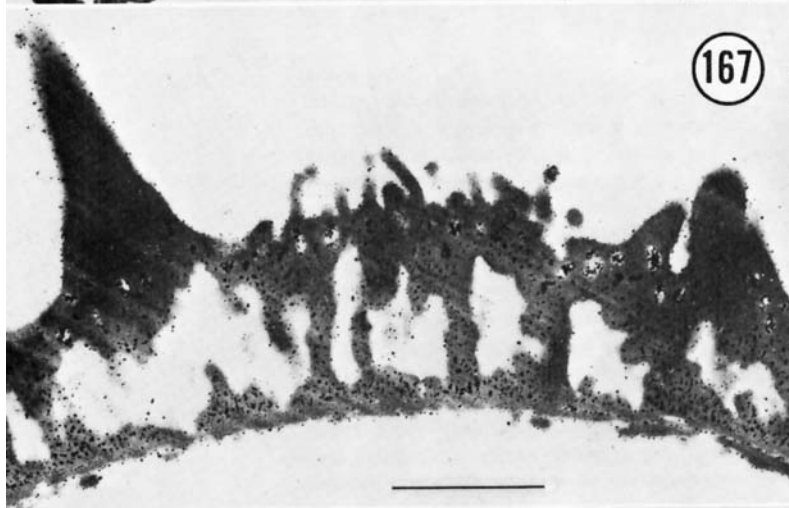
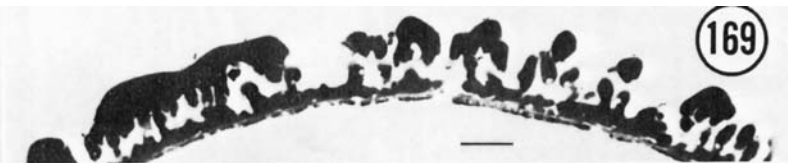
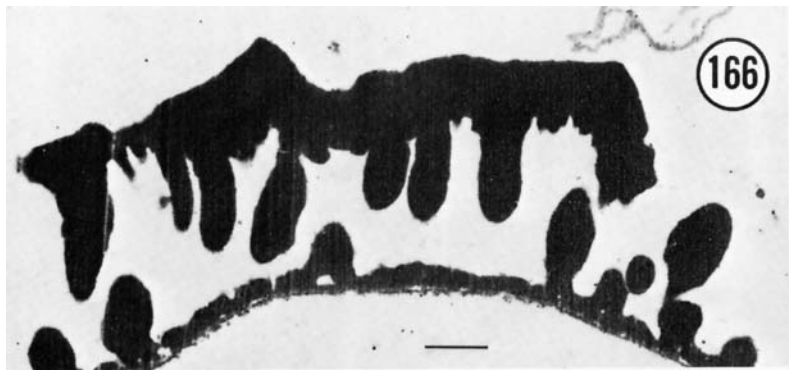
FIGURES 142-149.—Polygonaceae pollen, TEM: 142, *Antigonon guatemalense* Meisner, the endexine is narrow and plate-like; 143, *Atraphaxis buxifolia*, section somewhat oblique but endexine is thick and partially lamellar; 144, *Calligonum comosum*, the tectum and columellae are well developed but the foot layer is greatly reduced; 145, *Chorizanthe breweri* S. Watson, the tectum is thin and the lower part highly globular; the foot layer is reduced (or absent?) and the endexine narrow but uniform; 146, *C. paniculata*, this section is very similar to that of Figure 145, but there is a very thin foot layer and endexine; 147, *Coccoloba cordata*, section somewhat oblique; foot layer is extremely thick while the columellae and tectum are of smaller dimensions; extending from the tectum are large, irregularly shaped components; a vestigial endexine is suggested but additional work is necessary for confirmation; 148, *Eriogonum marifolium*, foot layer is very reduced as in Figures 144 and 145, but the endexine appears massive due largely to section through aperture; 149, *E. parishii*, S. Watson, very similar to Figure 145. (Scales equal 1 μ m.)



