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Pollen Morphology and Phylogenetic Relationships of the Berberidaceae

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ABSTRACT

Nowicke, Joan W., and John J. Skvarla. Pollen Morphology and Phylogenetic Relationships of the Berberidaceae. *Smithsonian Contributions to Botany*, number 50, 83 pages, 215 figures, 3 tables, 1981.—Pollen from 68 collections representing 14 genera and 40 species of the family Berberidaceae was examined by light microscopy, SEM, and TEM. In part, the pollen data reinforce the traditional view of closely related pairs or small groups of genera. In *Berberis* and *Mahonia* the pollen morphology would support separate family status as well as congeneric treatment. The unusual exine structure in *Nandina* would reinforce its treatment as a monotypic family, Nandinaceae. The distinction of *Bongardia* from *Leontice* and of *Dysosma* from *Podophyllum* is confirmed by pollen data. The presence of a fundamentally similar tectum in *Achlys*, *Dysosma*, *Epimedium*, *Jeffersonia*, *Podophyllum peltatum*, *P. hispidum*, and *Vancouveria* suggests closer relationship among these genera than has been previously thought. The close similarity of the pollen in *Jeffersonia* and *Plagiorhegma* confirms their congeneric treatment. Palynologically, *Bongardia*, *Caulophyllum*, and *Leontice* are more closely related to each other than to any remaining genera. In three taxa, *Diphylleia*, *Podophyllum hexandrum*, and *Ranzania*, certain characteristic(s) of the pollen render it unique and for the most part nullify any systematic value within the family. The pollen morphology of the Berberidaceae s.l. is not similar to that of the Ranunculaceae, *Hydrastis* excepted, nor to Lardizabalaceae. There appear to be unusual examples of parallelism between the Berberidaceae and Cistaceae, and between *Podophyllum* and *Croton.*

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Contents

Pollen Morphology and Phylogenetic Relationships of the Berberidaceae

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Introduction

The geographical distribution of the flowering plants presents some perplexing problems, but none more so than that of disjunct or discontinuous genera that, by definition, occupy widely separated regions. If these taxa are regarded as monophyletic, then it follows, largely by assumption, that either at one time their range must have included intervening areas or the taxa have fruits and/or seeds with adaptations for long distance dispersal. There are, in fact, floristic relationships based upon two regions (rarely three) having a high number of disjunct genera common to both, and it is more logical and probable that the high number is an indication of a previously more continuous range. The floras of eastern North America and eastern Asia are one of the classic examples, with as many as 80 genera having species in both regions. These genera are not randomly spread among the dicots or monocots, but tend to be concentrated in the more primitive families, one of which is the Berberidaceae. Even in the widest sense this is a small family, consisting of 10 to 12 genera and about 600 species, with as many as 500 of these belonging to *Berberis* L.

The genera most commonly regarded as belonging to the Berberidaceae are the following. *Achlys* De Candolle, *Berberis* L., *Bongardia* C. A. Meyer, *Caulophyllum* Michaux, *Diphylleia* Michaux, *Dysosma* R. E. Woodson, *Epimedium* L., *Jeffersonia* Barton (*Plagiorhegma* Maximowicz), *Leontice* L., *Mahonia* Nuttall, *Nandina* Thunberg, *Podophyllum* L., *Ranzania* Ito, and *Vancouveria* C. Morren and Decaisne. These genera are not considered to be a single closely related group, and this is reflected in the fact that few systematists have included all in one family.

Most modern generalists consider the genera as primitive or at least unspecialized and place them with the Rannuculaceae, Menispermaceae, Lardizabalaceae, and several very small families as the Order Ranunculales or even Berberidales.

This study of pollen morphology in the Berberidaceae is part of an extensive and continuing research project on the phylogenetic relationships of the Order Centrospermae. This unusual group of families with the unique nitrogen-containing pigments, the betalains, and distinctive sieve tube plastids (Behnke, 1976) has pollen with an ektexine characterized as spinulose and punctate/tubuliferous. This particular surface pattern,

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found in 85% of the taxa examined, is the predominant type in each of the betalain families as well as the two anthocyanin families, Caryophyllaceae and Molluginaceae. Both authors have regarded this ektexine type as unspecialized and consider that the significance attached to it resides mainly in its high frequency. These results have been published in two papers, one based on light microscopy and SEM (Nowicke, 1975) and the other emphasizing TEM (Skvarla and Nowicke, 1976).

In the first investigation of families outside the Centrospermae, the pollen of the Plumbaginaceae, Polygonaceae, and Primulaceae was examined in a study that combined and integrated results from light microsocpy, SEM, and TEM (Nowicke and Skvarla, 1977). Examination of 136 taxa in these families, considered to be related to the Centrospermae by various authors, revealed a wide range of variation in the ektexines, but not the common one in the Centrospermae. The Polygonaceae may be one of the most palynologically diverse families in the angiosperms, with variation in shape, apertures, tecta, and exine structure.

The Order Ranunculales is the second group of families to be investigated palynologically for evidence of relationships to Centrospermae. At this writing almost 150 species have been examined in the Ranunculaceae, 40 species in the Berberidaceae s.l., 14 in the Lardizabalaceae, seven in the Coriariaceae, four in the Sabiaceae, and three in the Corynocarpaceae. Due to the large number of taxa and the general conclusions that the palynological data do not support a close relationship among any of the above families, the decision was made to treat each family in a separate publication.

For purposes of comparison and the reader's convenience, we have included electron micrographs of the common pollen type in the Centrospermae (Figures 1–6) as well as the predominant type in the Ranunculaceae (Figures 7–12).

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Previous Treatments of the Family

The Japanese botanist Masao Kumazawa worked on both the Ranunculaceae and Berberidaceae for a number of years (1930a, 1930b, 1932a, 1932b, 1935, 1936a, 1936b, 1937a, 1937b, 1937c, 1938a) and published a paper in 1938 (1938b) in which he reviewed and discussed the relationship within and between the families. Kumazawa (1938a:9) regarded both families as including "extremely heterogeneous types" with the systematic affinities of some genera still undecided. The Berberidaceae and Ranunculaceae have peculiar anatomical features not commonly found in dicots: fused cotyledons, trimerous parts, V-shaped xylem. The developmental mode of the pollen grains and endosperm are more characteristic of the monocots than dicots.

Although numerous authors have considered that the connecting links between the Ranunculaceae and Berberidaceae were to be found in the transitional genera *Glaucidium-Hydrastis* and *Podophyllum-Diphylleia*, Kumazawa (1938a) regarded the above generic pairs as widely separated, citing differences in vegetative structures and anther dehiscence, as well as the results from his most recent investigation of ovular structures in the two families (1938b).

Kumazawa (1938a:12) considered *Nandina* as the "farthest deviated" genus in the Berberidaceae; in fact, he would support family status based on the combination of vegetative and ovular characteristics as well as a type of anther dehiscence not found in any other berberidaceous genera. He no longer regarded *Diphylleia* as closely related to *Podophyllum*, the two differing in dehiscence of the anthers, the pollen, and the type of vernation. He segregated *Podophyllum* as a monogeneric family, but left the fate of *Diphylleia* "for consideration" (1938a:13). For the remaining genera, Kumazawa established a Berberidaceae consisting of two subfamilies: Berberidoideae with only *Berberis* and *Mahonia*; and Epimedioideae with three tribes, Epimedeae with *Epimedium* (*Vancouveria*?), *Leontice* (*Bongardia*?), *Caulophyllum*, *Jeffersonia*, and *Plagiorhegma*, Achylieae with *Achlys*, and Ranzanieae with *Ranzania*. He cited the pollen of *Berberis* and *Mahonia* as the most striking distinction between the two subfamilies, possibly indicating a large phylogenetic gap between them.

Buchheim (1964) maintained the relationship of *Diphylleia* and *Podophyllum* by segregating the two genera in a subfamily, the Podophylloideae. The second and much larger subfamily, Berberidoideae, has the remaining genera, but their similarities and distinctions are maintained by the establishment of three tribes: Nandineae with only *Nandina*; Berberideae with *Berberis*, *Mahonia*, and *Ranzania*; and the Epimedieae with *Aceranthus*, *Achlys*, *Bongardia*, *Caulophyllum*, *Epimedium*, *Jeffersonia*, *Leontice*, *Plagiorhegma*, and *Vancouveria*. His concept of the Order Ranunculales, which he described for the *Syllabus der Pflanzenfamilien*, includes the following families: Ranunculaceae, Berberidaceae, Lardizabalaceae, Menispermaceae, Nympheaceae, Ceratophyllaceae, and Sargentodoxaceae (only *Sargentodoxa*).

Buchheim's (1964) interpretations of the relationships of the above families are of significance because he also described the Magnoliales, considered, at least by Hutchinson (1959), to be the woody counterpart of the Ranunculales. Undoubtedly his treatment of each order benefited from the knowledge and perspective provided by the treatment of the other.

Cronquist (1968) placed the Berberidaceae in the Order Ranunculales, consisting of Ranunculaceae, Circaeasteraceae, Lardizabalaceae, Menispermaceae, Coriariaceae, Corynocarpaceae, and Sabiaceae. In his list (1968:365) of orders and families, Podophyllaceae are indicated as belonging to the Ranunculaceae, but no genera are listed; Nandinaceae are a part of the Berberidaceae.

Takhtajan (1969:208) separated *Podophyllum* and *Diphylleia* as the Podophyllaceae and also gave *Nandina* family status. The remaining genera are assumed to be in the Berberidaceae since they do not appear elsewhere in his scheme as families. In addition to the above families, he regarded Lardizabalaceae, Sargentodoxaceae, Menispermaceae, Ranunculaceae, Glaucidiaceae, Hydrastidaceae, and Circaeasteraceae as belonging to the Order Ranunculales.

Hutchinson (1959) designated the second order in his division Herbaceae as Berberidales, but the Berberidaceae are very reduced, consisting of only *Berberis* and *Mahonia*; *Nandina* is placed in a separate family in this order. The remaining berberidaceous genera are united as the Podophyllaceae, but placed in the first order, the Ranales (Ranunculales).

Thorne (1974) designated the first superorder in the dicotyledons as the Annoniflorae, which he segregated into three orders: the Annonales, the largest with about 23 families; the Berberidales with six families; and the Nymphaeales with only four families. The significant difference between Thorne's concept of the Berberidales and that of most other generalists is the addition of the Papaveraceae whose distinction is partially acknowledged by treating it as a suborder. The other suborder, the Berberidineae, includes Lardizabalaceae, Sargentodoxaceae, Menispermaceae, Berberidaceae, and Ranunculaceae. Thorne maintained a wide family concept, preferring to recognize the traditional generic alliances as subfamilies or tribes.

In a more recent study utilizing comparative serology, Jensen (1974) concluded: that *Berberis* and *Mahonia* are very closely related, even congeneric; that *Podophyllum* and *Diphylleia* are similar in serological aspect; and that *Nandina* is very similar to the above four genera, but closer to *Berberis* and *Mahonia*. He also suggested that these five genera be segregated as a unit such as subfamily, and the distinction between the above be maintained by establishing three tribes. In comparing the reactions of other genera to the *Berberis vulgaris* antiserum and to the *Podophyllum emodi* (= *P. hexandrum*) antiserum, Jensen found that *Vancouveria* and *Jeffersonia* indicated at least some similarities to each system, but *Caulophyllum* and *Epimedium* had only a very weak reaction to each. Jensen also noted that *Caulophyllum* and *Leontice* are very similar in serological respects. But pending further studies, he would place the remaining genera of the Berberidaceae, *Achlys*, *Bongardia*, *Caulophyllum*, *Epimedium*, *Jeffersonia*, *Leontice*, and *Vancouveria*, in a second subfamily.

Chapman (1936), in a study of carpel morphology in the Berberidaceae, used serial sections to trace the distribution of the vascular bundles and proposed that only an original condition of three separate, spirally arranged carpels from which two distinct lines evolved would satisfactorily explain the present variation. The two lines that Chapman suggested would require a fusion of the carpels with the loss or suppression of one or two. For *Berberis*, *Mahonia*, *Leontice*, and *Caulophyllum* the distribution of the vascular bundles could be the result of suppression of the upper two carpels and an expansion of the lowest one. In the other line, the two fused carpels found in *Epimedium*, *Vancouveria*, *Nandina*, *Achlys*, *Jeffersonia*, *Diphylleia*, and *Podophyllum* could be derived by the loss of one carpel in the process of fusion. She concluded that the separation of *Berberis* and *Mahonia* with their independent evolution occurred very early; that the lack of a close relationship of *Nandina* to the other genera would also indicate an early separation; that *Jeffersonia* and *Achlys* are more closely related to *Epimedium* than to each other; and that the carpel morphology of *Diphylleia* and *Podophyllum* does not support a close relationship to each other.

According to Kumazawa's developmental studies (1938a) the basilary placentation accorded to *Berberis*, *Mahonia*, *Caulophyllum*, and *Achlys* is in fact a modification of the parietal placentation found in *Epimedium*, *Nandina*, and *Plagiorhegma* (*Jeffersonia*), differing only in the area of elongation at a later stage. Furthermore, the ovules of the basilary types are in reality slightly dislocated towards the lateral walls, which also supports Kumazawa's view that parietal placentation is the original type.

Not all of Kumazawa's results (1938a) are relevant here, but those on *Nandina* are significant in the later discussion. It was the only genus investigated in which the funiculus was absent; in the other genera it ranged from very short to prominent. *Nandina* had an atypical micropyle in which the outer integument did not project at the point of closure.

The following review of the size and distribution of the berberidaceous genera is essential to the discussion of the results of this study. If a genus has been the subject of a separate study, the pertinent conclusion or observations are included. Closely related genera are discussed together.

Achlys De Candolle has two species, *A. triphylla* (Smith) De Candolle in Pacific North America, and *A. japonica* Maximowicz from Asia. This is the only disjunct genus in the family with a Pacific North America and Asia distribution.

Berberis L. is the largest genus in the family with as many as 500 species widely distributed in both the Old World and the New World. The closely related *Mahonia* Nuttall, with approximately 75 species, is the second largest genus. Although Ahrendt (1961) published an exhaustive study of these two genera, it is unfortunate that he did not discuss the relationships of *Berberis* and *Mahonia* to the remaining berberidaceous genera.

Bongardia C. A. Meyer has a single species, *B. chrysogonum* (L.) Grisebach, found along the Afghanistan-Iran-U.S.S.R. border. It was first described as a species of *Leontice* by Linnaeus (1753).

Caulophyllum Michaux is a disjunct genus of two very similar species, *C. thalictroides* (L.) Michaux in eastern North America as far west as Nebraska and Missouri, and *C. robustum* Maximowicz from China, Japan, and Korea. The latter sometimes has been treated as a variety of the former.

Diphylleia Michaux has three species, one in eastern North America, *D. cymosa* Michaux, and two in Asia, *D. grayii* R. Schmidt in Japan and *D. sinensis* Li from China, and is a disjunct genus.

Dysosma R. E. Woodson was established as a monotypic genus based on *Podophyllum pleianthum* Hance. At that time (1928), Woodson regarded all the following taxa as variations of *Dysosma pleiantha* (Hance) Woodson: *Podophyllum versipelle* Hance, *P. veitchii* Hemsley and E. H. Wilson, *P. difforme* Hemsley and E. H. Wilson, *P. esquirolii* Leveille, and *P. onzoi* Hayata. Later, Hu (1937) transferred two species of *Podophyllum*: *P. delavayi* Franchet, now *Dysosma delavayi* (Franchet) Hu and *P. aurantiocaule* Handel-Mazzetti, now *Dysosma aurantiocaule* (Handel-Mazzetti) Hu.

Epimedium L. and the closely related *Vancouveria* C. Morren and Decaisne were treated by Stearn in a monograph published in 1938. He reduced two monotypic genera, *Aceranthus* C. Morren and Decaisne, and *Vindicta* Rafinesque, to *Epimedium* since the type species for each was *E. diphyllum* Loddiges; but he maintained the generic status of *Vancouveria*, citing a group of morphological distinctions that occur only individually in various species of *Epimedium.*

Stearn (1938) recognized 21 species of *Epimedium*, all with an Old World distribution, but remarked on the difficulty of assessing their relationships to each other, the characteristics seeming to be either on a generic level and applicable to all, or on a species level and applicable to one. He did segregate the 21 species into eight small groups which he then placed in two sections defined by the origin or position of the leaves: section Rhizophyllum in which all leaves are basal with only one "group" of two species; and section Phyllocaulon in which all leaves are attached to the flowering stem, with the remaining seven "groups" and 19 species. Stearn (1938:428) based the four subsections, some of which include more than one "group," on the number of leaves on the floral stem, but noted that "this is liable to some variation." After attempting to verify the identification of some voucher specimens, the authors would agree.

For *Vancouveria*, Stearn (1938) recognized three species: *V. hexandra* (Hooker) C. Morren and Decaisne, the most common and the most widely distributed (California, Oregon, and Washington), and *V. chrysantha* Greene and *V. planipetala* Calloni, both found in California and Oregon. The report of *V. hexandra* from Vancouver Island or continental Canada is apparently erroneous; Stearn did not see any collections from these regions.

Jeffersonia Barton has two species, *J. diphylla* (L.) Persoon from eastern North America, and *J. dubia* (Maximowicz) Bentham and Hooker, which occurs in southeastern Manchuria, adjacent Korea, and eastern Siberia. The disjunct status of *Jeffersonia* depends on the validity of the reduction of *Plagiorhegma dubia* Maximowicz; most authors follow Bentham and Hooker in this, Hutchinson excepted (1959).

Leontice L., an Old World genus of eight to 10 species, is sometimes given separate family status, the Leonticaceae (Airy-Shaw, 1966), including *Bongardia* and *Caulophyllum.*

Nandina Thunberg is a monotypic genus from China whose distinctions have been acknowledged by Chapman (1936), Ernst (1964), Kumazawa (1938a), and most generalists.

Podophyllum L. is a disjunct genus with one species, *P. peltatum* L., very common in the eastern half of North America, and an uncertain number, but not more than four or five species, distributed in eastern Asia. The present authors follow Soejarto, Faden, and Farnsworth (1979) in the use of *Podophyllum hexandrum* Royale rather than *P. emodi* Wallich for the most common Asian species.

Ranzania Ito is a monotypic genus with the single species, *R. japonica* (Ito) Ito, restricted to the northern part of Honshu, the largest of the Japanese Islands. Kumazawa (1937c) concluded after a detailed study that this species did bear some resemblance to *Caulophyllum* and *Epimedium*, but that it also had in the stamens, petals, and fruit some of the restricted or peculiar characteristics found in *Berberis* and *Mahonia.* He proposed that *R. japonica* represented an intermediate type and was not as closely related to the Epimedieae as he had previously thought.

The cytological data on the genera of the Berberidaceae are almost complete and are of significance to "General Discussion" herein. The following reports were taken from Darlington and Wylie (1956): *Achlys* 2n = 12; *Berberis* x = 14, 2n = 28, 56; *Bongardia* x = 6, 2n = 14; *Caulophyllum* x = 8, 2n = 16; *Diphylleia* x = 6, 2n = 12; *Epimedium* x = 6, 2n = 12; *Jeffersonia* x = 6, 2n = 12; *Mahonia* x = 14, 2n = 28; *Nandina* x = 10, 2n = 20; *Podophyllum* x = 6, 2n = 12; *Ranzania* x = 7, 2n = 14; *Vancouveria* x = 6, 2n = 12. *Leontice armeniaca* with 2n = 14, and *L. leontopetalum* with n = 8 + 1B, and 2n = 16, were taken from Ornduff (1968). Six genera, *Achlys*, *Diphylleia*, *Epimedium*, *Jeffersonia*, *Podophyllum*, and *Vancouveria*, have chromosome number of 2n = 12.

There are two monotypic genera, *Glaucidium* Siebold and Zuccarini and *Hydrastis* Ellis ex L., that are always included in the Order Ranunculales and are associated with Berberidaceae and Ranunculaceae but at different levels of recognition. Wettstein (1935) placed both genera in the Berberidaceae; Cronquist (1968) included both in the Ranunculaceae; Hutchinson (1959) divided the Ranunculaceae s.l. into the Ranunculaceae s.s. and Helleboraceae with both genera in the latter family; Takhtajan (1969) acknowledged their distinction from the Ranunculaceae, from the Berberidaceae, and from each other by separate family status, Glaucidiaceae and Hydrastidaceae. Thorne (1974:187) summarized their characteristics and relationships as follows.

> *Hydrastis* and *Glaucidium*, sometimes placed with the Bericadeae or as a distinct family, do have the berberidaceous rhizomatous habit of growth and *Glaucidium* frequently has only one carpel. However, their flowers have numerous stamens, many to two carpels or one carpel, no petals or nectaries, and their leaves are simple and palmately lobed. They are distinguishable from the other Ranunculaceae by the absence of nectaries, ovules with longer outer integument, rather fleshy fruit, and distinctive haploid chromosome numbers of *n* = 10 and 13. Their chemistry is very similar to that of the other Ranunculaceae (Hammond, 1955; Jensen, 1968) but they possess several alkaloids in common also with the Berberidaceae (Willaman and Schubert, 1961). They seem better treated as an intermediate group but close enough to the other ranunculads to warrant subfamily treatment in the Ranunculaceae (Kumazawa, 1938; Buchheim, 1964).

The most comprehensive study of the pollen of the Berberidaceae to date may well be a paper published in 1936 which also included the Ranunculaceae and Lardizabalaceae. Kumazawa (1936a) provided descriptions and discussions for 46 genera and 230 species with 72 illustrated by line drawings. Although his terminology differs somewhat from those currently in vogue, there is no problem in translation, e.g., expansion furrow being the equivalent of colpus. He recognized four pollen types based on apertures: Type 0, inaperturate; Type I, 3-zonocolpate, rarely 6–8-zonocolpate; Type II, pantocolpate; and Type III, pantoporate. Since Kumazawa (1936a) regarded *Diphylleia* as pantoporate, and *Berberis* and *Mohonia* as inaperturate, the Berberidaceae, in his estimation, had all four types.

In a more recent contribution, Roland-Heydacker (1974) described the pollen of *Berberis vulgaris* L. and *Mahonia aquifolium* Nuttall as having unique helicoid colpi as well as a compacted ektexine, a granular endexine, and a persistent intine that reacted positively to tests for polysaccharides.

Materials and Methods

The pollen of 40 species assigned to 14 genera in the Berberidaceae (Table 1) has been examined in light microscopy (LM) and in scanning electron microscopy (SEM) and a limited number in transmission electron microscopy (TEM). The pollen of three species from the Order Centrospermae (Table 2) and seven from the Ranunculaceae (Table 3) have also been included. Anthers were removed from herbarium specimens and all material acetolyzed according to procedures outlined in Erdtman (1966). Samples for SEM were vacuum coated with gold and examined with a Cambridge Stereoscan MK IIa, and S410, or a Coates and Welter 106B Field Emission 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). Pollen samples were stained in 0.125% OsO_4 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.

Light slides of all samples are deposited at the Palynological Laboratory, Department of Botany, Smithsonian Institution.

The species examined, the collector and number, and country or U.S. state, as well as figure number(s) if illustrated, are given in Tables 1, 2, and 3. For the most part the names used are taken from the herbarium label or the most recent annotation; each collection sampled was similar to those remaining of a particular species as identified. For most of the disjunct berberidaceous genera, the geographical location, North America as opposed to Asia, provided sufficient identification for the purposes of this study.

The investigation of the Berberidaceae is part of a study comparing pollen morphology of the Ranunculales with that in the Centrospermae and detailed measurements and/or descriptions are usually not included. However, within the Berberidaceae s.l. a significant difference in size, as indicated by polar length, does distinguish two groups of genera from each other. Size could have been a factor in the transfer of *Hydrastis* L. from the Ranunculaceae to the Berberidaceae. For this reason the longest dimensions of ten grains in collections of Berberidaceae and Ranunculaceae were recorded. The high, low, and the mean are given in Tables 1 and 3, respectively; these figures should be treated with reserve in view of the small sample size.

The results from the pollen investigation of each genus are presented first, along with a discussion of the generic relationships as indicated by palynology. A general discussion follows and attempts to evaluate and integrate the pollen data with those from vegetative and floral morphology (Kumazawa 1930a, 1930b, 1932a, 1932b, 1935, 1936a, 1936b, 1937a, 1937b, 1938a, 1938b; Takeda, 1915; Terabayashi, 1977, 1978), carpel morphology (Chapman, 1936), serology (Jensen, 1974), and cytology as reported by Darlington and Wylie (1956) and Ornduff (1968).

Results and Discussion of Pollen Analyses

Pollen from three families in the Centrospermae is illustrated in Figures 1–6: *Anacampseros filamentosa* Sims (Portulacaceae), Figures 1, 2, has an aperture condition that can be described as pantocolpate but the configuration and the shape of the individual "colpi" are not always uniform, the tectum is spinulose and perforate; *Tunica stricta* (Bunge) Fischer and Meyer (Caryophyllaceae), Figures 3, 4, has a pantoporate aperture type and a tectum that is spinulose and sparsely punctate; *Acrodon bellidiflorus* N. E. Brown (Aizoaceae), Figures 5, 6, is 3-colpate with a tectum that has been described as reticulate (Radulescu, 1974), but the size of the perforations varies within a sample and those illustrated in the high magnification micrographs are, in fact, unusually large.

The possibility of a close relationship between the Berberidaceae and any families in the Centrospermae is unlikely, but most taxonomists consider the Berberidaceae and Ranunculaceae to be closely related and for this reason the latter family is illustrated by seven species: in SEM, Figures 7–18, in TEM, Figures 115–123, and in the data of Table 3. It should be noted that the following discussion of Ranunculaceae pollen is based on the examination of almost 150 species (Nowicke and Skvarla, unpublished data).

Ranunculus oreophytus Delile (Figures 7, 8) and *Hepatica transsilvanica* Fuss (Figures 15, 16) have a pantocolpate aperture condition; *Clematis heracleifolia* De Candolle (Figures 9, 10) has apertures best described as pores but neither their shape nor their distribution over the surface of the grain is uniform; *Glaucidium palmatum* Siebold and Zuccarini (Figures 11, 12), *Batrachium aquatile* Dumortier (Figures 13, 14), and *Hamadryas magellanica* Lamarck (Figures 17, 18) have a 3-colpate condition. All six species have, in a general sense, a spinulose and punctate/perforate tectum.

Many of the Ranunculaceae taxa examined in thin section have prominent or very large columellae, e.g., *Ranunculus oreophytus* (Figure 115), *Batrachium aquatile* (Figure 119), *Hamadryas magellanica* (Figure 121), and to a lesser extent in *Clematis heracleifolia* (Figure 117) and in *Hepatica transsilvanica* (Figure 120). *Glaucidium palmatum* (Figure 118) illustrates reduced columellae, a condition that is found in *Aconitum* (Nowicke and Skvarla, unpublished data) and *Adonis* (Nowicke and Skvarla, 1980, fig. 158). For the most part the pollen in this family has a well developed endexine layer (Figures 115, 116, 118, 120, 121). The perforations of the tectum, obscure in SEM (Figures 8, 10, 12, 14, 16, 18), are more conspicuous in thin section. *Hydrastis canadensis* L. (Figures 122, 123), will be discussed with the tribe Epimedieae.

There is an unusual characteristic, demonstrated only in transmission microscopy, that is common to some Berberidaceae and to some Ranunculaceae: columellae-shaped ektexine units penetrate the endexine in the apertures (hereafter referred to as aperture columellae). This condition has been found in all species of *Ranunculus* examined in TEM, illustrated here by *R. oreophytus* (Figure 116), in *Batrachium aquatile* (Figure 119), and in *Hepatica transsilvanica* (Figure 120). It is also present in some species of *Anemone* and some species of *Clematis* (Nowicke and Skvarla, 1980, figs. 155, 156). In the Berberidaceae s.l., it is most conspicuous in the two closely related genera *Epimedium* and *Vancouveria* (Figures 149, 154, 155, 159, 160, 161; see discussion of these genera).

Santisuk (1979) investigated the pollen of 124 taxa in the tribe Ranunculeae using light and scanning electron microscopy and established 10 pollen types "based on the types of columellae and aperture and on the nature of the tectum" (Santisuk, 1979:3). For the same taxa his data and ours do not conflict (Nowicke and Skvarla, unpublished data).

In addition to the Ranunculaceae all modern generalists (see "Introduction") consider the Lardizabalaceae to be closely related to the Berberidaceae. The results from pollen studies do not support this contention. For the most part the 14 species examined in the Lardizabalaceae have similar pollen: 3-colpate, the tectum can be psilate with punctae, or indentations, or finely punctate-striate; in thin section the tectum is the most conspicuous unit of the ektexine, the columellae are diminutive in size and sparsely distributed, the foot layer is very thin, the endexine is well developed in the region of the colpus but very reduced in the mesocolpus (Skvarla and Nowicke, unpublished data).

We are of the opinion that most of the taxonomic difficulty associated with the Berberidaceae s.l. can be attributed to exceptional and restricted sporophytic characteristics: the perianth absent in *Achlys*, multiseriate in *Nandina*; petals spurred and/or retroflexed in *Epimedium* and *Vancouveria*; stamens tactile in *Berberis*, *Mahonia*, and *Ranzania*; filaments connivent in *Vancouveria*; the fruits bladder-like in *Bongardia* and *Leontice*, follicle-like in *Epimedium* and *Vancouveria*, horizontally cleft in *Jeffersonia*; seeds large, fleshy, and glaucous in *Caulophyllum*; the habit woody in *Berberis*, *Mahonia*, and *Nandina*, and semisucculent in *Bongardia* and *Leontice*.

Close scrutiny of the entire sections "Results and Discussion of Pollen Analyses" and "General Discussion" will reveal that the authors have not been consistent, from genus to genus, on the degree of importance attached to the same palynological characteristics. The endexine layer is a case in point: it is taxonomically significant in *Nandina*, but insignificant in all remaining genera; another, the condition in which the pollen is shed (monads versus tetrads) is significant in only one species and insignificant in all the remaining ones. The above statements are not intended to justify or validate any or all of the generic realignments proposed here, but to point out that we have been forced to evaluate irregular pollen data against an already uneven background of floral and vegetative morphology.

Within the Berberidaceae the following range of variation was found in apertures, tectum, and exine structure. There are three types of apertures, irregular or spiral found in *Berberis* and *Mahonia*, 6-pantocolpate in *Ranzania*, and 3-colpate, found in all the remaining genera examined. The tectum can be psilate, punctate, punctate-striate, finely reticulate, striate, striate-reticulate, two layers of striae, "random" rods (small, variously distinct rods with one end projecting outward), spinose, or gemmate, with some of the categories grading into another. The structure of the exine is typical of angiosperms: foot layer, columellae, and tectum for all genera except *Berberis*, *Mahonia*, and *Ranzania*, which have an unstratified exine.

Berberis L. (Figures 19–24, 124–132), and *Mahonia* Nuttall (Figures 25–30, 133–138) are considered to be closely related by generalists and specialists alike (see "Introduction"). The pollen of all species examined (Table 1) in these two genera is very similar (Figures 19–30, 124–138) and cannot be distinguished from each other using LM, SEM, or TEM. Of far greater significance than the expected similarity of the pollen is the fact that the unifying characteristics are unmistakably primitive and serve to emphasize the extent of the separation of *Berberis* and *Mahonia* from the remaining genera.

Within the taxa examined in *Berberis* and *Mahonia* the shape and extent of formation of the apertures, i.e., some grains appear inaperturate, is highly variable but could be classified as either irregular or spiral. The irregular category applies to grains with cracks or breaks, e.g., *Berberis fendleri* A. Gray (Figures 21, 22), *B. grandiflora* Turczaninow (Figure 24), *Mahonia fremontii* (Torrey) Fedde (Figures 25, 26), *M. oiwakensis* Hayata (Figure 29), and *M. haematocarpa* (Wooton) Fedde (Figure 30). Occasionally the "furrows" delimit the surface of the grain into plate-like areas, e.g., *M. fremontii* (Figure 25) or *M. oiwakensis* (Figure 29). More rarely some grains have areas with pebble-shaped pieces of exine, e.g., *B. ilicifolia* Forster (Figure 19). The spiral apertures could be designated as preformed but the configuration of the furrows is not uniform, e.g., *Berberis vulgaris* L. (Figure 23) and *Mahonia nervosa* (Pursh) Nuttall (Figures 27, 28).

Kumazawa, who examined four species of *Berberis* and two of *Mahonia*, made the following points about their germinating apparatus (1936a: 35).

> (1) The margin of the furrow expanded is irregularly denticulated in surface view, suggesting the breaking of the exine.
>
> (2) In some cases no furrows are found on the surface of the shrunken and swollen pollens.
>
> (3) There is no rule concerning the position of the furrow.
>
> (4) The shrunken pollens with furrows may represent the reshrunken form of the swollen pollens.

The surface of the exine is unspecialized and randomly variable: punctate, psilate and punctate, psilate, or punctate-striate occur within a species or even within a sample, e.g., *Mahonia fremontii* (Figures 25, 26).

In thin section the exine structure of *Berberis* (Figures 124–132) and *Mahonia* (Figures 133–138) are indistinguishable from each other. The ektexine is nearly amorphous and not organized into typical foot layer, columellae, and tectum units. Because of this lack of structural organization the pollen of *Berberis* and *Mahonia* was examined in both the acetolyzed and unacetolyzed conditions. Following acetolysis, the ektexine contains numerous channels and cavities of a highly pleomorphic nature, which for purposes of this discussion are classified as follows: (1) some completely bisect the ektexine (Figures 128, 130, 136), (2) some partially bisect the exine and occur with sufficient frequency as to resemble highly irregular columellae (Figures 125, 126, 128, 131–133), and (3) some channels appear as irregular, isolated, open holes in the ektexine (Figures 125, 126, 128, 129, 131, 133). Without acetolysis there appears to be a fourth category of channels: extremely short, abundant, randomly oriented and "closed" or filled with electron-dense material (Figure 124).

The primary difference between the examination of acetolyzed and unacetolyzed ektexine images is that of stain density: the images from acetolyzed grains have considerably greater density than those from unacetolyzed grains. This no doubt explains the appearance or visibility of the fourth category of channels. Whether or not the lack of staining of unacetolyzed pollen was due to the dried (i.e., herbarium) nature of the pollen before processing is not known and certainly it would be useful in future work to collect pollen directly from the field and immediately process for TEM. This might clarify the nature of the thin electron-translucent layer or membrane(?) found on the ektexine of unacetolyzed *Berberis* (Figure 124) pollen. The extent of such a layer or specificity (it was not observed in *Mahonia*, Figure 138) as well as its equivalence to the fibrous-granular extra-ektexinous layer as indicated in the acetolyzed preparation of *Berberis ilicifolia* (Figure 131) is not clearly understood at this time.

In the aperture regions the ektexine is represented as knobs or isolated fragments (Figures 127, 132, 134–136). It appears identical in acetolyzed and unacetolyzed preparations.

The endexine in *Berberis* (Figures 124–127, 130–132) and *Mahonia* (Figures 133–137) is prominent and consists of a fibrous-granular layer; the inner surface is smooth and/or uniform but at the interface with the ektexine the endexine appears to partially fill or encroach upon the cavities and channels. It is present in the apertures and appears to support the ektexine fragments. The endexine is not noticeably altered by acetolysis.

The presence of irregular cavities (Figures 124–132) and the concomitant segregation of material suggest an early stage of columellae development.

In the six species of *Berberis*, the mean diameter ranges from a low of 38.4 μm in *B. vulgaris* to a high of 50.6 μm in *B. grandiflora*; in the four species of *Mahonia*, the low is 34.1 μm in *M. haematocarpa* and 33.8 μm in *M. oiwakensis* and the high is 51.2 μm in *M. nervosa*. This degree of size variation is not unexpected since *Berberis* is known to have tetraploid entities as well as diploid; *Mahonia* has not, to our knowledge, been reported as having either a haploid number of 28 or a diploid number of 56; this does not deny the existence of polyploidy in *Mahonia*.

Our results agree with those of Roland-Heydacker (1974), except for her characterization of all(?) apertures as spiral.

The presence of irregular apertures, a surface that is psilate or nearly so, and above all the unstratified exine, are primitive characteristics and are in agreement with the phylogenetic position accorded *Berberis* and *Mahonia* by most systematists.

Ranzania japonica (Ito) Ito (Figures 139–148), although widely cultivated in the United States, has a very restricted distribution, northern Honshu, Japan. Kumazawa (1936a) described the pollen and illustrated it with line drawings (1936a:fig. 67_a, 67_1, 67_2), but for purposes of comparison the authors preferred to examine the pollen of *Ranzania* in SEM and TEM.

Despite its appeal as an ornamental plant, none of the major U.S. herbaria had specimens identified as such. The material finally obtained (Table 1) consisted of one pollen sample sent from Japan by Terabayashi; one flowering specimen, partially dried, from the garden of a private individual in New York State, Epstein s.n.; and all material at the Royal Botanic Gardens, Kew, only two collections, one from a cultivated plant, the other a sterile specimen collected by *Takeda s.n.*, 27 August 1905 in the vicinity of Mount Shirouma, in Honshu.

The sample from Japan (*Terabayashi 154* KYO) was examined in LM and SEM and is illustrated in Figures 139 and 140. Although the grains were not numerous, they were uniform in size, shape, aperture type, and the surface of the exine, and the two in Figure 139 are representative. They also appear to be a dyad (see TEM discussion of Figure 147). The configuration of the six colpi is such that there are four threefold axes delineating the surface of the grain into four triangular areas. Most of the colpi have rounded ends and the resulting uniform width gives the impression of a precise aperture formation. The opening is frequently blocked by a protruding wedge of exine. The surface of the grain is psilate.

The cultivated specimen from New York was examined in LM, SEM, and TEM, but illustrated here only in TEM, Figures 142, 143, and 146. In the SEM preparation about one-third of the grains appear to be sterile, based on the much smaller size. The remaining material, frequently collapsed or ruptured, etc., is also variable in size, but intact grains measure 25–35 μm in diameter. The apertures are 6-pantocolpate, and almost all grains, including the smaller ones, manifest this condition to some extent, i.e., less than six furrows, the furrows extended so that some grains have a wide angle L-shaped opening but even in collapsed and ruptured material the furrows are straight and not irregular cracks or breaks as in *Berberis* and *Mahonia*, Figures 19–30.

Most of the minimal pollen sample from the cultivated collection (K) was prepared for TEM (Figures 141, 144, 145, 147, 148) but a small fraction was acetolyzed and examined in SEM. This material consists of a single expanded grain, ca 19 μm in diameter, and a half dozen clusters of collapsed grains, with as few as three and as many as ten. None of the grains had any evidence of apertures, neither the irregular cracks of *Berberis* and *Mahonia*, Figures 19–30, nor the 6-pantocolpate type as illustrated in Figure 139. The surface of the collapsed grains has a remarkably uniform texture, similar to small pebbles with no space between adjacent ones.

The pollen morphology in the collections of Terabayashi and the cultivated one from New York agrees with that described and illustrated by Kumazawa (1936a).

The pollen morphology found in the cultivated collection from Kew is perplexing due to the apparently complete absence of apertures. None of the grains split or ruptured, nor did the pattern of collapse suggest internal lines of weakness. If the pollen is considered to be anomalous or abnormal, the lack of any other aberrations (in the limited material examined in SEM), such as small grains, is in itself peculiar.

The two collections of *Ranzania* examined by TEM are basically similar in that both show a nearly amorphous ektexine and fibrous-granular endexine. The ektexines in the New York State collection (Figures 142–143) are highly channeled and virtually indistinguishable from sections of acetolyzed pollen from *Berberis* and *Mahonia* (Figures 125–136). The endexine, however, in contrast to *Berberis* and *Mahonia*, is proportionately thicker and contains fragments of the ektexine (Figures 142–143). Further, the outer (i.e., distal) surface of the endexine appears lamellate in some sections (Figures 142–143). The New York State collection apparently contained some heteromorphic or anomalous pollen: the oblique section represented by Figure 146 is of a whole pollen grain and indicates an ektexine that appears more gemmate or nodular than the amorphous structures illustrated in Figures 142–143. The ektexine from pollen of the Kew collection (Figures 141, 144–145) differs from the New York State collection in that it appears to contain extremely short, narrow to broad, irregular columellae and a thin but distinguishable foot layer (see particularly Figure 145). The sections represented by Figures 147 and 148 include dyad representatives in this collection and indicate that binding of adjacent grains is by fusion of their ektexine surfaces. Since pollen samples of *Ranzania* were so limited we were unable to prepare any samples without acetolysis.

Both Kumazawa (1938a) and Buchheim (1964) had very similar concepts of a tribe Epimedieae. The former placed *Epimedium* with *Leontice*, *Caulophyllum*, *Jeffersonia*, and *Plagiorhegma* as the tribe Epimedieae, but it is unclear whether *Vancouveria* is reduced to *Epimedium*, and whether *Bongardia* is reduced to *Leontice*, since neither genus is listed under any other subfamily or tribe. The latter author included *Achlys*, *Bongardia*, *Caulophyllum*, *Epimedium*, *Jeffersonia*, *Leontice*, and *Vancouveria* in the tribe Epimedieae. The only difference is that Kumazawa placed *Achlys* in its own tribe, Achlyieae.

All of the above genera have grains that are 3-colpate, the colpi long and narrow, and have an incomplete tectum. The structure of the exine in all of these genera conforms with the common type in the angiosperms: foot layer, columellae, and tectum, with the endexine present in varying amounts and distribution.

The present authors' use of the tribe Epimedieae is more restricted and includes *Achlys*, *Epimedium*, *Jeffersonia*, and *Vancouveria*.

Epimedium L. (Figures 31-36, 94, 99, 104, 105, 110, 112, 114, 149-156), the largest genus in the Epimedieae with at least 25 species distributed in the Old World, has a range of variation in the tectum with phylogenetic implications since it links various entities of the family. For the most part we follow Stearn's (1938) treatment of *Epimedium* and *Vancouveria*.

It should be emphasized that the designation applied to the tectum in each of the following species is based on the most common form. Almost all samples had sufficient variation to indicate a link to other species.