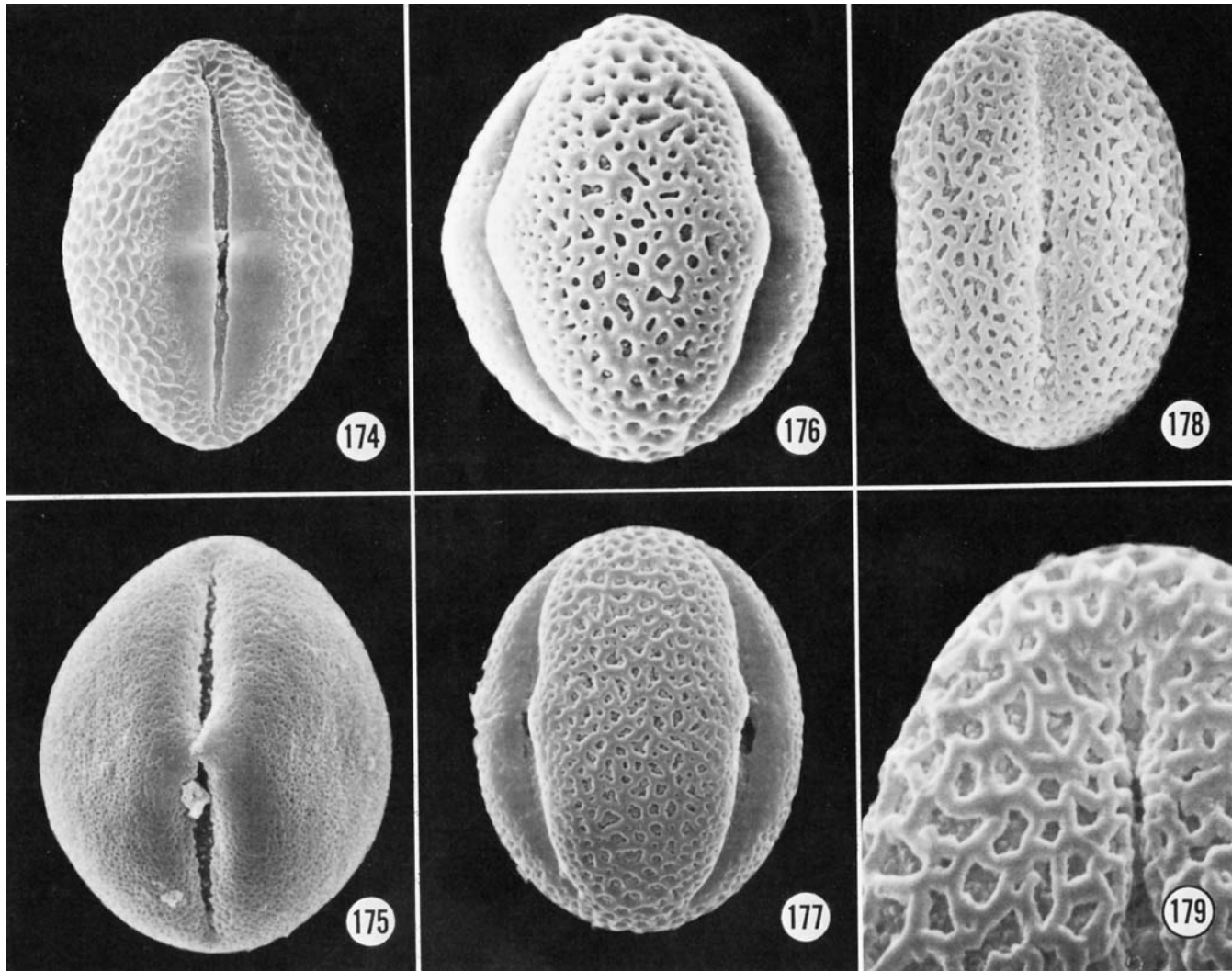
FIGURES 150–156.—Polygonaceae pollen, TEM: 150, *Fagopyrum esculentum*, the section is similar to *Antigonon guatemalense* (Figure 142) in the thickened tectum with funnel-like depressions (Figure 87), reduced foot layer, and thin but recognizable endexine; 151, *Gymnopodium antigonoides*, the endexine is not clearly evident in this somewhat oblique view, but, the inset of a section including the colpus reveals uniform endexine (Goldman 743); 152, *Harfordia macroptera*, section through the colpus with prominent endexine; the lower surface of the tectum is irregular (Figures 145, 146, 149, 157, 158); 153, *Muehlenbeckia chilensis*, except for the aperture regions the endexine is highly reduced; 154, *M. tamnifolia*, the endexine appears to be more uniform than in Figure 153; 155, *M. cunninghamii*, the tectum is thick with few perforations and the highly lamellar endexine and foot layer are approximately equal in thickness (Aston 984); 156, *M. polybotryar* Meisner, section somewhat oblique; the foot layer reduced and endexine prominent. (Scales equal 1 μm .)



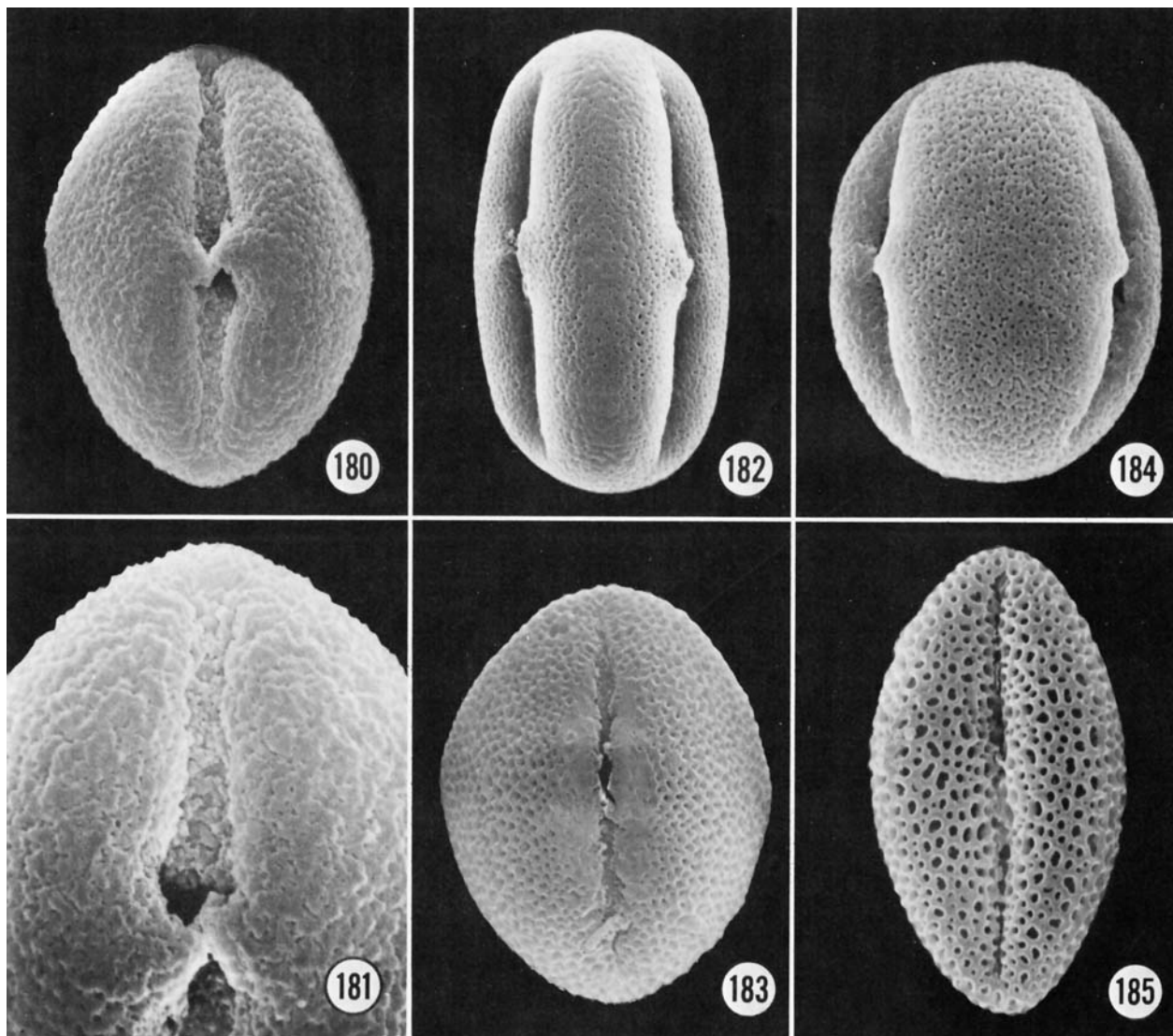
FIGURES 157–165.—Polygonaceae pollen, TEM: 157, *Nemacaulis denudata*, the section illustrates several characteristics of the punctate type, i.e., tectum with granular lower surface, very reduced foot layer, and an endexine which at least in the region of the colpus is very prominent; 158, *Oxytheca trilobata*, same as 157, the double arrows indicate the extremely thin foot layer, single arrows indicate acetolysis resistant material, which can be readily mistaken for exine layering; 159, *Polygonum orientale*, long columellae fused at the apex to form the muri alternate with smaller free columellae in the lumina (Figures 114, 115); a thin endexine can be recognized in the aperture region to the left; 160, *Podopterus mexicanus*, an endexine cannot be recognized but the lower part of the foot layer appears to consist of a thin, less electron-dense zone; 161, *Polygonella fimbriata*, the section reveals a well-developed foot layer and thickened endexine, an unusual combination in the family; 162, *Polygonum amphibium*, section at right angle through muri; 163, *P. amphibium*, section parallel through murus; 164, *P. bistorta*, section, which includes entire pollen grain, is oblique; the densely packed columellae are rare and limited to *Bistorta* complex (Cantlon & Malcolm 580085); 165, *P. convolvulus*, section through polar region where tectum is psilate; this taxon and *Polygonella fimbriata* (Figure 161) are the only two in which both the foot layer and endexine are well developed; this supports their parallel exomorphology observed in SEM (Figures 130, 140, 141) and discussed in text. (Scales equal 1 μm .)



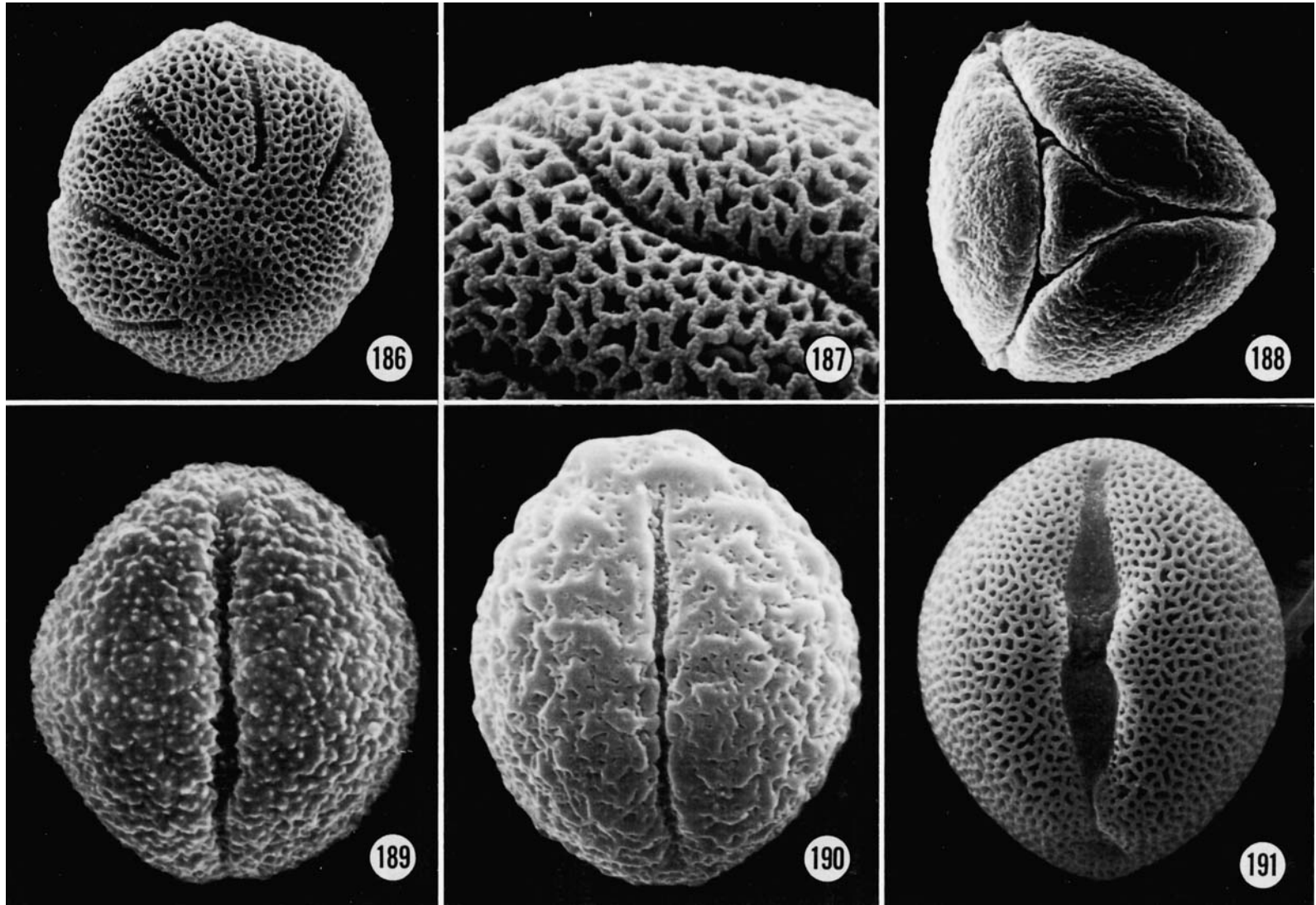
FIGURES 166-173—Polygonaceae pollen, TEM: 166, *Polygonum dielsii*, section \pm oblique, solid tectum indicates section is through muri; 167, *P. forrestii*, the most distinctive member of the genus in TEM; the endexine is thin, the ectexine contains abundant holes or internal foramina, and the tectum is composed of very large, solid spines on an irregular or granular base; 168, *P. vacciniifolium*, very similar to Figure 164, densely packed columellae and also a member of the Bistorta complex; 169, *P. virginianum*, the discontinuous tectum reflects reticulate sculpture; 170, *Rumex acetosa*, the foot layer is either greatly reduced or absent; endexine thickness and rupture indicate colpus; 171, *Ruprechtia laxiflora*, foot layer is consistent and well developed; arrows point to what appears to be a lamellar endexine in colpial region; 172, *R. pallida*, similar to Figure 171 but endexine somewhat better developed; the accumulation of apparent foot layer material in colpus region is unusual; 173, *Triplaris americana*, similar to Figure 151, thickened tectum, thin foot layer and endexine. (Scales equal 1 μm .)