Epimedium diphyllum (Morren & Decaisne) Loddiges (Figures 31, 32, 149), *E. cremeum* Nakai (Figures 114, 151-154), *E. grandiflorum* Morren (Figures 112, 155, 156), and *E. sempervirens* Nakai (Figures 33, 34, 110) all have a tectum consisting of small rods with one end projecting as a very small tip. These rods are illustrated best in the high magnification SEMs (Figures 32, 34, 110, 112, 114). Although the distribution of the rods appears to be random, there are some grains in which the free tips are arranged like the vanes of a pinwheel. This configuration is also found in *Podophyllum peltatum* (Figures 77, 78, 109, 111, 113). The similarity of the pinwheel tectum to the crotonoid one (Lynch and Webster, 1975) is discussed under "Ektexine Relationships" at the end of the palynological section.

Epimedium alpinum L. (Figures 36, 104), classified here as having a striate-reticulate tectum, nonetheless has lost some of the distinction of the individual striae.

The tectum of *Epimedium brevicornu* Maximowicz (Figures 35, 105, 150) is also classified as striate-reticulate, but, of the species of *Epimedium* examined, it has, at least in some grains, the longest and most distinct striae. A predominantly striate condition such as that found in *Achlys* DeCandolle (Figures 49-51, 96, 175-179), *Jeffersonia* Barton (Figures 43-48, 93, 95, 98, 107, 170-174), and *Vancouveria planipetala* Calloni (Figures 37, 38, 101, 102, 165-169) very likely exists in *Epimedium*, but not in the specimens available for this study.

Epimedium membranaceum K. Meyer (Figure 94) and *E. sagittatum* (Siebold & Zuccarini) Maximowicz (Figure 99) have a perforate tectum in which only the angular shape of the perforations and occasional long ridge (muri or striae?) indicate that it is a modification of the striate-reticulate type.

Four species, *Epimedium brevicornu* (Figures 35, 105, 150), *E. cremeum* (Figures 114, 151-154), *E. diphyllum* (Figures 31, 32, 149), and *E. grandifllorum* (Figures 112, 155, 156) were examined in thin section, and found to be almost indistinguishable from each other. The endexine is present only in the apertures and is penetrated by aperture columellae (see previous discussion of Ranunculaceae). This condition is illustrated in Figure 149 of *Epimedium diphyllum* and in the higher magnification sections in Figure 154 (*E. cremeum*) and especially in Figure 155 (*E. grandiflorum*). The foot layer is thin, irregular and with notable radial channels (Figures 150, 153, 156). Columellae are short and fairly regular. The structure of the tectum in Figures 149, 153, 154, and 155 is consistent with that depicted in SEM (Figures 31-34, 110, 112, 114); the gaps reflect the loose packing of the rods, and the small peaks reflect their free tips. In Figures 150, 151, and 152 the unattached dots or circles represent a cross section of the free tip.

The mean polar length calculated for each of the eleven collections of *Epimedium* (Table 1) ranges from 28.2 μm for *E. diphyllum* to 33.9 μm for *E. brevicornu* and *E. sagittatum*.

In *Epimedium* and closely allied genera—*Achlys* (Figure 177), *Jeffersonia*, *Vancouveria* (Figures 157-160, 163)—and in all material of *Bongardia* (Figure 193), *Caulophyllum* (Figures 184, 188, 189), and of *Leontice* (Figures 180-183) that was examined in thin section, the foot layer has radially oriented channels. These channels separate the foot layer into units that appear to be the result of columellae expanding laterally at the base. Since the foot layer is formed developmentally in this manner, it seems more likely that these channels should be interpreted as evidence of incomplete fusion as opposed to the idea that they have formed in an already solid wall.

The three species of *Vancouveria* Morren and Decaisne (Figures 37–42, 97, 100–102, 157–169) have ektexines in which the variation illustrates a near perfect continuum in the degree of distinction of the individual striae: *V. hexandra* Morren and Decaisne (Figures 39, 40, 100, 160–164) is finely striate-reticulate; *V. chrysantha* Greene (Figures 41, 42, 97, 157–159) is striate-reticulate with the striae more prominent than *V. hexandra*; and *V. planipetala* Calloni (Figures 37, 38, 102, 165–169) has a ± striate ektexine.

Each species was examined in thin section: *Vancouveria chrysantha*, Figures 157–159; *V. hexandra*, Figures 160–164; and *V. planipetala*, Figures 165–169. All are similar to *Epimedium*, Figures 149–156: the endexine is restricted to the aperture regions and has aperture columellae, and there are channels in the foot layer. Differences in the structure of the tectum among the three species are in agreement with the differences illustrated by SEM: the more open striate-reticulate pattern of *V. chrysantha*, Figure 97, is reflected in the irregularity and gaps of the tectum, Figures 157–159; the finely striate-reticulate pattern of *V. hexandra*, Figures 40 and 100, is reflected in the more continuous tectum illustrated in Figures 160 and 163; the mostly striate pattern of *V. planipetala*, Figures 38, 101, and 102, reflects this condition in Figure 166 and in the lower grain in Figure 169 in which the tectum appears to consist of a "string of beads" due to the mostly parallel striae being cut at right angle.

Within *Vancouveria* the difference between the mean polar length of the two collections of *V. hexandra*, 34.6 μm for *Allen 66* and 39.4 μm for *Ebert s.n.*, was greater than differences among the three species; however, both collections were cited as *V. hexandra* by Stearn (1938).

The American species of *Jeffersonia* Barton, (Figures 43–48, 93, 95, 98, 107, 170–174), *J. diphylla* (L.) Persoon (Figures 46–48, 98, 107, 170, 171) and the Asian representative, *J. dubia* (Maximowicz) Bentham and Hooker (Figures 43–45, 93, 95, 172–174), have grains that are 3-colpate with a striate ektexine.

In each of five collections examined (Table 1) there are some grains in which the individual stria appears to consist of an outer or surface section and an inner or subsurface section. In the high magnification SEMs of both species (Figures 45, 48, 93, 95, 98, 107), at least some of the surface striae are branched and can be traced to the point where they sink, alter direction, and become part of the inner layer.

One logical interpretation of such exine structure is that it provides a strong wall by the lamellation of cross grained layers since the long axis of the striae in the outer layer is at right angle or less to the long axis of the striae in the inner layer.

In Figure 45 of *Jeffersonia dubia* and especially in Figure 48 of *J. diphylla* the wider spacing of the striae in both layers produces the effect of one layer of slats upon another. In the Pennsylvania collection of *J. diphylla* (Figures 47, 48, 98), the surface striae are shorter, are not closely packed and are deposited in a patchwork design, whereas in the New York collection (Figures 46, 107) the surface striae are longer, more densely packed, and with a nondescript or interwoven pattern. Most of the grains in each collection of *J. dubia* (Figures 43–45, 93, 95) have tecta in which the surface striae are parallel; in Figure 93 of the Korean collection some of the distinction of the individual striae has been lost.

This particular tectum type, designated here as "two layers of striae," is widely distributed in the dicots: Aceraceae (Clarke and Jones, 1978; Biesboer, 1975), Cneoraceae (Lobreau-Callen et al., 1978), Cistaceae (Saenz de Rivas, 1979; Nowicke and Skvarla, unpublished data), Gentianaceae (Jonsson, 1973), Leguminosae (Graham and Barker, in press; Larsen, 1975).

In TEM, the pollen of *Jeffersonia* (Figures 170–174) has a narrow, smooth to fragmented endexine, the foot layer appears very uneven, irregular, and has occasional channels, and the columellae are not well formed. In *J. diphylla* (Figure 171) the oblique angle of section has somewhat distorted the characteristics of the various layers but the endexine is present in non-apertural regions. In Figure 172 of *J. dubia*, the median section (at right angle to the long axis) depicts the endexine as thin and fragmented except near the apertures. The foot layer is not uniform and has channels, and the tectum consists of almost touching circular units, which is how the mostly parallel striae of *J. dubia* would appear in cross section (see also *Vancouveria planipetala*, Figure 169). In Figures 173 and 174 the endexine is more uniform than in Figure 172. In Figure 174 there are small units of 3, 4, 5, or even 6 circles connected below by a solid line. This probably represents a cut that is at right angle to the outer striae and parallel with part or all of an inner stria.

The striate tectum of *Jeffersonia* pollen (Figures 43–48, 93, 95, 98, 107) is similar to that of *Vancouveria planipetala* (Figure 102), *Achlys triphylla* (Figures 49–51, 96) and especially to that of *Hydrastis* (Figures 52–54). Comparison of the high magnification SEMs of *J. dubia* (Figure 45) and *J. diphylla* (Figure 48) with some whole grains of *Hydrastis* (Figures 53 and 54) reveals the same type of structure: two layers of striae. The size of the *Jeffersonia* pollen (the mean of the five collections, reported in Table 1, varies from 29.3 μm to 33.9 μm), would support a closer relationship to *Achlys*, *Epimedium*, *Vancouveria*, and even *Hydrastis* than to *Bongardia*, *Caulophyllum*, and *Leontice*.

None of the sections of *Jeffersonia* (Figures 171–173) have apertures with ektexinous material that could be designated, with confidence, as aperture columellae (see discussion of Ranunculaceae, *Epimedium*, and *Vancouveria*).

The pollen morphology of *Jeffersonia* is taxonomically significant in the following ways: the distinction of *J. diphylla* (Figures 46–48, 98, 170, 171) from *Podophyllum* (Figures 73–78, 81–84, 91, 106, 109, 111, 113, 198–202) supports the separate generic status accorded by Barton (1793); the similarity of the pollen in the American (Figures 46–48, 107) and Asian (Figures 43–45, 93, 95) taxa supports the congeneric status of *Jeffersonia* and *Plagiorhegma.* This does not, however, deny any palynological relationship between *Jeffersonia diphylla* and *Podophyllum peltatum*: there are occasional grains in *J. diphylla* (Figure 107) with a tectum that is similar to some grains of *P. peltatum* in which one of the pinwheel vanes (small rods) is predominant (Figure 108).

The genus *Achlys* De Candolle is represented by numerous collections of *A. triphylla* (Smith) De Candolle (Figures 49–51, 96, 175–177), but only by a depauperate type collection of *A. japonica* Maximowicz (Figures 178, 179). The two collections examined of the American species have grains that are 3-colpate and have a striate tectum. The only pollen sample of *A. japonica*, *Terabayashi 209* (KYO), was unsatisfactory due to a paucity of material and evidence of sterility. Some of the grains, however, are 3-colpate with a tectum similar to that of *A. triphylla* (Figure 49), i.e., coarse striae mostly parallel to each other.

In TEM (Figures 175–179), the endexine is thin in the mesocolpal regions and thicker near the apertures (Figure 175), the foot layer uneven with occasional channels and is much thicker than the endexine. The columellae are narrow and short, the tectum is thick and the striae appear to be closely packed. As in *Jeffersonia* (Figures 170–174) none of the sections of *Achlys* have clearly defined aperture columellae.

In comparing the striate grains of *Achlys*, *Jeffersonia*, and *Vancouveria planipetala*, the striae in *Achlys* and in *V. planipetala* are usually parallel and more compacted than in either species of *Jeffersonia.* All of the above have the same fundamental ektexine structure but modifications in the deposition of the striae produce variation in the tectum. There are, in fact, grains in each of the collections examined that have striae similar to that in Figure 43, and are indistinguishable from each other (*Calder and Savile 8323* and *Terabayashi 209* of *Achlys* excepted).

Although the two collections of *Achlys triphylla* had a high incidence of sterility, which could negate a size characteristic, the longest grains in the *Evert* sample are 28.6 μm and in the *Calder and Savile* sample, 33.0 μm.

The pollen morphology of *Hydrastis canadensis* L. (Figures 52–54, 103, 122, 123) has considerable taxonomic significance: the striate-reticulate tectum (Figures 52–54, 103, 122 and 123) distinguishes this species from all other Ranunculaceae examined, 150 species and 44 genera (illustrated here by Figures 7–18, 115–121), including *Glaucidium* (Figures 11, 12, 118), with which it is frequently paired.

The two collections (Table 3) examined in SEM have grains that are slightly different, but this type of variation is not uncommon in the Berberidaceae (nor Ranunculaceae). The collection from Arkansas (Figures 52 and 103) is similar to some grains of *Epimedium alpinum* (Figure 104), *E. brevicornu* (Figure 105), and *Jeffersonia diphylla* (Figure 107). The collection from Ohio, illustrated by a polar and equatorial view (Figures 53 and 54), has a tectum that closely resembles that found in many grains of *Jeffersonia diphylla* (Figure 48), in which two layers of striae can be seen.

In thin section (Figures 122, 123), the structure of the exine in *Hydrastis* is also different from that in the Ranunculaceae (Figures 115–121). The prominent columellae and more or less continuous tectum that characterize many Ranunculaceae examined in thin section (Skvarla and Nowicke, unpublished data) are not found in *Hydrastis*. This conforms with impressions based on SEM micrographs.

Achlys, *Epimedium*, *Hydrastis*, *Jeffersonia*, and *Vancouveria* have pollen with 3-colpate apertures, a tectum that is striate or striate-reticulate with overlapping variation, an endexine (mostly) in the region of the aperture, channeled foot layer, and a thin tectum.

On the basis of all taxa examined to date in the Order Ranunculales, more than 250 collections in Ranunculaceae, Berberidaceae, and Lardizabalaceae, only five genera, *Achlys*, *Epimedium*, *Hydrastis*, *Jeffersonia*, and *Vancouveria* (four of which have three species or less), have the pollen morphology described above. As such the palynological data challenge the inclusion of *Hydrastis* in the Ranunculaceae, as well as the close relationship with *Glaucidium*.

In *Leontice* L. (Figures 61–66, 69–72, 180–183), an Old World genus with as many as 10 species, the pollen of *L. altaica* Pallas (Figures 61, 62), *L. armeniaca* Boivin (Figures 65, 66, 180–182), *L. eversmannii* Bunge (Figures 71, 72), *L. leontopetalum* L. (Figures 69, 70, 183), and *L. odessana* Fischer (Figures 63, 64) were examined. All have similar grains: the colpi are very long, almost to the poles (Figures 61–63, 65, 69, 71, 72); the margins sometimes undulate (Figure 61); the tectum is almost continuous in *L. altaica* (Figures 61, 62) and in *L. odessana* (Figures 63, 64), but in *L. armeniaca* (Figures 65, 66), *L. leontopetalum* (Figures 69, 70), and in *L. eversmannii* (Figures 71, 72), the tectum is incomplete and the lumina are smaller near the colpi, and/or larger in the mesocolpus.

In thin section *Leontice armeniaca* (Figures 180–182) and *L. leontopetalum* (Figure 183) have a well-developed endexine, a foot layer with radial channels, small irregular columellae, and a thick, perforate tectum.

In the disjunct genus *Caulophyllum* Michaux (Figures 55–60, 184–189), two collections of each of the two entities have been examined (Table 1). The results are ambiguous with reference to the status of the Asian taxon, either as a species, *C. robustum* Maximowicz (Figures 55, 56, 59, 184), or as a variety of the American species, *C. thalictroides* (L.) Michaux (Figures 57, 58, 60, 185–189).

All four collections (Figures 55–60) have very similar pollen, long narrow colpi (Figures 55, 57) with an incomplete or reticulate tectum (Figures 55–60), and would be difficult to distinguish from each other using light microscopy.

In TEM (Figures 184–189), both species of *Caulophyllum* have a consistent endexine, readily defined in the mesocolpal regions (Figures 184, 189) as well as in the colpus (Figures 184, 188), an irregular foot layer, short columellae, and an incomplete tectum. Channels (Figure 184) or even gaps (Figure 189) are present in the foot layer.

The pollen of *Caulophyllum* closely resembles that of *Leontice*. The tecta of *C. robustum* (Figure

55) and *C. thalictroides* (Figure 57) are almost indistinguishable from *L. leontopetalum* (Figure 69) and *L. eversamannii* (Figure 71). The exine structure of *C. robustum* (Figure 184) is almost indistinguishable from that of L. *leontopetalum* (Figure 183). Both genera have larger pollen, the mean polar lengths of the five species of *Leontice* as listed in Table 1 are 48.8 μm, 54.7 μm, 43.7 μm, 55.1 μm, and 46.5 μm, and in the two collections of each species of *Caulophyllum*, 51.5 μm, 50.2 μm, 48.9 μm, and 45.1 μm.

The pollen of the monotypic genus *Bongardia* C.A. Meyer (Figures 67, 68, 190–197) has grains that are 3-colpate with an incomplete tectum of an apparently reticulate configuration. The high magnification (× 7500) SEM of the surface (Figure 68) and the tangential thin section (Figure 195) illustrate lumina or perforations (?), angular in shape and not noticeably larger in the mesocolpal region, and "muri," without small perforations, all of which could indicate a modification of an originally striate-reticulate tectum.

Bongardia chrysogonum (L.) Grisebach (Figures 67, 68, 190–197) was first described as a species of *Leontice* and in SEM the tectum of *Bongardia* is remarkably similar to that found in some grains of at least one species of *Leontice*, *L. altaica.* The larger size (the two collections recorded in Table 1 have a mean of 48.9 μm and 54.5 μm) would align *Bongardia* with *Leontice* and *Caulophyllum.*

However, in thin section in TEM (Figures 190–193, 195–197) and fracture in SEM (Figure 194), the pollen of *Bongardia* can be distinguished from all other taxa examined in the family, including *L. altaica*, by the presence of long columellae (Figures 190, 193, 194, 196), which may account for 75% of the thickness of the ektexine, whereas in *Leontice* (Figures 180, 183) or in *Caulophyllum* (Figures 184, 188, 189) the columellae are very short, making up less than 20% of the total thickness. The magnitude of the difference is such that *Bongardia* could be identified in LM alone, but it is transmission microscopy that reveals the different structure under a very similar surface. The foot layer, with radial channels (Figure 193), is thicker and more prominent than the tectum. Typically, the endexine is prominent in the region of the colpus (Figures 190, 192, 196), and much thinner, almost absent, in the mesocolpus.

Certain characteristics of the pollen support a relationship among *Bongardia*, *Caulophyllum*, and *Leontice.* All three have large grains (relative to *Achlys*, *Epimedium*, *Hydrastis*, *Jeffersonia*, and *Vancouveria*) and a tectum that is reticulate. The difference between the tectum of *Bongardia*—angular-shaped lumina and uniformly thin "muri" without small perforations (Figure 68)—and that found in *Caulophyllum* and in *Leontice*—circular lumina and "muri" that are variable in size but frequently larger than the lumina (Figures 56, 58–60, 70, and 72)—suggests different origins. The variation in the size of the lumina in *Caulophyllum* and *Leontice* indicates derivation from a tectum that was continuous, whereas in *Bongardia* the restriction of a tectum to the distal fusion of long, narrow, and evenly distributed columellae indicates that this condition was original, or if it has evolved from a continuous tectum, then a very long period of time must have occurred. However subtle the above distinctions (long columellae, angular lumina, thin muri) may appear to nonpalynologists, the data reinforce the separate generic status accorded *Bongardia* on other bases.

None of the material examined in *Bongardia*, *Caulophyllum*, and *Leontice* (two, four, and five collections, respectively) have any grains that might indicate a relationship to the tectum in the tribe Epimedieae, and *Podophyllum peltatum. Achlys*, *Epimedium*, *Jeffersonia*, *Vancouveria*, *Bongardia*, *Caulophyllum*, and *Leontice* do have in common the channeled foot layer.

There are a number of generic pairs in the Berberidaceae that undoubtedly are closely related, *Berberis* (Figures 19–24) and *Mahonia* (Figures 25–30), *Epimedium* (Figures 31–36) and *Vancouveria* (Figures 37–42), *Caulophyllum* (Figures 55–60) and *Leontice* (Figures 61–66, 69–72), and the pollen morphology supports these traditional views. But the distinction of the pollen found in *Diphylleia* (Figures 85–88, 203–205) from that of *Podophyllum* (Figures 73–78, 81–84, 91, 106, 108, 109, 111, 113, 198–202) appears to challenge their common association by almost all modern generalists. Buchheim (1964) acknowledged the supposed relationship by treating the two genera as the only members of a subfamily Podophylloideae. Hutchinson (1959), while not assigning genera to subfamily categories, did have *Podophyllum* and *Diphylleia* key out as the first and second genus. Takhtajan (1969) gave separate family status to these two genera.

Our investigation of the genus *Podophyllum* L. (Figures 73–78, 81–84, 91, 106, 108, 109, 111, 113, 198–202) reveals an unusual range of variation in the pollen morphology, but the significance of the variability remains obscure due to a paucity of material. The following discussion is based on one collection of *P. hispidum* Hao (Figures 81, 91), eight of *P. peltatum* L. (Figures 73–78, 106, 108, 109, 111, 113, 200–202), and two of *P. hexandrum* Royale (Figures 82–84, 198–199).

The variation in the tectum of *Podophyllum peltatum* (Figures 109, 111, 113) overlaps with that of some species of *Epimedium* (Figures 110, 112, 114).

The pollen (Figures 73–78, 106, 108, 109, 111, 113, 200–202) of the widespread and common May Apple, *Podophyllum peltatum* L., is shed as a monad, 3-colpate, the colpi long, the membrane covered with flecks of exinous material. The tectum could be described as consisting of short, flattened "rods" with one end projecting. There is considerable variation in the distinction of the rods or striae and the degree to which one end is free and projecting. Figures 74, 76, and 78 illustrate this variation. In each of the eight collections there are some grains in which the free tips are arranged like the vanes of a pinwheel, as shown in Figures 77, 78, 109, 111, and 113.

Podophyllum peltatum (Figures 200–202) is as variable in TEM as in SEM. For the most part, all material sectioned has a thin foot layer, short slender columellae, and a predominant tectum. However, in each collection there is some evidence of radial channels in the foot layer as well as aperture columellae. The difference within the *Nunan* collection of the thickness of the tectum (Figures 200, 201) illustrates the problem.

Although the pinwheel configuration is more precise in *Podophyllum peltatum* (Figures 77, 78, 109, 111, and 113) than in *Epimedium diphyllum* (Figures 31, 32), *E. cremeum* (Figure 114), *E. grandiflorum* (Figure 112), or *E. sempervirens* (Figures 33, 34, 110), the similarity is undeniable. However, all species of *Epimedium* examined in thin section (Figures 149, 150, 153–156) have a well defined foot layer with channels, while *P. peltatum* has perhaps the most reduced foot layer of all species examined in the family.

The mean polar lengths in the nine collections of *Podophyllum peltatum* (Table 1), 37.3 μm, 36.0 μm, 35.4 μm, 33.9 μm, 36.5 μm, 35.3 μm, 35.4 μm, 38.5 μm, and 37.7 μm respectively, overlap with some species of *Epimedium*, of *Jeffersonia*, and of *Vancouveria*. While the mean length of *P. hispidum*, 38.9 μm, is slightly larger than any of *P. peltatum*, the high for each of the nine would include the low, 36.4 μm, for *P. hispidum*.

Podophyllum hexandrum (Figures 82–84, 198, 199) is the only taxon examined in all the Order Ranunculales that has the pollen shed as tetrads, with the members arranged in either tetrahedral or rhomboidal configuration. The elongate apertures (Figures 82, 83) can be regarded as colpi and their distribution, while not irregular, is not necessarily consistent from one tetrad to the next. The surface is covered with gemmae of variable size that in turn have a ripplelike surface (Figures 84, 198, 199).

The tetrad mechanism is fusion of the gemmae-producing layer along the common wall (Figure 198) and the cytoplasm of each tetrad member would be discrete. Both the endexine and foot layer are thin and fairly uniform, and delicate columellae support gemmae of widely disparate sizes (Figures 198, 199). It should be noted that Figure 199 is somewhat oblique. Sections through the larger gemmae illustrate the undulate surface characteristic. The tectum is probably represented by a fusion of the small gemmae.

Pollen of the above two species of *Podophyllum* Figures 73–78, 82–84, 106, 108, 109, 111, 113, 198–202) examined in this study could scarcely appear more different. In *P. hexandrum* it is shed as tetrads and thin section confirms fusion by the gemmae-producing layer between adjacent grains. The apertures are furrow-like and not always in the same position from tetrad to tetrad, and the tectum consists of gemmae of variable sizes. In contrast, the pollen of *P. peltatum* is shed as a monad, is 3-colpate, and the ektexine or tectum has a "pinwheel" configuration or modifications thereof.

A minimal pollen sample from an Arnold Arboretum collection identified as *Podophyllum hispidum* (Figures 81, 91) has 3-colpate grains, the colpi long and narrow with flecks of exine material on the membrane. The SEMs depict an almost complete or continuous tectum with faint lines (Figure 91), indicating that it might be a modification of the striate-reticulate type found elsewhere in the genus and family. These results should be treated with reserve.

The only material available for the genus *Dysosma* R. E. Woodson was that of *D. pleiantha* (Hance) Woodson (Figures 79, 80, 92, 206), the type species. The 3-colpate grains (Figures 79, 80), in which the tectum is again regarded as a modification of the striate-reticulate type, contribute little new information regarding the extent of *Dysosma's* relationship with *Podophyllum.* The monad condition and the surface of the tectum appear much closer to *Podophyllum peltatum* than to *P. hexandrum.*

In thin section (Figure 206), however, *Dysosma* could be distinguished from all remaining genera by a prominent tectum and foot layer that has a complementary, undulating interface bridged by delicate, uniform columellae. The endexine is thin and uniform in the mesocolpal regions and noticeably thickened in the colpus.

Diphylleia Michaux (Figures 85–88, 203–205) has at least three species and an eastern North America and eastern Asia type of disjunction. The pollen of the North American species, *D. cymosa* Michaux (Figures 85, 86, 203, 204) and that of an Asian one, *D. sinensis* Li (Figures 87, 88, 205), are 3-colpate and have a tectum composed of irregularly placed rods that form the base of stout, blunt spines. The sparse distribution of the rods makes the tectum appear punctate (Figures 85, 88).

In TEM (Figures 203–205) the most striking feature is the delicate structure that supports massive spines. The tectum in each species appears irregular and broken, but it is consistent with the surface depicted in SEM; small sparsely distributed columellae connect the tectum with an equally irregular foot layer. The endexine is thin and fragmented.

Like the other disjuncts, the two species of *Diphylleia* have subtle differences in the pollen, i.e., the Asian taxon (Figures 87, 88, 205) has more numerous and more slender spines than the North American one (Figures 85, 86, 203, 204), but this distinction might not be maintained if additional collections were examined.

Podophyllum has two strikingly different pollen types, the tetrads of *P. hexandrum* (Figures 82–84, 198, 199) and the monads of *P. hispidum* (Figures 81, 91) and *P. peltatum* (Figures 73–78, 106, 108, 109, 111, 113, 200–202) and the pollen of *Diphylleia* has to be compared with each. But the tectum found in *Diphylleia*, stout blunt spines, has no counterpart in any of the other taxa examined in the family.

Nandina domestica (Figures 89, 90, 207–211) was described by Thunberg (1781) ostensibly from a Chinese collection, but the origin of this subshrub remains a matter of conjecture since the plant has a long history of cultivation and can be found in many parts of Asia as an escape.

The distinction of this monotypic genus has been acknowledged by segregating it as a tribe or even as a family, Nandinaceae. The pollen morphology (Figures 89, 90, 207–211) supports Kumazawa's (1938a:12) opinion that it is the "farthest deviated" if it is included in the Berberidaceae.

As demonstrated in SEM (Figures 89 and 90), the pollen morphology is among the most common types in the dicotyledons: the apertures are 3-colpate and the tectum is deeply punctate with the punctae evenly distributed.

In thin section (Figures 207–211), the exine of *Nandina* can be distinguished from all members of the Berberidaceae s.l. by the presence of a massive endexine. Compared with most members of the family, the tectum is thick and almost complete (Figure 207), except for the punctae (Figure 208), and it is uniform in the sense that it is the same thickness in the mesocolpal regions as well as near the colpi; the columellae are diminutive (Figures 207, 209), the foot layer is much thinner than the tectum but recognizable and consistent. The massive endexine is lamellar at the interface with the foot layer, and uneven and less electron dense on the inner surface (Figure 211). The continuity of this layer is disrupted by small gaps where the colpus and mesocolpus meet.

This study is concerned with generic relationships within the Berberidaceae s.l., and no other taxa examined had a thick punctate tectum similar to that of *Nandina*. *Dysosma pleiantha* (Hance) Woodson (Figure 206) had a thick tectum but this is the only characteristic that these two species have in common.

The remarkable development of the endexine layer of *Nandina* as revealed in thin section (Figure 207) is unique and has not been found in any taxa examined to date in the Centrospermae (Skvarla and Nowicke, 1976), or in Plumbaginaceae, Polygonaceae, or Primulaceae (Nowicke and Skvarla, 1977). Moreover, the distinction of the pollen of *Nandina* applies to the Order Ranunculales as well. Considering each of the various families as a whole, the Ranunculaceae does have the most consistent and well developed endexine (Figures 115–121), but at least to date none rivals the one found in *Nandina*. Palynologically this species may be more closely related to certain taxa in the Lardizabalaceae, *Akebia trifoliata* (Thunberg) Koidzumi and *Decaisnea fargesii* Franchet, in that all three have at least the components of the ektexine represented in the same proportions, thick tectum, diminutive columellae, and thin foot layer (Skvarla and Nowicke, unpublished data).

Just as there are exceptional and restricted sporophytic characteristics, e.g., perianth absent in *Achlys* (see page 8), there are palynological distinctions that occur in only one or two genera: tetrads only in *Podophyllum hexandrum*, 6-pantocolpate aperture type only in *Ranzania*, a massive endexine only in *Nandina*, very long columellae only in *Bongardia*, spinose tectum only in *Diphylleia*, gemmate tectum only in *P. hexandrum*, and aperture columellae only in *Epimedium* and *Vancouveria*. An unstratified exine is found in three genera, *Berberis*, *Mahonia*, and *Razania*.

EKTEXINE RELATIONSHIPS.—The 24 high magnification SEMs, Figures 91–114, of tecta found in *Achlys*, *Epimedium*, *Dysosma*, *Hydrastis*, *Jeffersonia*, *Podophyllum hispidium*, *P. peltatum*, and *Vancouveria* have been arranged to demonstrate a continuum in variation and the existence of a relationship among these taxa. The relationships exist within and between groups of figures so that the series should be viewed as a foldout. While the discussion could start with any one group, that of Figures 103–108, representing four genera, *Hydrastis*, Figure 103, *Epimedium brevicornu*, Figure 105, *E. alpinum*, Figure 104, *Jeffersonia diphylla*, Figure 107, and *Podophyllum peltatum*, Figures 106 and 108, might serve this purpose best. Palynologically, *Hydrastis*, Figure 103, is more closely related to the *Epimedium* species, Figures 104 and 105, and to *Jeffersonia*, Figure 107, than to any member of the Ranunculaceae (Nowicke and Skvarla, unpublished data). The similarity of the striae configuration in *Jeffersonia*, Figure 107, with that in the collection of *Podophyllum peltatum* in Figure 108 could suggest a relationship. The difference between the two collections of *P. peltatum*, Figures 106 and 108, is a loss of some of the distinction of individual rods and the fact that the free tip is no longer free. The difference between the tectum of *Hydrastis*, Figure 103, and that of *Epimedium alpinum*, Figure 104, can also be considered as a loss of some distinction.

There is a hypothetical series, Figures 98, 97, 92, 91, in which the tectum from one taxon could be derived from the preceding one by a loss of some distinction of either rods or striae. The tectum found in *Vancouveria chrysantha*, Figure 97, could be derived from *Jeffersonia diphylla*, Figure

98; the tectum of *Dysosma*, Figure 92, could be derived from *Vancouveria chrysantha*, Figure 97; and *Podophyllum hispidum*, Figure 91, could be derived from *Dysosma*, Figure 92, by the loss of all distinction of the striae or rods.

A second similar series, consisting of Figures 106, 105, 100, 99, 94, 93, illustrates a continuum in variation from a striate-reticulate tectum to one that is almost complete, and could link *Podophyllum peltatum*, *Epimedium brevicornu*, *Vancouveria hexandra*, *E. sagittatum*, *E. membranaceum*, and *Jeffersonia dubia*, respectively.

A third series, Figures 108, 107, 102, 101, 96, 95, illustrates the possible stages of the transition from a striate-reticulate tectum to ones that are striate, the striae being mostly parallel to each other. The taxa linked include *Podophyllum peltatum*, *Jeffersonia diphylla*, *Vancouveria planipetala*, *Achlys triphyla*, and *J. dubia*.

The group consisting of Figures 109–114, illustrates a tectum condition found in some species of *Epimedium*, Figures 110, 112, and 114, and in certain collections of *Podophyllum peltatum*, Figures 109, 111, and 113. All six micrographs have at least some areas where the free tips are arranged like the vanes of a pinwheel.

In a review paper (Nowicke and Skvarla, 1980) the authors documented the existence of similar tectum patterns (as illustrated by SEM) in families or genera that are widely separated on the basis of other characters. This phenomenon as well as the existence of very diverse (apparently) morphologies in closely related species raises the fundamental question of the origin and persistence of such forms.

One possible interpretation of these results is that there are a limited number of structurally defined tectal types, each with a potential variation that may or may not be manifested. The two layers of striae tectum, known to occur in at least half a dozen families, could serve as an illustration of such a tectal type.

Jeffersonia may be an example in which the potential variation is, at least in part, realized: in Figure 48 the tectum consists of two layers of striae, in Figure 95 the tectum is striate, in Figure 45 the tectum appears intermediate between that in Figures 48 and 95, in Figure 107 the tectum is irregularly striate.

Hydrastis canadensis may be another example: in the collection illustrated in Figures 53 and 54 the tectum consists of two layers of striae, while in a second collection, illustrated in Figures 52 and 103, the tectum is striate-reticulate.

Another tectal type may be that found in the euphorbiaceous genera *Croton* (Nowicke and Skvarla, unpublished data) and *Manihot* (Lynch and Webster, 1975, figs. 1–8; Nowicke and Skvarla, unpublished data), in the icacinaceous genus *Platea* (Lobreau-Callen, 1973, pl. 3: figs. 1–3), in the cistaceous genera *Fumana* (Saenz de Rivas, 1979, figs. 3A–3C; Nowicke and Skvarla, unpubished data) and *Lechea* (Nowicke and Skvarla, unpubished data), in the Myristicaceae (Walker and Walker, 1980), in the Buxaceae (Nowicke and Skvarla, unpublished data), in *Aquilaria*, *Cryptadenia*, *Lachnaea*, *Lophostoma*, *Phaleria*, and *Wikstroemia*, all members of the Thymelaeaceae (Erdtman, 1966; Nowicke and Skvarla, unpublished data), in *Podophyllum peltatum* (Figures 77, 78, 109, 111, 113), and in some species of *Epimedium* (Figures 110, 112, 114). These tecta could be classified as a continuous triangular array. In *Scyphocephalium* (Walker and Walker, 1980, figs. 20, 21), *Aquilaria*, *Croton*, *Lachnaea*, *Manihot* (Lynch and Webster, 1975, fig. 7), and *Wikstroemia* the configuration of the triangular or prism-shaped subunit is very precise, whereas in *Fumana*, *Podophyllum*, *and Epimedium* it is identifiable only in some grains, sometimes only in certain areas, e.g., along the colpus.

Most species of *Croton* have a tectum as defined above—a continuous triangular array—however, *C. californicus* (Solomon et al., 1973, figs. 46a–46c; Nowicke and Skvarla, unpublished data) represents a variation in this type by having the subunits rounded or gemmate and with a ripple surface. This is more or less paralleled in *Podophyllum*: those grains of *P. peltatum* that have a tectum of uniform "pinwheels" (Figure 78), would be equivalent to most species of *Croton*, with the "vanes" of the pinwheel equivalent to the traingular subunits; *P. hexandrum* (Figures 82–

84), with a tectum of ripple-surfaced gemmae would be equivalent to *C. californicus.*

Of far greater interest is the remarkable parallelism of the pollen morphology in the family Cistaceae with that of the Berberidaceae. Saenz de Rivas (1979) examined 36 species representing five of the eight genera in the Cistaceae. He classified the exine sculpturing (1979, table 1) into five types, rugulose, retipilate, reticulate, striate, and reticulate-granular, all of which were documented by SEM micrographs, and most of which have a close counterpart in the Berberidaceae s.l.

The close similarity between Saenz de Rivas' rugulose type (1979, figs 1E, 1F), and the reduced striae distinction type in the Berberidaceae, as illustrated by *Vancouveria chrysantha* (Figure 97) and *Dysosma* (Figures 79, 80, 92), would be difficult to refute.

The retipilate exine in some species of *Fumana* (Saenz de Rivas, 1979, figs 3A–3C), in another cistaceous genus *Lechea* (Nowicke and Skvarla, unpublished data), and the pinwheel pattern found in *Podophyllum peltatum* (Figures 77, 78, 109, 111, 113) and some species of *Epimedium* (Figures 110, 112, 114) are probably derivations of a continuous triangular array as discussed above.

The striate type in the Cistaceae as illustrated by *Halimium atriplicifolium* (Saenz de Rivas, 1979, fig. 2A) is very similar to the striate-reticulate type in some species of *Epimedium*: *E. alpinum* (Figure 104) and *E. brevicornu* (Figure 105). Other examples of striate types in the Cistaceae (Saenz de Rivas, 1979, figs. 2B–2F) are equivalent to the two layers of striae as illustrated in *Jeffersonia* (Figures 45, 48), and in *Hydrastis* (Figures 53, 54).

The reticulate-granular type in the Cistaceae (Saenz de Rivas, 1979, figs. 1A–1D) has its counterpart in the Berberidaceae in those species of *Epimedium* (Figures 31–34, 110, 112, 114) that have a tectum of small rods with one tip projecting.

The parallel pollen morphology in the Berberidaceae and Cistaceae suggests that the tecta described by the present authors as two layers of striae, "randomly" placed small rods, and a continuous triangular array are closely related and may be variants of, or derived from, a major structural type.

General Discussion

The following discussion considers data from other sources—gross morphology, carpel morphology, serology, and cytology—together with the implications of pollen analyses.

That *Berberis* and *Mahonia* are closely related is beyond question. Of more fundamental interest is the extent of their separation or isolation from the remaining genera traditionally aligned as the Berberidaceae. To regard the woody habit of *Berberis* and *Mahonia* as secondarily derived from a herbaceous one is a situation where Occam's Law should be applied: there is no reason to assume that *Berberis* and *Mahonia* were ever anything but woody in habit. Certainly the distinguishing characteristics of their pollen are unequivocally primitive. Carpel morphology (Chapman, 1936) indicates the *Berberis-Mahonia* line separated very early from the ancestral stock. Both genera have tactile stamens, chromosome numbers of 2n = 28 or 56 and their interfertility as well as their mutual susceptibility as the alternate host for wheat rust clearly supports Jensen's (1974) proposal that they are congeneric. All available evidence indicates that *Berberis* and *Mahonia* are primitive, isolated genera, and the present authors would agree with Hutchinson's (1959) restricted view of the Berberidaceae as consisting of only *Berberis* and *Mahonia.*

In a family that is said to consist of groups of genera not closely related to each other, the degree to which *Ranzania* is separated from the remaining genera may be exceeded only by *Nandina. Ranzania japonica*, found in an area of three degrees of latitude on northern Honshu, has one of the more restricted distributions in all of the dicots. This species possesses floral characteristics that align it with *Berberis-Mahonia*: petals with fleshy nectaries at the base, sensitive stamens, an unstratified exine, and baccate fruit. Certain vegetative characteristics, however, align it with *Caulophyllum-Leontice*: the habit, rhizome, leaf and petiole morphology. The type of aperture, 6-pantocolpate (Figure 139), is unique in the family s.l., a status that Kumazawa (1937c) also applied to the anther dehiscence. Kumazawa recognized four modes of dehiscence in the Berberidaceae: three were monogeneric, *Nandina*, *Podophyllum*, and *Ranzania*, and the fourth included all remaining genera. However, the distinctions of the four types as illustrated by Kumazawa (1937c:59, fig. 3) do not, at least to the present authors, seem very great.

Terabayashi's first publication in his studies of floral morphology of the Berberidaceae was on *Ranzania* (1977) and the second one on *Berberis* and *Mahonia* (1978). If the flower parts of *Ranzania* as depicted in line drawings by Terabayashi (1977, fig. 1) are compared with those of *Berberis* and *Mahonia* by the same author (1978, figs. 1, 2), the close similarity would make it difficult to deny a relationship between the three genera. Certainly the presence of an unstratified exine in both the *Berberis-Mahonia* alliance (Figures 124–138) and in *Ranzania* (Figures 141–145) supports this contention.

Herbarium specimens of *Ranzania*, consisting of the only two collections at Kew, were obtained in April 1979. Unfortunately, one was cultivated, the other sterile. Nevertheless when these two collections (Figures 212, 213) were compared with a Japanese species of *Berberis*, *B. amurensis* Ruprecht (Figure 214) and one of *Mahonia*, *M. japonica* (Thunberg) De Candolle (Figure 215), the contrast was striking: *Ranzania* is a slender, delicate herb with a single stem arising from a small rhizome, and at a height of six to eight inches the stem divides producing two petioles and the peduncle, which supports a single flower (the cultivated, partially dried New York State specimen is ± identical).

The difference in aperture type may be more significant than the similarity in exine structure. An unstratified exine is a generalized condition found in many primitive angiosperms, and in *Berberis*, *Mahonia*, and *Ranzania* it most likely represents an original, unchanged state. However, the 6-pantocolpate aperture of *Ranzania* is an advanced type, especially in regard to the irregular type found in *Berberis* and *Mahonia*.

The similar floral morphology and exine structure would support the view that *Ranzania*, *Berberis*, and *Mahonia* are monophyletic, but the great disparity in vegetative morphology and aperture type strongly suggests that the ancestral stock of *Ranzania* separated very early in time from that which produced *Berberis and Mahonia*. The present authors would maintain *Ranzania* as a taxon incertae.