FIGURES 174-179.—Primulacae pollen, SEM: 174, *Coris monspeliensis* L., equatorial view, $\times 2500$; 175, *Lysimachia hybrida* Michaux, equatorial view, $\times 5000$; 176, *Naumbergia thyrsiflora* (L.) Reichenbach, mesocolpial view, $\times 4620$; 177, *Lysimachia terrestris* (L.) Britton, Stern, & Poggenberg, mesocolpial view, $\times 4400$; 178, *Stimpsonia chamaedryoides* C. Wright, equatorial view, $\times 3200$; 179, ectexine surface, $\times 7500$. (Photo reduced to 72 percent.)

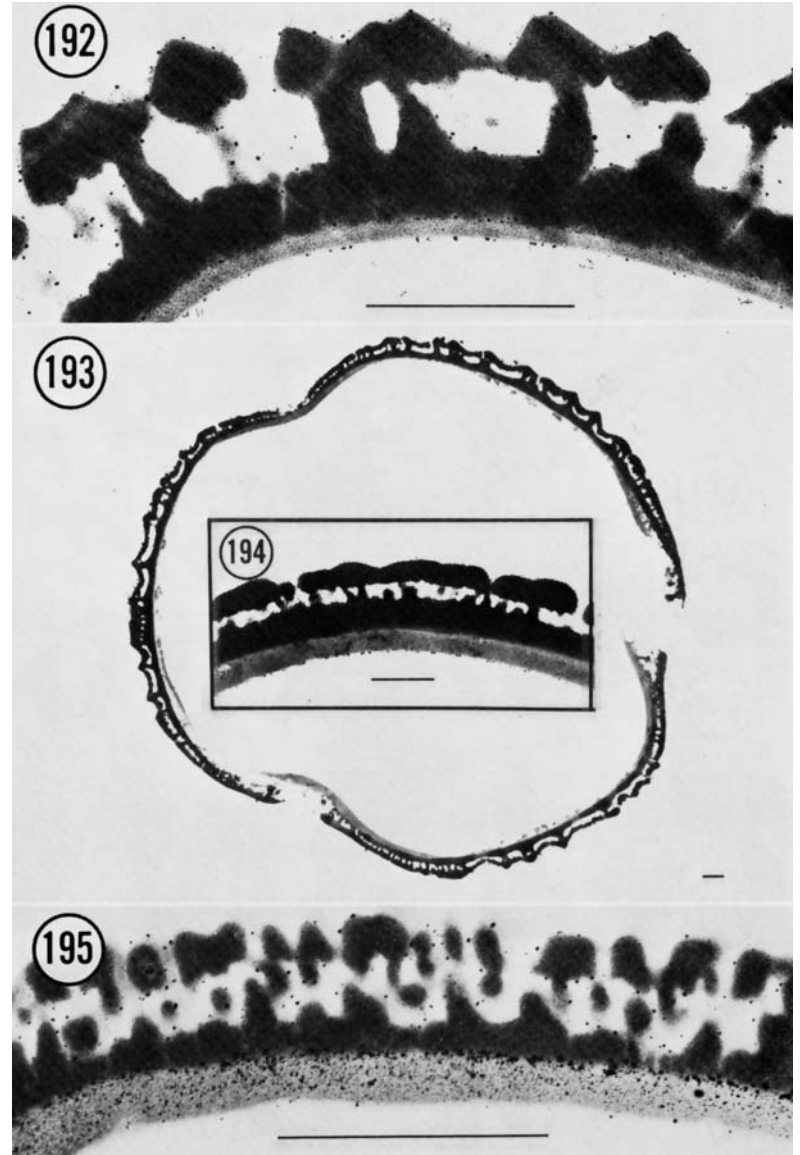


FIGURES 180-185.—Primulaceae pollen, SEM: 180, *Dodecatheon alpinum* (A. Gray) Greene, equatorial view, $\times 4000$; 181, ektexine surface, $\times 7500$; 182, *Douglasia montana* A. Gray, mesocolpial view, $\times 4250$; 183, *Anagallis linifolia* L., equatorial view, $\times 3900$; 184, *Cyclamen neapolitanum* Tenore, mesocolpial view, $\times 6500$; 185, *Hottonia palustris* L., equatorial view, $\times 5250$. (Photo reduced to 78 percent.)



FIGURES 186-191.—Primulaceae pollen, SEM: 186, *Primula veris* L., oblique view, $\times 3200$; 187, ectexine surface, $\times 7500$ (186, 187, *Charpin et al. s.n.*); 188, *Cortusa matthioli* L., polar view with triangular apocolpial field, $\times 5000$; 189, *Soldanella alpina* L., equatorial view, $\times 6060$; 190, *Glaux maritima* L., equatorial view, $\times 4300$ (*Redfield s.n.*); 191, *Omphalogramma vincaeflora* Franchet, equatorial view, $\times 3550$. (Photo reduced to 76 percent.)