The almost complete agreement on the close relationship of *Epimedium* and *Vancouveria* is not surprising since the latter genus has been treated as a section of the former (Baillon, 1871). The range of variation found in the tectum of *Epimedium* and *Vancouveria* would indicate that Stearn's (1938) treatment as closely allied but separate genera is the most valid. Both genera have a chromosome number of 2n = 12, the basic one for the Berberidaceae. Chapman (1936) placed *Epimedium* and *Vancouveria* with the other predominantly two-carpellate genera (*Achlys*, *Diphylleia*, *Epimedium*, *Jeffersonia*, *Nandina*, *Podophyllum*), but emphasized their special relationship by her statement (1936:344), "The structure of the ovaries of the species commonly placed in the genus *Vancouveria* helps clarify the interpretation of conditions in *Epimedium*." Comparison of herbarium specimens leaves little doubt as to their close association.

Comparison of *Bongardia*, *Caulophyllum*, and *Leontice* collections, unfortunately, leaves considerable doubt as to the extent of their affinities to each other. Vegetatively, *Bongardia* and *Leontice* are almost succulent, a sharp contrast to the thin leaves and slender stems of *Caulophyllum*. All three genera have fruits described as bladder-like; but *Caulophyllum* has this condition only in the earliest stage of fruit development, and the large (ca. 1 cm in diameter), exposed seeds with a dark blue, glaucous coat are "easily mistaken for fruits" (Ernst 1964:19). Moreover, each of the two seeds is attached to an erect, conspicuous funiculus, as much as 7 mm long and 2 mm in diameter, a structure lacking in the other two genera. It could be argued that the fundamental difference between the fruits of *Caulophyllum* and those of *Leontice* and *Bongardia* is the rapid and extensive growth of the seeds in the former genus. But the disparity of the mature fruits and/or seeds as well as the unusual funiculus would scarcely support a close relationship.

Results from carpel morphology (Chapman, 1936) and serology (Jensen, 1974) support Airy-Shaw's (1966) viewpoint of a close relationship between *Caulophyllum*, *Leontice*, and *Bongardia*, but not necessarily separate family status since the same results also indicate some affinity to other berberidaceous genera.

The palynological data alone are paradoxical: of all the 3-colpate taxa, *Bongardia*, *Caulophyllum*, and *Leontice* have the largest individual grains, averaging 49–55 μm long; all three have an incomplete tectum, and in eleven collections there were no variants that indicated a relationship to the tectum found in the tribe Epimedieae and *Podophyllum peltatum*. The type of tectal perforation in *Bongardia* differs sufficiently from that of *Caulophyllum* and *Leontice* to suggest different origins of the "incomplete" characteristic. In thin section and LM, the pollen of *Bongardia* can be distinguished from that of *Caulophyllum*, *Leontice*, and all remaining genera by the predominance of the columellae, which account for 80% of the exine.

In a discussion following Jensen's presentation of the serological results (1974), A. Takhtajan refers to his study of seed coat characteristics in *Bongardia*, *Caulophyllum*, and *Leontice*, and the fact that *Bongardia* differs considerably from the other two.

All three genera have been reported as having chromosome numbers other than, or in addition to, the basic x = 6: *Bongardia* n = 6, 7, 2n = 12; *Leontice* n = 7, 8, 2n = 14, 16; *Caulophyllum* has to our knowledge only been reported as 2n = 16.

Ultimately any statement regarding their relationship depends on the value attached to each of the above characteristics: habit, fruit, seeds, carpel morphology, serology, pollen morphology, and cytology. The paradoxical results indicate an early separation or a differential rate of evolution among the characteristics investigated. Nevertheless, *Caulophyllum*, *Leontice*, and *Bongardia* appear to be more closely related to each other than to any remaining genera and could be segregated as the tribe Leonticeae.

The similarity of pollen morphology in *Achlys* and *Jeffersonia*, a more or less striate tectum, consistent endexine, and small size range, prompted a comparison of the two genera on other characteristics. There are, however, differences of such magnitude as to preclude the possibility of any close relationship: the compact, spicate inflorescence of *Achlys* with numerous, small flowers which lack a perianth contrasts sharply with the scapose inflorescence of *Jeffersonia* with a single, showy flower. The fruit of *Jeffersonia* is as unusual as the inflorescence of *Achlys*: the oblong capsule opens by a horizontal cleft to release the numerous seeds. The fruit of *Achlys* is small, one-seeded, and either dehiscent (Hutchinson, 1959) or indehiscent (Rickett, 1971).

According to Chapman (1936:346), "The frequent coupling of the genera *Achlys* and *Jeffersonia* does not seem to be especially justified when the carpel morphology of the two is considered." She regarded them as no more related to each other than each is to *Epimedium*.

In a morphological and systematic study of *Achlys*, Takeda (1915) also dismissed the possibility of a close relationship to *Jeffersonia*, citing the much greater specialization of the latter genus. He regarded *Achlys* as being related to *Epimedium* and *Leontice*, and in fact characterized *Achlys* as a much reduced form of the latter genus.

Both genera have a chromosome number of 2n = 12, the basic one for the Berberidaceae, which contributes little to the clarification of the relationships of *Achlys* and *Jeffersonia* to each other or to any of the remaining genera.

Any discussion of the relationships and placement of *Podophyllum* must first attempt to resolve the vague circumscription of this genus.

Woodson (1928) elevated *Podophyllum pleianthum* Hance to separate generic status as *Dysosma* based primarily on the following characteristics: very large leaves with regular, equal lobes and a finely dentate margin, as opposed to smaller leaves with irregular lobes and an entire or uneven margin in *Podophyllum*; an inflorescence of four to 19 flowers, as opposed to one; and introrse anthers as opposed to extrorse in *Podophyllum* and all the rest of the Berberidaceae. He also cited differences in the pollen, that of *Dysosma* being spherical and relatively small, while that of *Podophyllum* is lobed and relatively large. The latter description can only mean that Woodson used *P. hexandrum* pollen as representative of *Podophyllum* and interpreted the tetrad as a large, lobed grain.

Kumazawa (1935:274) re-examined *Podophyllum pleianthum* in view of Woodson's elevation and concluded that "the anthers are quite laterally situated on the connective and the dehiscence is extrorse." He also commented that "the size of the pollen grain is larger in *P. pleianthum* than in *P. peltatum*, and this is quite contrary to his [Woodson's] description." Our data in Table 1 confirm this, although the difference is not very great: *Dysosma* has a mean length of 42.9 μm, and in eight collections of *P. peltatum*, the means are 37.3 μm, 36.0 μm, 35.4 μm, 33.9 μm, 36.5 μm, 35.4 μm, 35.3 μm, 38.5 μm, and 37.6 μm.

Woodson (1928) did not, in the opinion of the present authors, need a pollen difference to confirm the validity of *Dysosma*. However, the pollen of *Dysosma* (Figures 79, 80, 92) appears to be much closer to that of *Podophyllum peltatum* and *P. hispidum* than that of *P. hexandrum* is to these two species. Examination of the collections (US) seem to justify his treatment. Hu (1937) apparently agreed with Woodson since he transferred at least three other species of *Podophyllum* to *Dysosma*.

If the genus *Dysosma* and Hu's (1937) subsequent transfers (see page 5) are accepted as valid, *Podophyllum* s.s. still includes two very dissimilar entities regarding pollen morphology: the common and widely distributed *P. peltatum* L. in North America and, judging from the material at US, a similarly common and widely distributed *P. hexandrum* Royale from Asia. The tetrads of *P. hexandrum*, in which the tectum is covered with ripple surfaced gemmae, are radically distinct from the monads of *P. peltatum* or any other member of the Berberidaceae. However difficult it may be to reconcile the distinction of the pollen in these two species, they are very similar in vegetative and floral morphology and the present authors would maintain *Podophyllum* as including both species until samples and/or other data from other species of *Podophyllum* or *Dysosma* become available.

The pollen found in the two species of *Diphylleia* (Figures 85–88, 203–205), *D. cymosa* from North America and *D. sinensis* from Asia, is unique and reinforces their close relationship to each other and distinguishes them from all other members of Berberidaceae, s. l.

According to Chapman (1936:347), "the taxonomic association of *Diphylleia* and *Podophyllum* is one which the study of carpel structure does not confirm." Furthermore, "it seems likely that the two may be derived from the complex which gave rise to the two carpel forms, but the separation between them can probably be extended back to an early representative in that evolution." Her views of a remote connection between *Diphylleia* and *Podophyllum* agree with those of Kumazawa (1938a).

Li (1947) recognized three species of *Diphylleia*, mostly on the basis of the origin of the inflorescence and the extent of the lobing in the leaves: *D. cymosa* Michaux from eastern North America, *D. sinensis* Li from China, and *D. grayi* R. Schmidt from Japan. Examination of the collections at the US indicates that *Diphylleia* can be separated into three entities using Li's criteria.

Diphylleia and *Podophyllum* have a chromosome number of 2n = 12, basic in the family and therefore of limited value as an indicator of relationships.

According to Jensen (1974:223), *Diphylleia* and *Podophyllum* have "the possibility of great serological similarity," but the two genera have the reality of widely divergent (apparently) pollen morphologies (Figures 73–78, 81–88, 198–205).

In considering the variation in pollen morphology of the Berberidaceae s.l., the distinction of the grains in *Diphylleia* relative to the remaining members of the family is surpassed only by that of the tetrads in *Podophyllum hexandrum.*

Nandina domestica Thunberg is one of the few berberidaceous genera that has a woody habit and in this respect, as well as articulated leaves, it is similar to *Berberis* and *Mahonia*. Chapman (1936) placed *Nandina* with the 2-carpellate genera, but cited earlier work that recorded some 3-carpellate specimens among the predominantly 2-carpellate ones. She (1936:346) considered the variation in *Nandina* "as an index to the history of the forms in the other genera rather than indicating the genus as ancestral in the evolution of the family."

Kumazawa (1938b:12) made a strong case for elevating *Nandina* to separate family status.

> The outer integument of *Nandina* is strongly developed and the micropyle is not observed from outside; moreover, the nucellus is absorbed before the flower comes into bloom and the external epidermis and the internal one change into the thin walled columnar tissue. These vegetative and ovular characters, as well as the dehiscing type of anther described before (Kumazawa, 1937c), are quite unique among the berberidaceous genera.

The pollen of *Nandina* can be easily distinguished from all remaining members of the family by the massive endexine.

Nandina has a chromosome number of 2n = 20, unique in the Berberidaceae.

Jensen's (1974:225) serological study of the Berberidaceae does not support the separation of *Nandina* since "it features serological similarities of a high degree with *Berberis* and *Mahonia* and with *Podophyllum* and *Diphylleia*." He drew a parallel of the distinctive characteristics of *Nandina* relative to the Berberidaceae with certain groups in the Ranunculaceae relative to that family (1974:225): "The fact that the deviating chromosome number (n = 10) is by no means decisive is proved by the related family of Ranunculaceae, in which the Thalictreae and Coptideae also exhibit a completely different karyotypus." The present authors are of the opinion that variation in a family as large as the Ranunculaceae is to be expected; but in a family of 12 genera, such variation may indicate a lack of relationship.

In considering the disparity of the palynological results with Jensen's (1974) preliminary data from serology (see page 3), it should be noted that conclusions from the latter source are restricted to comparisons among the taxa investigated. While pollen morphology also relies heavily on comparison, this discipline has reached a stage where a number of characteristics have values attached, primitive or unspecialized, and advanced or specialized. Most palynologists would designate the unstratified exine, irregular apertures, and undifferentiated surfaces found in *Berberis* and *Mahonia* as primitive without any knowledge of the rest of the family's pollen morphology.

Reference has been made in the Introduction that the Berberidaceae have an unusually high number of disjunct or discontinuous genera, five of the 12 have species that are widely separated geographically. *Achlys* is the only one with a Pacific North America and eastern Asia distribution. Unfortunately, the paucity of material of the Asian taxon as well as the high incidence of sterility in both taxa compromises any statement about their relationships.

Caulophyllum, *Diphylleia*, and *Jeffersonia* have the more common eastern North America and eastern Asia type of disjunction. In each of these three genera, the pollen of the American species and that of the Asian species are fundamentally similar with only subtle differences in the tectum. The range of variation found within a sample and between collections of some species makes such differences suspect, and the paucity of Asian specimens curtailed any further investigation.

Podophyllum is another disjunct genus with a distribution similar to that of *Caulophyllum*, *Diphylleia*, and *Jeffersonia*, but if the pollen of *P. hexandrum* is arbitrarily dismissed due to unparalleled distinction (in all of the Order Ranunculales), and if the treatment of *P. pleianthum* as *Dysosma pleiantha* is considered valid, then for purposes of comparison the Asian possibilities are reduced to one pollen sample from a collection identified as *Podophyllum hispidum* at Gray Herbarium. The differences in the tectum between *P.*

hispidum and *P. peltatum* are more pronounced than in the other disjuncts, but the type found in *Dysosma pleianthum* could be interpreted as intermediate and link the two entities.

Summary

The pollen diversity in the Berberidaceae confirms, for the most part, previous characterization as "groups of genera" not closely related to each other, especially regarding the distinction of *Berberis* and *Mahonia*, and of *Nandina*. However, the pollen would suggest greater conformity or closer relationship among *Achlys*, *Dysosma*, *Epimedium*, *Jeffersonia*, *Podophyllum* species, and *Vancouveria*, than has been previously thought.

For *Berberis* and *Mahonia* the characteristics of the pollen, an unstratified exine with a random or unspecialized surface, irregular and/or spiral apertures, as well as their woody habit, indicate that they are primitive genera, additionally distinguished by a chromosome number of n = 14 (28 for some species of *Berberis*), susceptibility to *Puccinia graminis*, and articulated leaves. Hutchinson's (1959) concept of the Berberidaceae as consisting of only *Berberis* and *Mahonia* could be justified.

The pollen of the monotypic genus *Nandina* can be distinguished from those of all other taxa examined, which in combination with evidence from floral morphology (carpel morphology, development, anther dehiscence) and, above all, the unique chromosome number of 2n = 20, support the case for separate family status.

Palynologically, *Hydrastis* is more closely related to *Achlys*, *Epimedium*, *Jeffersonia*, and *Vancouveria* than to any genus examined thus far in the Ranunculaceae.

Pollen morphology reinforces the special relationship between *Epimedium* and *Vancouveria*: species assigned to these two genera were the only members of the Berberidaceae s.l. to have aperture columellae. They are additionally distinguished by the presence of saccate petals or nectar spurs, a follicle-like fruit, and seeds with a conspicuous aril. Both have a chromosome number of x = 6.

The close similarity of the pollen in the American *Jeffersonia diphylla* and the Asian *Plagiorhegma dubia* supports their congeneric treatment as *Jeffersonia* and allies them with *Achlys*, *Epimedium*, *Podophyllum peltatum*, and *Vancouveria*. While *Jeffersonia* has the typical chromosome number of x = 6, and an anther dehiscence by narrow valves attached at the apex found in at least six other berberidaceous genera, no one genus seems to be especially allied with this Asian-American disjunct. Certainly the fruit, which resembles a moss capsule, is unique within the taxa examined.

Achlys has pollen similar to *Epimedium*, *Jeffersonia*, *Podophyllum peltatum*, and *Vancouveria*, and a chromosome number of x = 6. The highly reduced flower (sepals and petals are absent) suggest no other generic relationships.

Achlys, *Epimedium*, *Jeffersonia*, and *Vancouveria* are similar in pollen morphology, chromosome number, anther dehiscence, and habit, and could be segregated as a tribe.

Palynologically the Old World genus *Leontice*, the monotypic *Bongardia* (based on *L. chrysogonum*), and the Asian-American disjunct *Caulophyllum*, are more closely related to each other than to any remaining taxa examined. Although the unifying characteristics are quantitative (larger size and thicker walled), the fact that their tecta are not related to the type found in *Achlys*, *Epimedium*, *Jeffersonia*, *Podophyllum peltatum*, and *Vancouveria* may be more significant. All three have chromosome numbers other than, or in addition to, n = 6: *Bongardia* n = 6, 2n = 14, *Caulophyllum* 2n = 16, and *Leontice* 2n = 14, 16. *Caulophyllum* and *Leontice* have very similar stamen morphology, and all three have anthers opening by valves. Their distinction could be acknowledged by treating them as a tribe, Leonticeae.

The structure of the exine supports the separate generic status of *Podophyllum pleianthum* as *Dysosma* Woodson, accorded on other bases. The tectum, aperture type, and size are similar to *P. peltatum*, and *Achlys*, *Jeffersonia*, *Epimedium*, and *Vancouveria*.

The pollen of *Podophyllum hispidum* and *P. pel-*

tatum is similar in the tectum, apertures, and size to that found in *Achlys*, *Epimedium*, *Jeffersonia*, and *Vancouveria*. *Podophyllum peltatum* has a 2n = 12, characteristic of the above genera, but this species has longitudinal anther dehiscence as opposed to valves. The pollen morphology of *Podophyllum hexandrum* is unique within the Order Ranunculales: tetrads with a tectum supporting ripple-surfaced gemmae. In leaf and floral morphology *P. hexandrum* is closely related to *P. peltatum*. The boundaries of *Podophyllum* have yet to be established.

The characteristics of the pollen of *Ranzania* are ambiguous: the 6-pantocolpate aperture type is unique within the Berberidaceae s.l., but the unstratified exine is similar to that in *Berberis* and *Mahonia*. The chromosome number of 2n = 14 has been reported only from *Bongardia* and one species of *Leontice*.

The pollen found in two species of the disjunct genus *Diphylleia* is unique, so much so that no clear relationships within the Berberidaceae are suggested, while the chromosome number, 2n = 12, is found in at least six other genera of the family. Evidence from floral morphology is inconclusive except to deny a close relationship with *Podophyllum*. Of all taxa examined in this study, *Diphylleia* is indeed a genus of uncertain affinities.

Pollen morphology does not support a close relationship between the Berberidaceae and Ranunculaceae nor between the Berberidaceae and Lardizabalaceae.

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Tables and Figures

TABLE 1.—Berberidaceae specimens examined, alphabetically by genus (grain size in µm; asterisk indicates longest dimension for tetrad member)

Species	Collection	Location	Longest dimension of ten grains			Figure numbers
			Low	*Mean*	*High*	
Achlys japonica Maximowicz	Terabayashi 209 KYO	Japan	22.1	24.3	26.0	178, 179
A. triphylla (Smith) De Candolle	Calder & Savile 8323 US	Canada	27.3	30.2	33.0	49, 51, 175–177
	Evert s.n. 1920 US	Washington	24.7	26.3	28.6	50, 96
Berberis fendleri A. Gray	Eastwood 5272 US	Colorado	37.7	39.9	42.9	21, 22, 124, 125
B. grandiflora Turczaninow	Arbelaez & Cuatrecasas 5908 US	Colombia	39.0	43.2	45.5	24
	Mexia 7628 US	Colombia	48.1	50.6	53.3	126, 127
B. ilicifolia Forster	Goodall 834 US	Argentina	45.5	49.9	53.3	19, 20, 128–132
B. tischleri C. K. Schneider	Rock 17544 US	China	36.4	41.9	49.4	
B. vulgaris L.	Soper & Dale 3950 US	Canada	32.5	38.4	41.6	23
Bongardia chrysogonum (L.) Spach	Balls 776 US	Turkey	44.2	48.9	54.6	194
	Sintenis 35 US	U.S.S.R.	50.7	54.5	58.5	67, 68, 190–193, 195–197
Caulophyllum robustum Maximowicz	Kirino 713 US	Japan	49.4	51.5	54.6	55, 56
	Moran 5204 US	Korea	46.8	50.2	53.3	59, 184
C. thalictroides (L.) Michaux	Harper 3864 US	Alabama	44.2	48.9	52.0	60, 185–189
	Henry 571 US	Pennsylvania	42.9	45.1	48.1	57, 58
Diphylleia cymosa Michaux	Braun s.n. 25 Apr 27 US	Tennessee	32.5	36.4	39.0	86
	Pollard s.n. 16 May 01 US	North Carolina	36.4	40.4	44.2	85, 203, 204
D. sinensis Li	Rock 4230 US	China	35.1	39.5	44.2	87, 88, 205
Dysosma pleiantha (Hance) R. E. Woodson	Steward & Cheo 210 GH	China	39.0	42.9	50.7	79, 80, 92
	Wilson 3203 GH	China				206
Epimedium alpinum L.	Porta s.n. Jun 1894 US	Italy	29.9	31.5	33.8	36, 104
E. brevicornu Maximowicz	Rock 12302 US	China	29.9	33.9	37.7	35, 105, 150
E. cremeum Nakai	Togasi 1281 US	Japan	32.5	33.2	33.8	151–154
	Kirino 618 US	Japan	26.0	28.7	31.2	114
E. diphyllum (Morren & Decaisne) Loddiges	Anon. 1314887 US	Japan	26.0	28.2	29.9	31, 32, 149
E. grandiflorum Morren	Togasi 1031 US	Japan	28.6	31.3	33.8	112, 155, 156
E. membranaceum K. Meyer	Forrest 25471 US	China	29.9	33.2	35.1	94
E. sagittatum (Siebold & Zuccarini) Maximowicz	Anon. 1314880 US	Japan	32.5	34.1	36.4	99
E. sempervirens Nakai	Masayuki Oue 33 US	Japan	31.2	33.1	36.4	33, 34, 110
Jeffersonia diphylla (L.) Persoon	Baxter s.n. 15 Apr 11 US	New York	29.9	32.9	36.4	46, 107
	Chandler s.n. 30 Apr 16 US	Michigan	28.6	31.9	33.8	
	Shafer & Miller 180a US	Pennsylvania	31.2	33.9	36.4	47, 48, 98, 170, 171

Table 1.—Continued

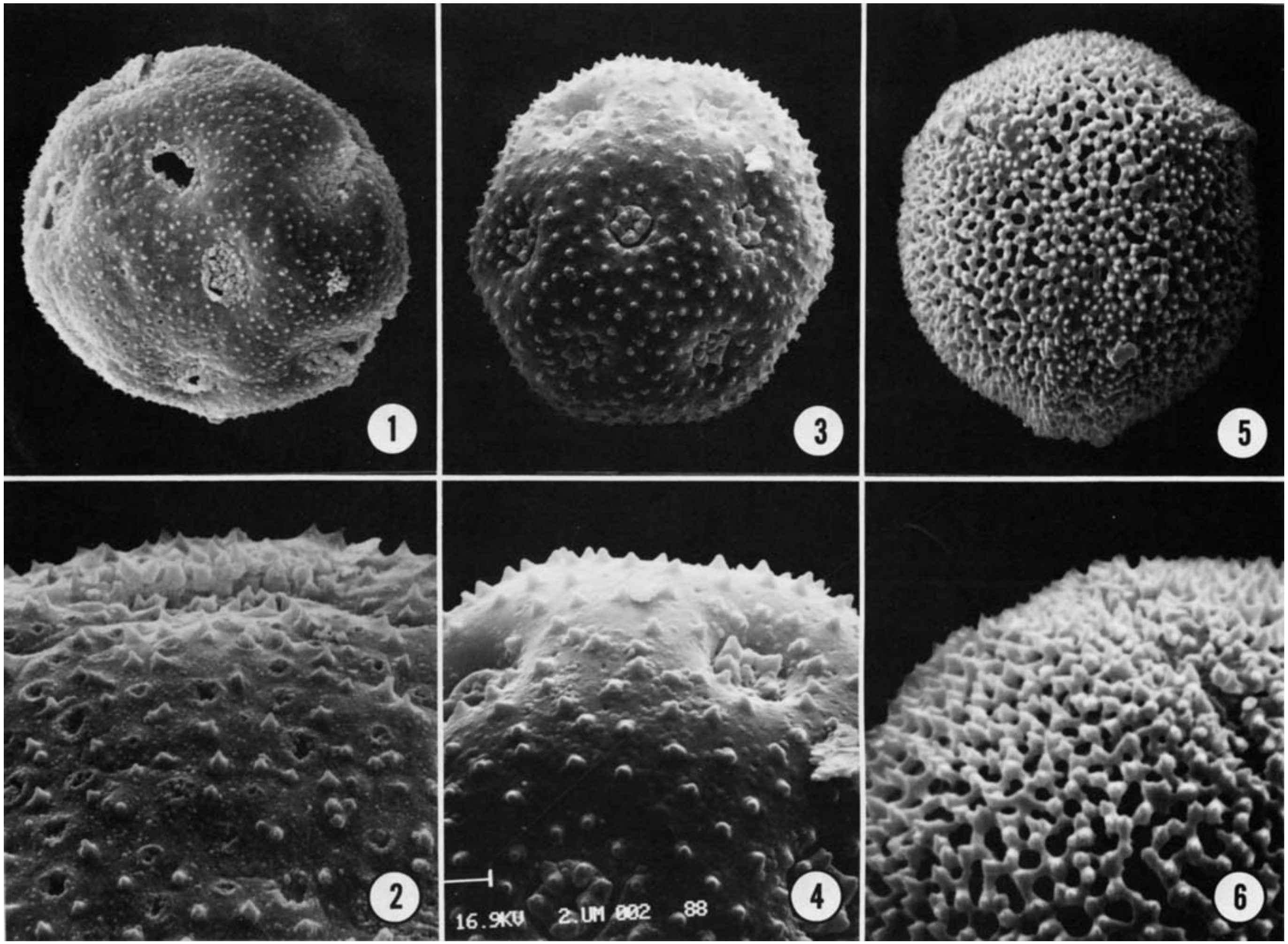
Species	Collection	Location	Longest dimension of ten grains: Low	Mean	High	Figure numbers
J. dubia (Maximowicz) Bentham & Hooker	Palczevsky 3616 US	U.S.S.R.	27.3	29.3	31.2	43, 95, 172–174
	Mrs.R. K. Smith s.n. 30 May 38 US	Korea	29.9	32.5	35.1	44, 45, 93
Leontice altaica Pallas	Anon. 597803 US	U.S.S.R.	42.9	48.8	53.3	61, 62
L. armenaica Boivin	Koelz 14701 US	Iran	52.0	54.7	57.2	65, 66, 180–182
L. eversmannii Bunge	Sintenis 121 MO	U.S.S.R.	39.0	43.7	48.1	71, 72
L. leontopetalum L.	Gillett & Rawi 10275 US	Iraq	52.0	55.1	58.5	69, 70, 183
L. odessana Rogowicz	A. Dojcz s.n. 5 Apr 08 MO	U.S.S.R.	42.9	46.5	49.4	63, 64
Mahonia fremontii (Torrey) Fedde	Hope 9396 US	Arizona	31.2	35.2	41.6	25, 26
M. haematocarpa (Wooton) Fedde	McKelvey 1225 US	Arizona	31.6	34.1	39.0	30
M. nervosa (Pursh) Nuttall	Belton s.n. 26 May 43 US	Oregon	49.4	51.2	53.3	27, 28, 133–135
M. oiwakensis Hayata	Wilson 10844 US	Formosa	29.9	33.8	37.7	29, 136–138
Nandina domestica Thunberg	Cheng 2098 US	China	41.6	44.2	48.1	207–211
	Tai & Class 4034 US	China	35.1	39.4	42.9	89, 90
	Wilson 2379 US	China	35.1	38.9	41.6	
Podophyllum hexandrum Royale	Rock 12259 US	China	31.5*	33.3*	35.8*	83, 84
	Rock 12259 GH	China	32.5*	33.3*	34.2*	198, 199
	Rock 12424 GH	China	27.3*	28.9*	31.3*	82
P. hispidum Hao	T. T. Yu, 15977 A	China	36.4	38.9	41.6	81, 91
P. peltatum L.	Braun 3911 US	Kentucky	33.8	37.3	40.3	109, 202
	Crampton 76 US	Illinois	29.9	36.0	40.3	77, 78, 113
	Jones s.n. 21 Mar 62 US	Alabama	32.5	35.4	39.0	
	McDougall 1231 US	Mississippi	31.2	33.9	36.4	75, 76, 108, 111
	Nease 310 US	Tennessee	32.5	36.5	41.6	
	Nunan 1914 US	Georgia	32.5	35.3	39.0	200, 201
	Ricksecker s.n. 20 May 95 US	Ohio	32.5	35.4	39.0	
	Rowell, York & Tharp 47171 US	Texas	35.1	38.5	41.6	73, 74, 106
	Thieret 10356 US	Louisiana	35.1	37.7	41.6	
Ranzania japonica (Ito) Ito	Cult. 12 Apr 47 K	England				141, 144, 145, 147, 148, 212
	Epstein s.n. Cult. US	New York	36.0		38.0	142, 143, 146
	Takeda s.n. 27 Aug 05 K	Japan				213
	Terabayashi 154 KYO	Japan	30.0	32.6	35.0	139, 140
Vancouveria chrysantha Greene	Thompson 4605 US	Oregon	32.5	34.7	37.7	41, 42, 97, 157–159
V. hexandra Morren & Decaisne	Allen 66 US	Washington	32.5	34.6	36.4	
	Ebert s.n. Aug 1920 US	Washington	33.8	39.4	41.6	39, 40, 100, 160–164
V. planipetala Calloni	Constance 2514 US	California	33.8	36.5	40.3	101
	Hoover 5046 US	California	35.1	38.1	41.6	37, 38, 102, 165–169

TABLE 2.—Centrospermae specimens examined, alphabetically by family (grain size in μm)

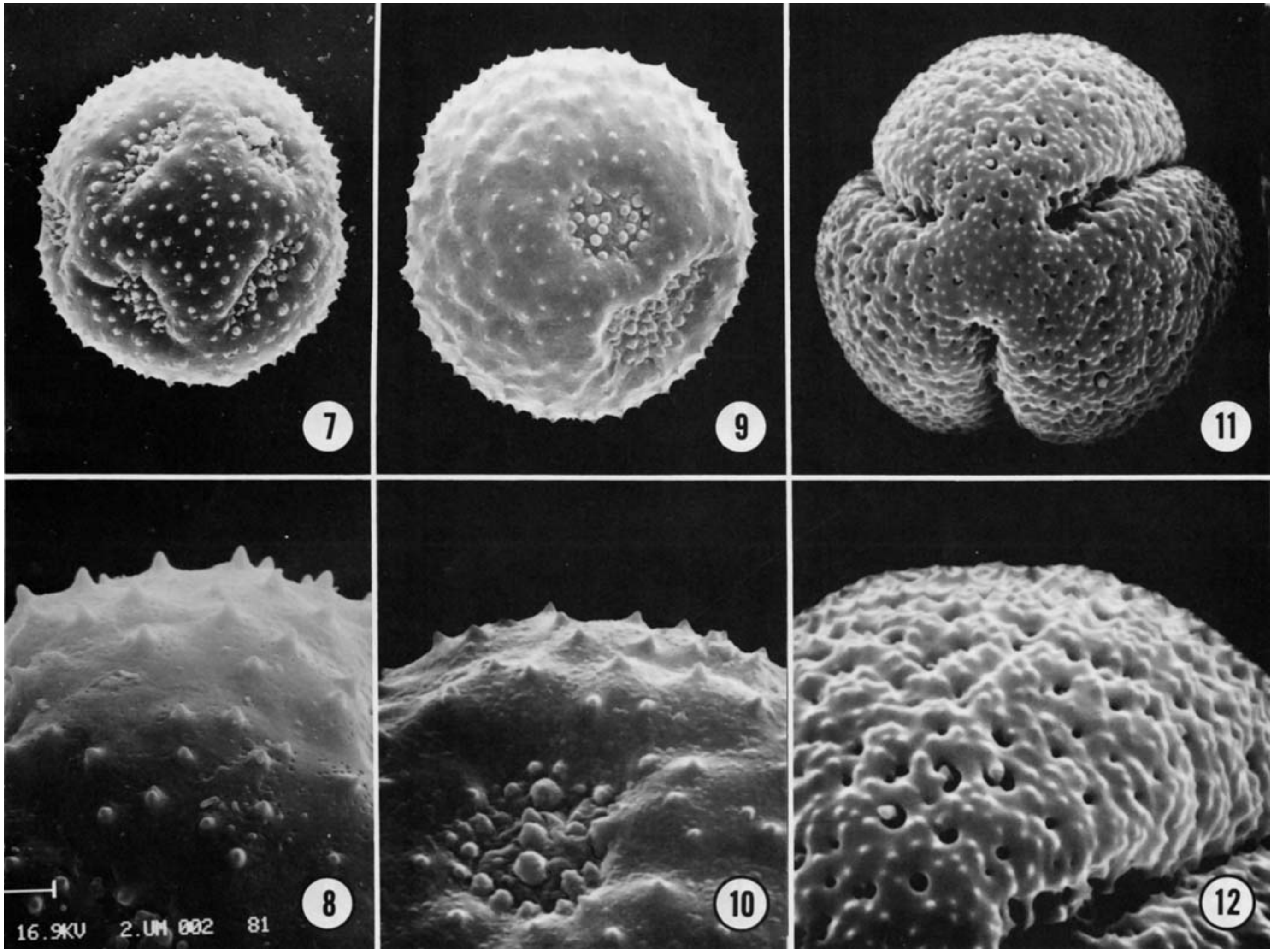
Species	Collection	Location	Longest dimension of ten grains: Low	Mean	High	Figure numbers
AIZOACEAE						
Acrodon bellidiflorus N. E. Brown	Van der Bijl 33 K	S. Africa	26.9	27.0	28.6	5, 6
CARYOPHYLLACEAE						
Tunica stricta (Bunge) Fischer & Meyer	Goloskokov s.n. 20 Jun 59 US	U.S.S.R.	22.1	23.1	24.7	3, 4
PORTULACACEAE						
Anacampseros filamentosa Sims	Rose & Stewart s.n. 1912 US	S. Africa	51.0	54.3	58.5	1, 2

TABLE 3.—Ranunculaceae specimens examined, alphabetically by genus (grain size in μm)

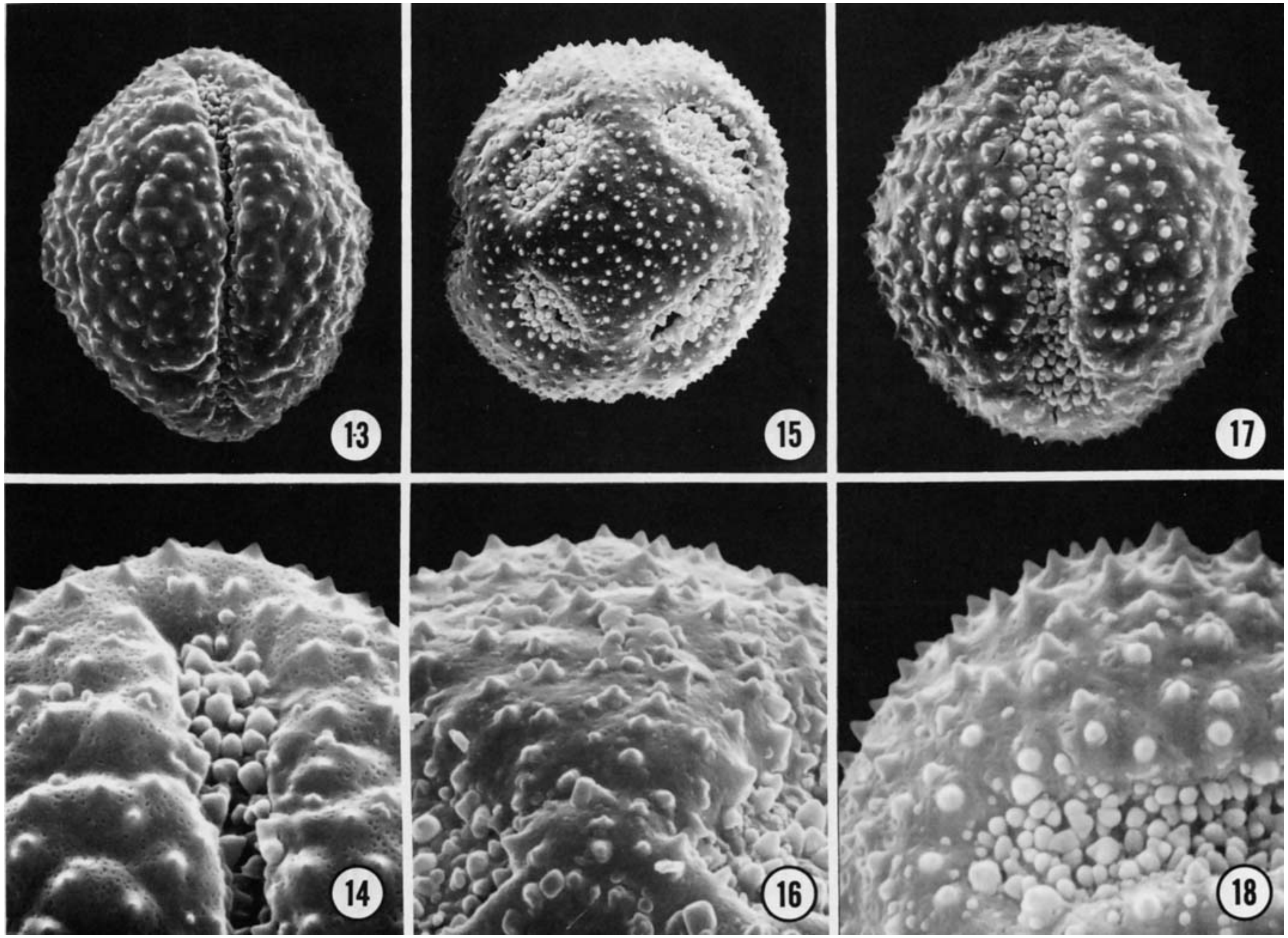
Species	Collection	Location	Longest dimension of ten grains: Low	Mean	High	Figure numbers
Batrachium aquatile Dumortier	Larsen & Pedersen s.n. 12 Jun 67 US	Denmark	29.9	33.4	36.4	13, 14, 119
Clematis heracleifolia De Candolle	Mrs. R. K. Smith s.n. 11 Aug 34 US	Korea	22.1	24.7	26.0	9, 10, 117
Glaucidium palmatum Siebold & Zuccarini	Takeda s.n. 23 May 07 US	Japan	24.7	26.3	27.3	11, 12, 118
Hamadryas magellanica Lamarck	Goodall 1073 US	Argentina	26.0	28.7	29.9	17, 18, 121
Hepatica transsilvanica Fuss	Richter s.n. 2 Apr 02 US	Hungary	33.8	38.0	41.6	15, 16, 120
Hydrastis canadensis L.	Hardin 610 US	Arkansas	19.5	22.8	26.0	52, 103, 122, 123
	Ricksecker s.n. 12 May 95 US	Ohio	19.5	22.6	26.0	53, 54
Ranunculus oreophytus Delile	Mearns 1402 US	Kenya	36.4	37.8	39.0	7, 8, 115, 116



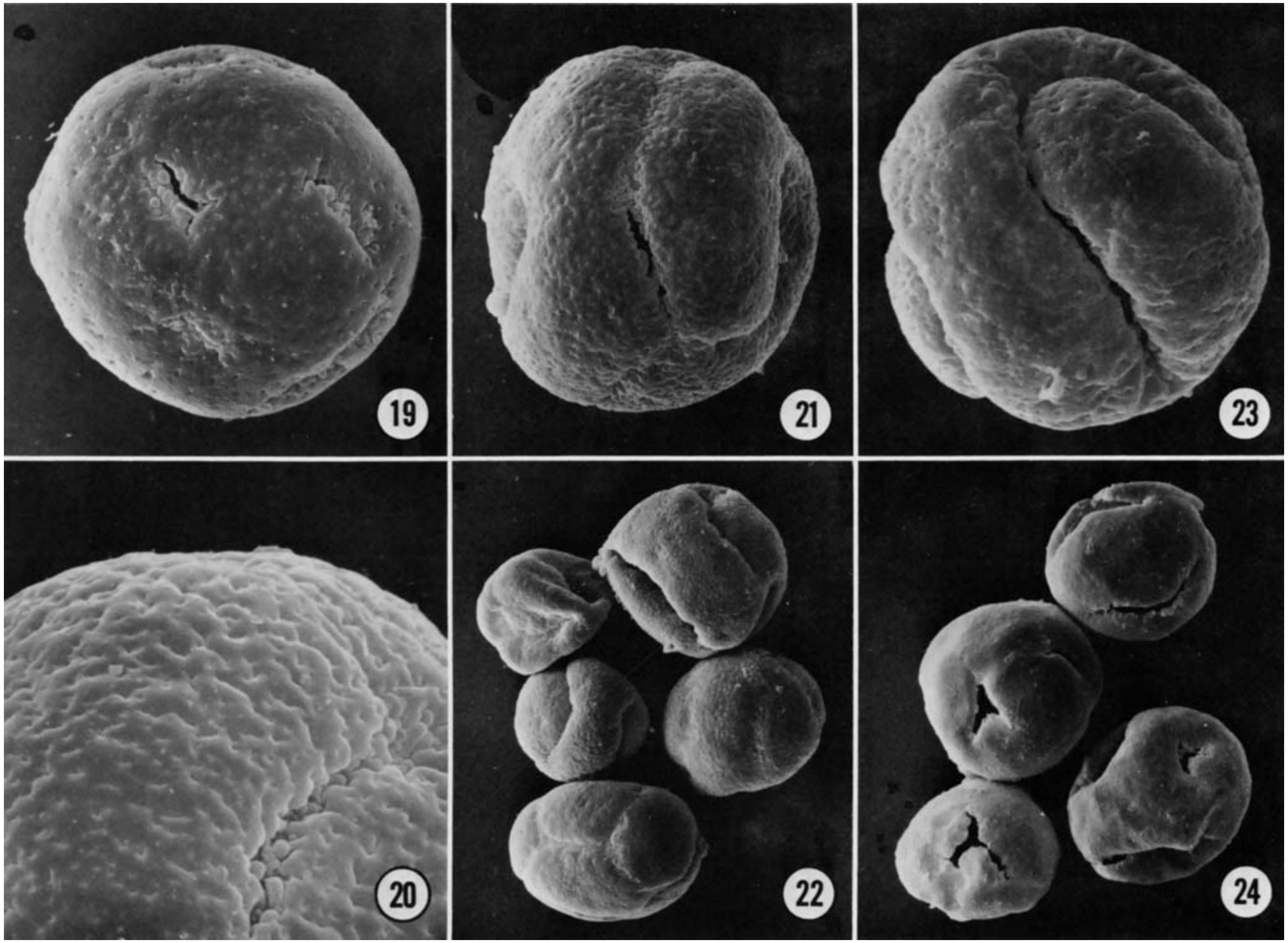
FIGURES 1–6.—Centrospermae pollen, SEM: 1, *Anacampseros filamentosa* Sims (Portulacaceae), pantocolpate, × 1300 (Rose & Stewart s.n. 1912 US, S. Africa); 2, *A. filamentosa*, ektexine surface, × 5000 (same collection); 3, *Tunica stricta* (Bunge) Fischer & Meyer (Caryophyllaceae), pantoporate, × 3520 (Goloskokov s.n. 20 Jun 59 US, U.S.S.R.); 4, *T. stricta*, ektexine surface, × 7500 (same collection); 5, *Acrodon bellidiflorus* N. E. Brown (Aizoaceae), 3-colpate, polar view, × 3465 (Van der Bijl 33 K, S. Africa); 6, *A. bellidiflorus*, ektexine surface, × 7500 (same collection). (Micrographs reduced to 74%.)