FIGURES 192-195.—Primulaceae pollen, TEM: 192, *Anagallis linifolia*, a uniform endexine is notable as is the prominent foot layer; 193, *Coris monspeliensis*, the section includes the entire grain and reflects the variation of the sculpture as seen in SEM (Figure 174); the endexine is greatly thickened in the region of the apertures; 194, *Glaux maritima*, the foot layer and endexine are both prominent and approximately equal in thickness (Redfield s.n.); 195, *Lysimachia hybrida*, the oblique section enhances the thickness of the foot layer and endexine. (Scales equal 1 μm .)



FIGURES 196-200.—Primulaceae pollen, TEM: 196, *Naumbergia thrysiflora*, thickened tectum is supported by reduced columellae on a well-defined foot layer and prominent endexine; 197, *Omphalogramma vincaeflora*, similar to Figure 196 except for more massive columellae; 198, *Primula officinalis* (L.) Jacquin, in contrast to all other taxa of Primulaceae examined in TEM, those in the genus *Primula* are without a foot layer; however in light microscopy and SEM, the samples appeared at least partially sterile; 199, *Stimpsonia chamaedryoides*, oblique section of entire grain illustrating consistent foot layer, and an endexine that is massive in aperture regions and thin but recognizable in the mesocolpial areas; 200, *Primula veris* L., see Figure legend 198 (*Skvortsoo s.n.*). (Scales equal 1 μm .)