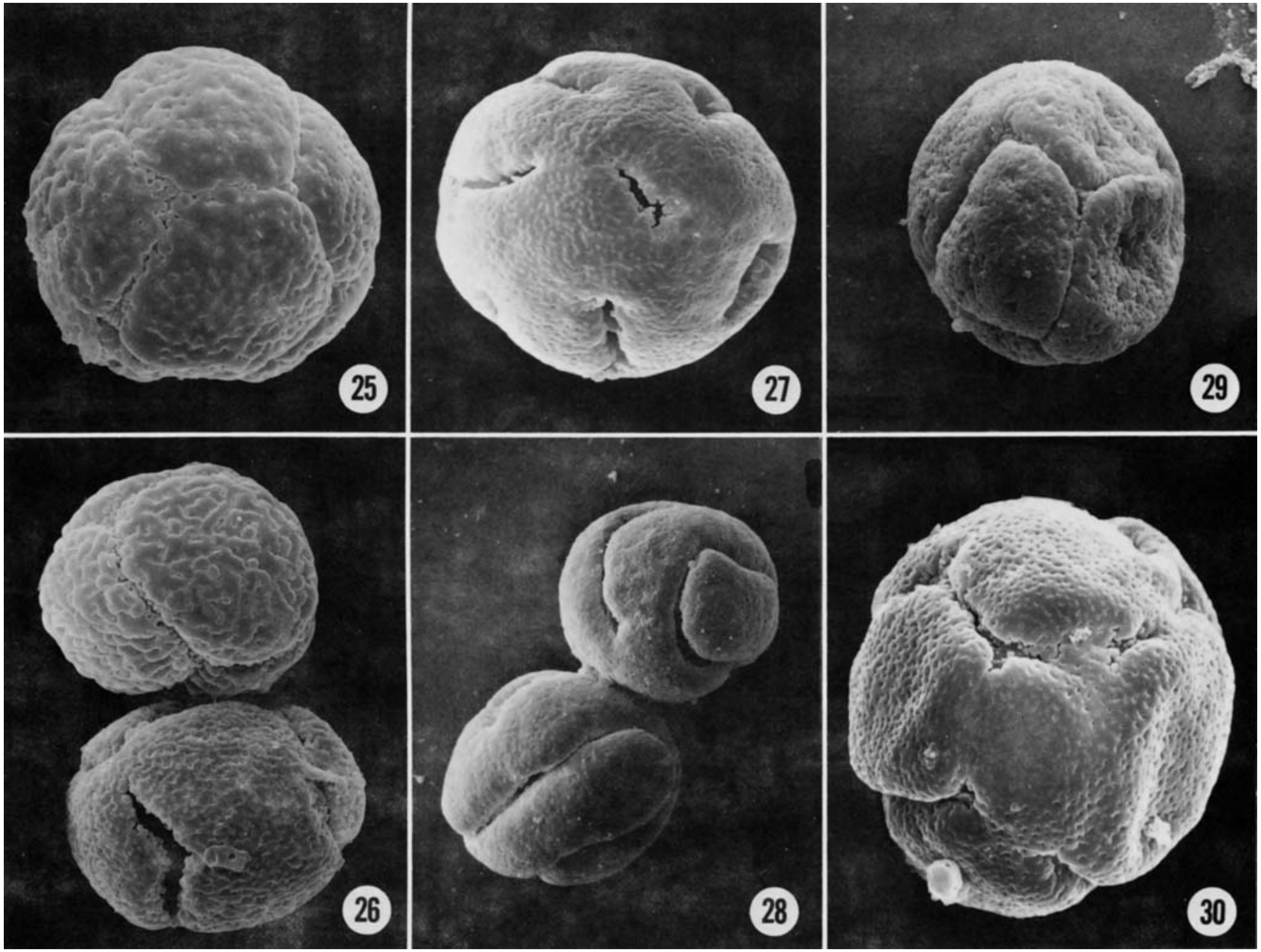
FIGURES 7–12.—Ranunculaceae pollen, SEM: 7, *Ranunculus oreophytus* Delile, pantocolpate, polar view, × 2260 (Mearns 1402 US, Kenya); 8, *R. oreophytus*, ektexine surface, × 7560 (same collection); 9, *Clematis heracleifolia* De Candolle, irregularly (panto)porate, × 3000 (Mrs. R. K. Smith s.n. 11 Aug 34 US, Korea); 10, *C. heracleifolia*, ektexine surface, × 7500 (same collection); 11, *Glaucidium palmatum* Siebold & Zuccarini, 3-colpate, polar view, × 4500 (Takeda s.n. 23 May 07 US, Japan); 12, *G. palmatum*, ektexine surface, × 10,000 (same collection). (Micrographs reduced to 76%.)



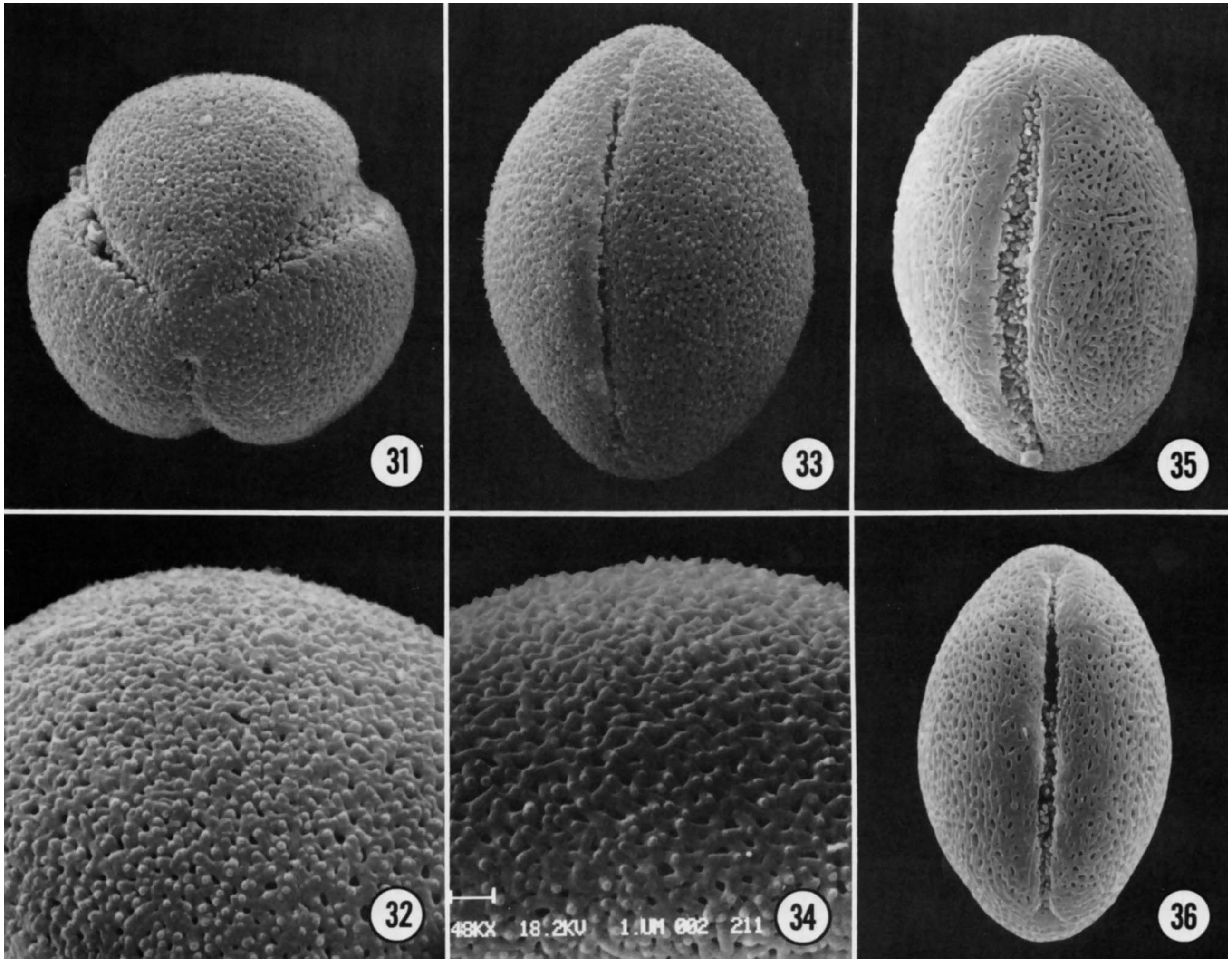
FIGURES 13–18.—Ranunculaceae pollen, SEM: 13, *Batrachium aquatile* Dumortier, 3-colpate, equatorial view, × 2425 (Larsen & Pedersen s.n. 12 Jun 67 US, Denmark); 14, *B. aquatile*, ektexine surface, × 7500 (same collection); 15, *Hepatica transsilvanica* Fuss, pantocolpate, polar view, × 2220 (Richter s.n. 2 Apr 02 US, Hungary); 16, *H. transsilvanica*, ektexine surface, × 7500 (same collection); 17, *Hamadryas magellanica* Lamarck, 3-colpate, equatorial view, × 3300 (Goodall 1073 US, Argentina); 18, *H. magellanica*, ektexine surface, × 7500 (same collection). (Micrographs reduced to 75%.)



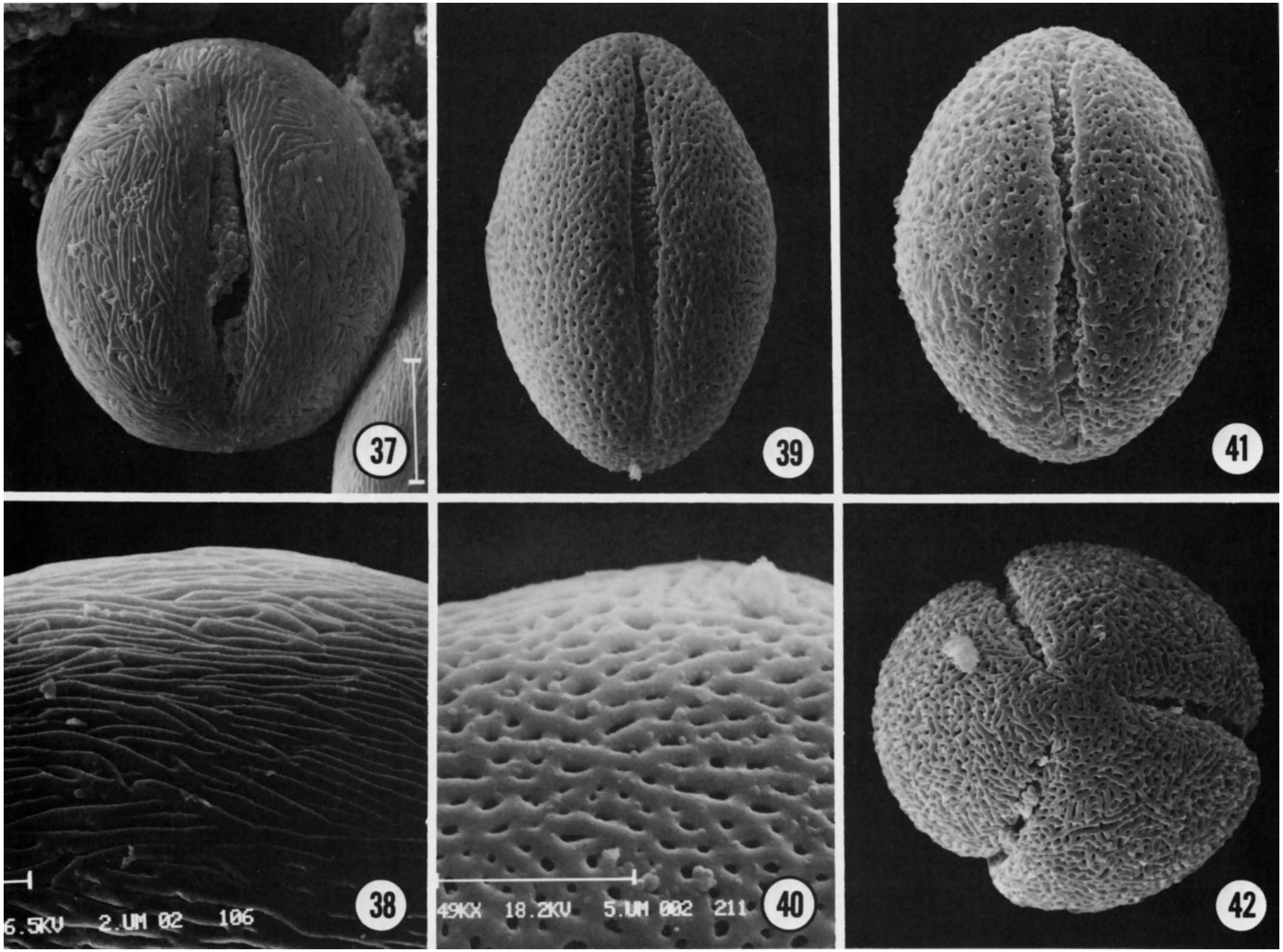
FIGURES 19–24.—Berberidaceae, *Berberis* pollen, SEM: 19, *B. ilicifolia* Forster, irregular apertures, × 1700 (Goodall 834 US, Argentina); 20, *B. ilicifolia*, ektexine surface, × 3000 (same collection); 21, *B. fendleri* A. Gray, irregular apertures, × 2000 (Eastwood 5272 US, Colorado); 22, *B. fendleri*, five grains (one at upper left may be sterile) illustrating variation in size and apertures, × 940 (same collection); 23, *B. vulgaris* L., spiral apertures, × 2050 (Soper & Dale 3950 US, Ontario); 24, *B. grandiflora* Turczaninow, four grains illustrating variation in apertures, × 790 (Arbelaez & Cuatrecasas 5908 US, Colombia). (Micrographs reduced to 71%.)



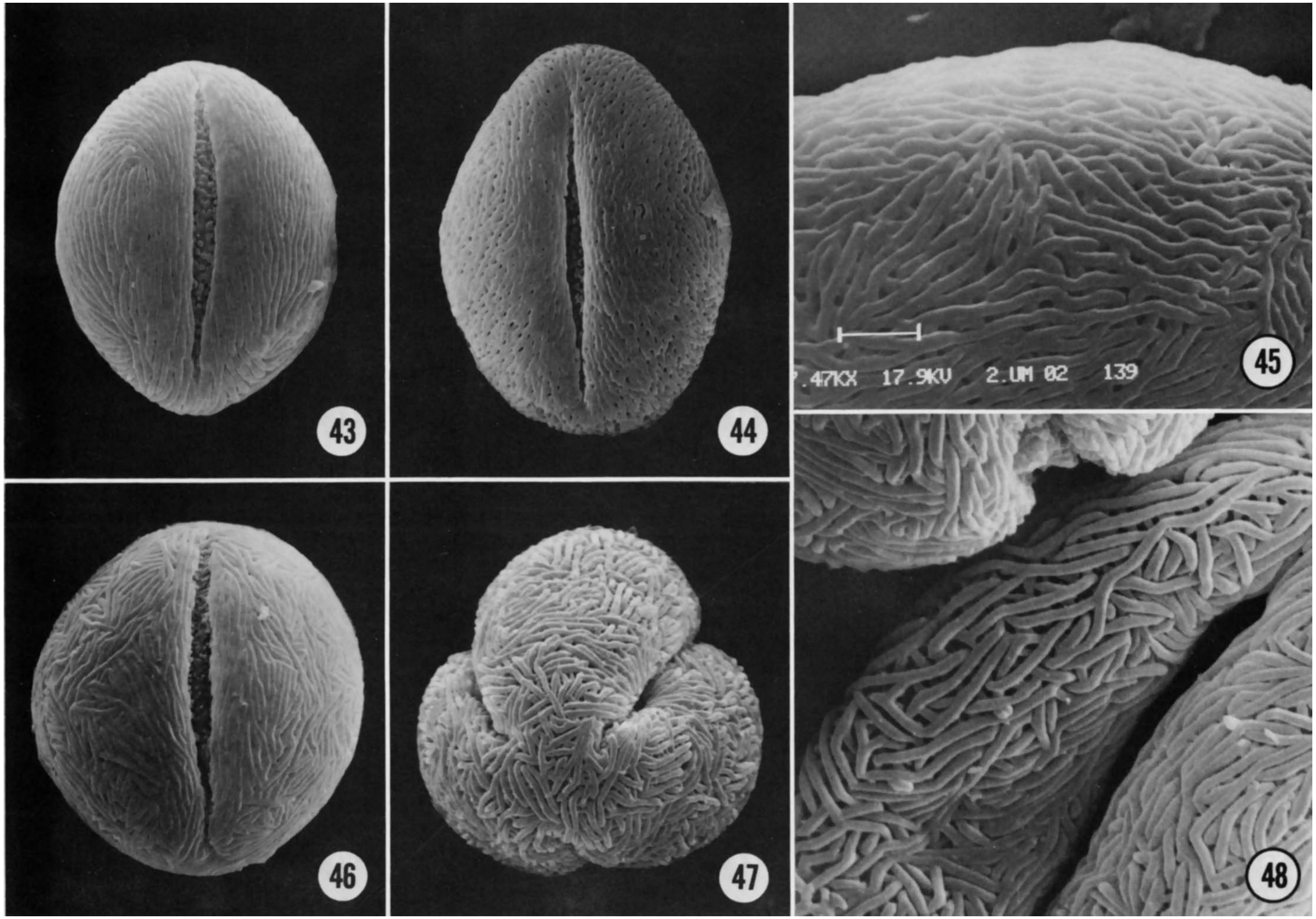
FIGURES 25–30. Berberidaceae, *Mahonia* pollen, SEM: 25, *Mahonia fremontii* (Torrey) Fedde, irregular apertures, × 2400 (Hope 9396 US, Arizona); 26, *M. fremontii*, 2 grains illustrating the variation in punctate-striate exine, × 1620 (same collection); 27, *M. nervosa* (Pursh) Nuttall, spiral apertures, × 1600 (Belton s.n. 26 May 43 US, Oregon); 28, *M. nervosa*, 2 grains illustrating the spiral apertures, × 928 (same collection); 29, *M. oiwakensis* Hayata, irregular apertures, × 2040 (Wilson 10844 US, Formosa); 30, *M. haematocarpa* (Wooton) Fedde, irregular apertures, × 2400 (McKelvey 1225 US, Arizona). (Micrographs reduced to 72%.)



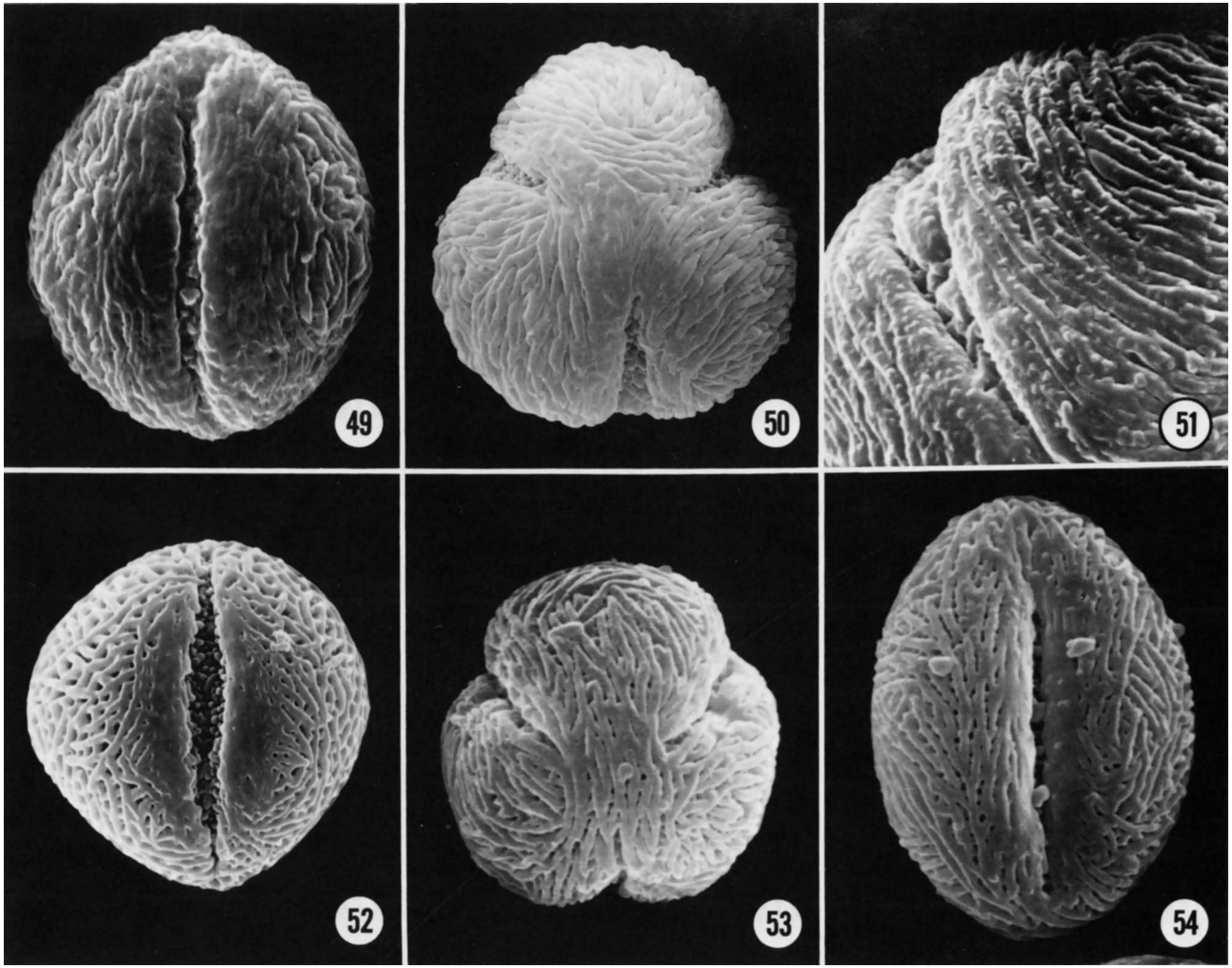
FIGURES 31–36.—Berberidaceae, *Epimedium* pollen, SEM: 31, *Epimedium diphyllum* (Morren & Decaisne) Loddiges, 3-colpate, polar view, × 3400 (Anon. 1314887 US, Japan); 32, *E. diphyllum*, ektexine surface, × 7500 (same collection); 33, *E. sempervirens* Nakai, 3-colpate, equatorial view, × 3000 (Masayuki Oue 33 US, Japan); *E. sempervirens*, ektexine surface, × 7480 (same collection); 35, *E. brevicornu* Maximowicz, 3-colpate, equatorial view, × 2700 (Rock 12302 US, China); 36, *E. alpinum* L., 3-colpate, equatorial view, × 2500 (Porta s.n. Jun 1894 US, Italy). (Micrographs reduced to 75%.)



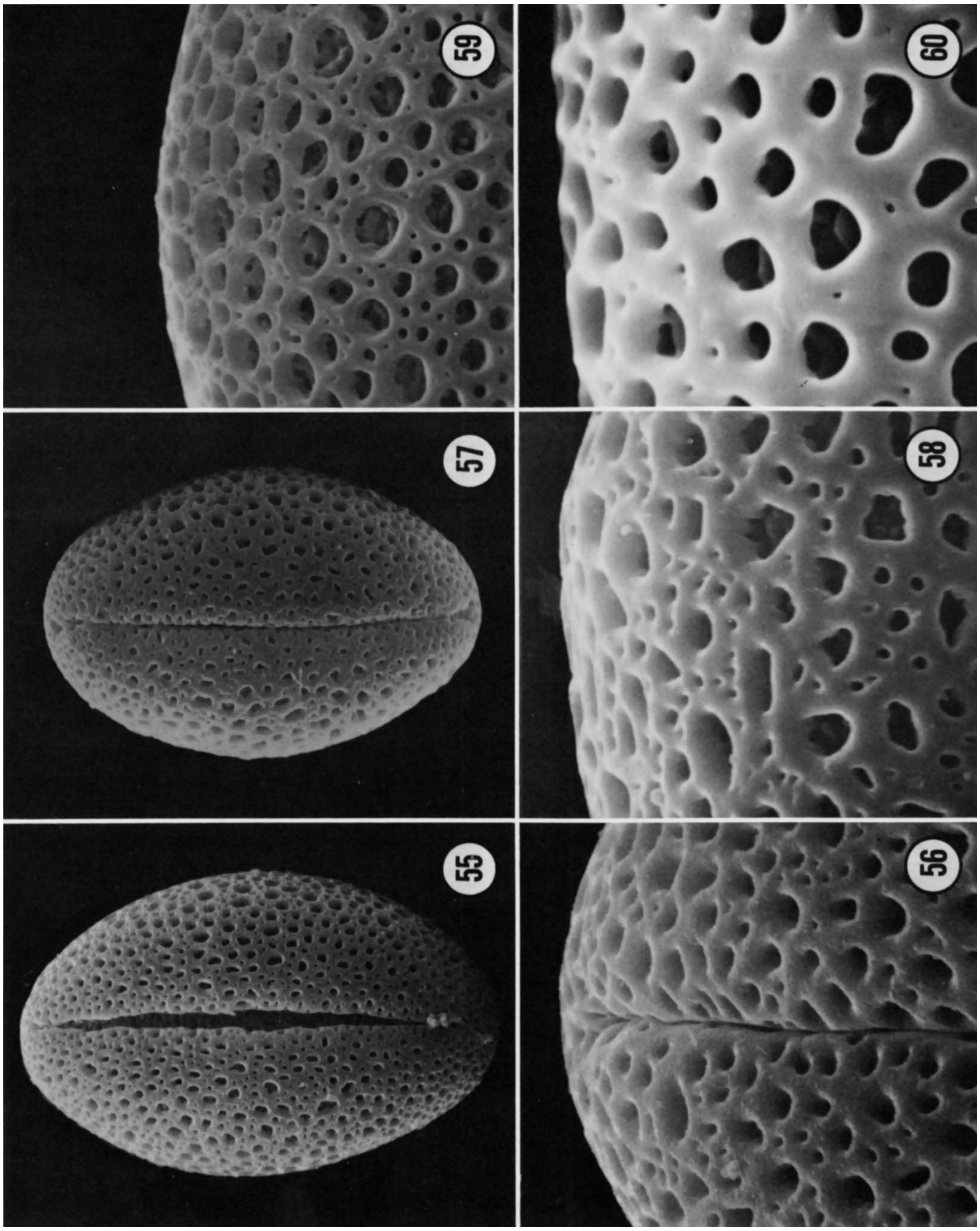
FIGURES 37–42.—Berberidaceae, *Vancouveria* pollen, SEM: 37, *V. planipetala* Calloni, 3-colpate, equatorial view, × 2400 (Hoover 5046 US, California); 38, *V. planipetala*, ektexine surface, × 7500 (same collection); 39, *V. hexandra* Morren & Decaisne, 3-colpate, equatorial view, × 2320 (Ebert s.n. Aug 1920 US, Washington); 40, *V. hexandra*, ektexine surface, × 7500 (same collection); 41, *V. chrysantha* Greene, 3-colpate, equatorial view, × 2700 (Thompson 4605 US, Oregon); 42, *V. chrysantha*, 3-colpate, polar view, × 3000 (same collection). (Micrographs reduced to 77%.)



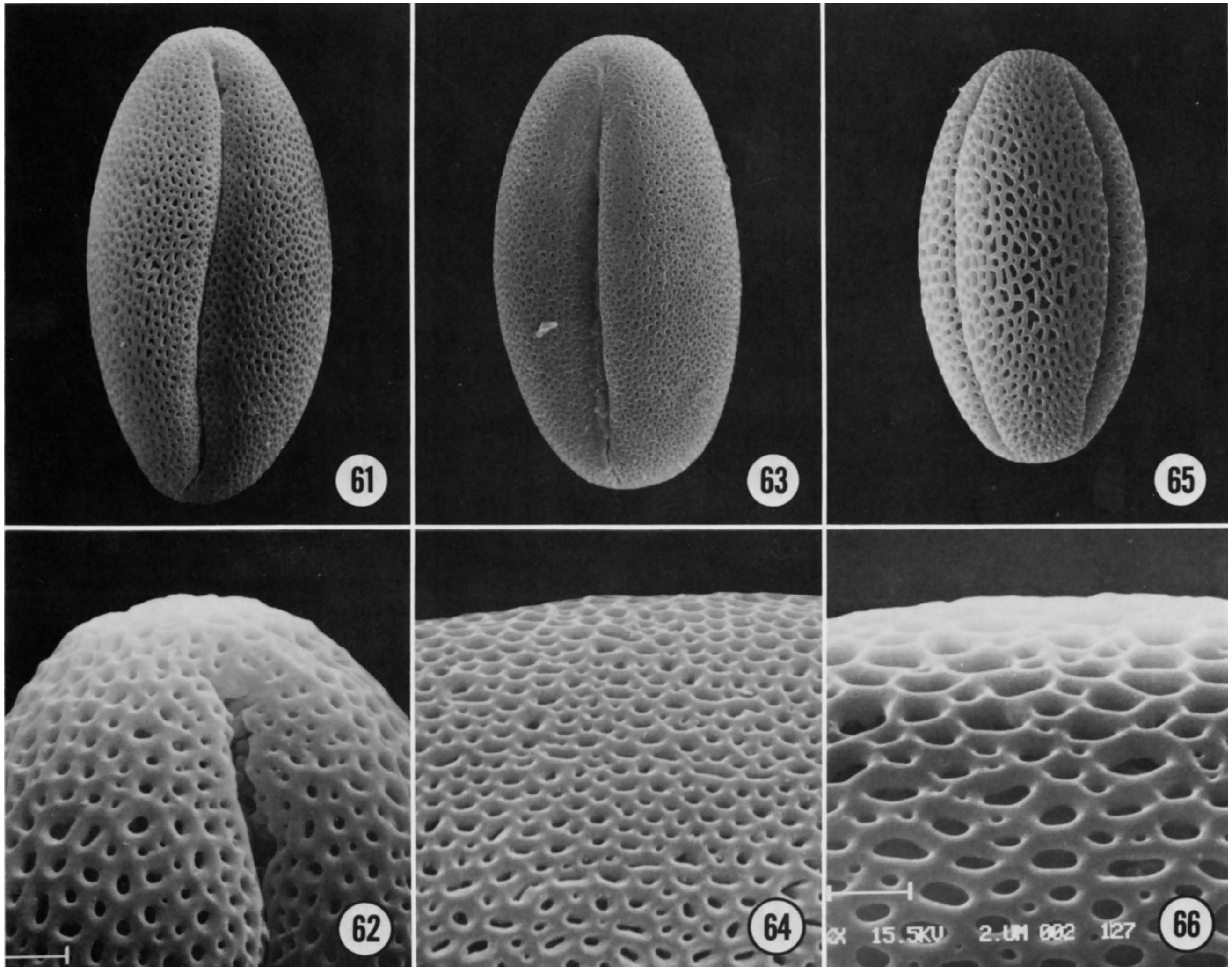
FIGURES 43–48.—Berberidaceae, *Jeffersonia* pollen, SEM: 43, *Jeffersonia dubia* (Maximowicz) Bentham & Hooker, 3-colpate, equatorial view, × 3000 (Palczevsky 3616 US, U.S.S.R.); 44, *J. dubia*, 3-colpate, equatorial view, × 2880 (Mrs. R. K. Smith s.n. 30 May 38 US, Korea); 45, *J. dubia*, ektexine surface, × 7470 (same collection); 46, *J. diphylla* (L.) Persoon, 3-colpate, equatorial view, × 2500 (Baxter s.n. 15 Apr 11 US, New York); 47, *J. diphylla*, 3-colpate, polar view, × 3200 (Shafer & Miller 180a US, Pennsylvania); 48, *J. diphylla*, ektexine surface, × 5280 (same collection). (Micrographs reduced to 75%.)



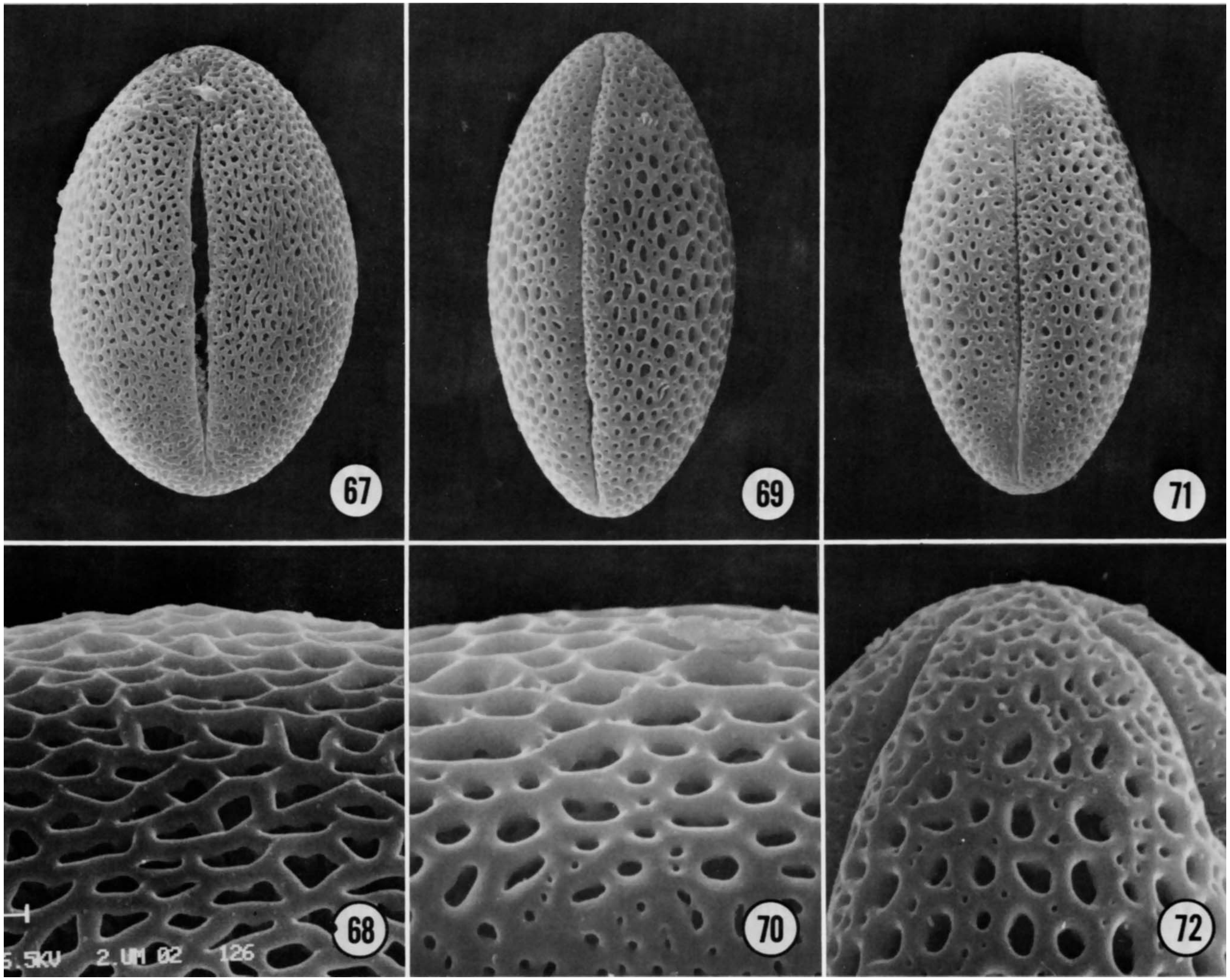
FIGURES 49–54.—Berberidaceae, *Achlys* and *Hydrastis* pollen, SEM. 49, *Achlys triphylla* (Smith) De Candolle, 3-colpate, equatorial view, × 3400 (Calder & Savile 8323 US, Canada); 50, *A. triphylla*, 3-colpate, polar view, × 2800 (Evert s.n. 1920 US, Washington); 51, *A. triphylla*, ektexine surface, × 6300 (Calder & Savile 8323 US, Canada); 52, *Hydrastis canadensis* L., 3-colpate, equatorial view, × 4000 (Hardin 610 US, Arkansas); 53, *H. canadensis*, 3-colpate, polar view, × 4750 (Ricksecker s.n. 12 May 95 US, Ohio); 54, *H. canadensis*, 3-colpate, equatorial view, × 5000 (same collection). (Micrographs reduced to 71%.)



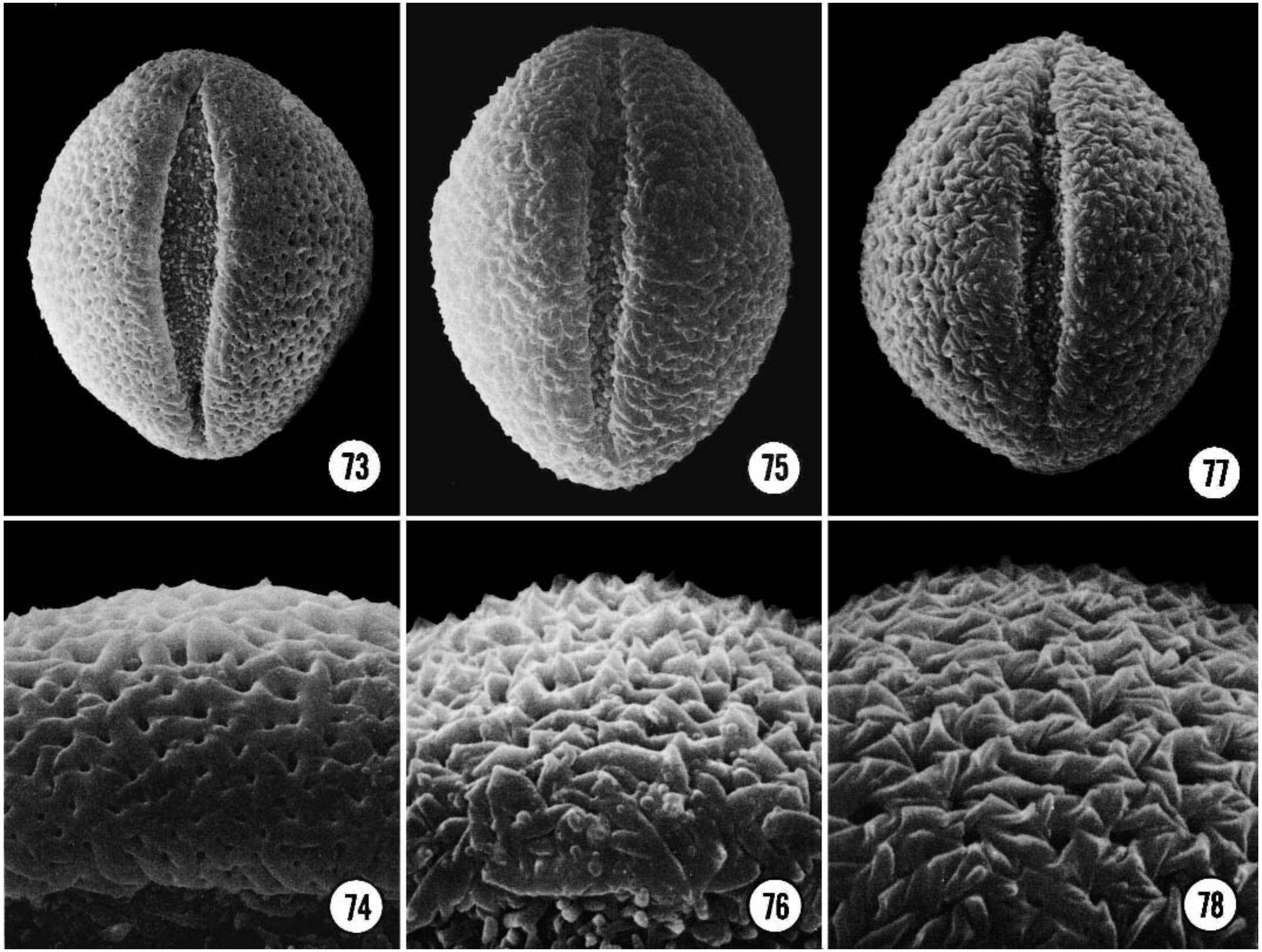
FIGURES 55–60.—Berberidaceae, *Caulophyllum* pollen, SEM: 55, *C. robustum* Maximowicz, 3-colpate, equatorial view, × 1700 (Kirino 713 US, Japan); 56, *C. robustum*, ektexine surface, × 5000 (same collection); 57, *C. thalictroides* (L.) Michaux, 3-colpate, equatorial view, × 1900 (Henry 571 US, Pennsylvania); 58, *C. thalictroides*, ektexine surface, × 7500 (same collection); 59, *C. robustum*, ektexine surface, × 5000 (Moran 5204 US, Korea); 60, *C. thalictroides*, ektexine surface, × 10,000 (Harper 3864 US, Alabama). (Micrographs reduced to 77%.)



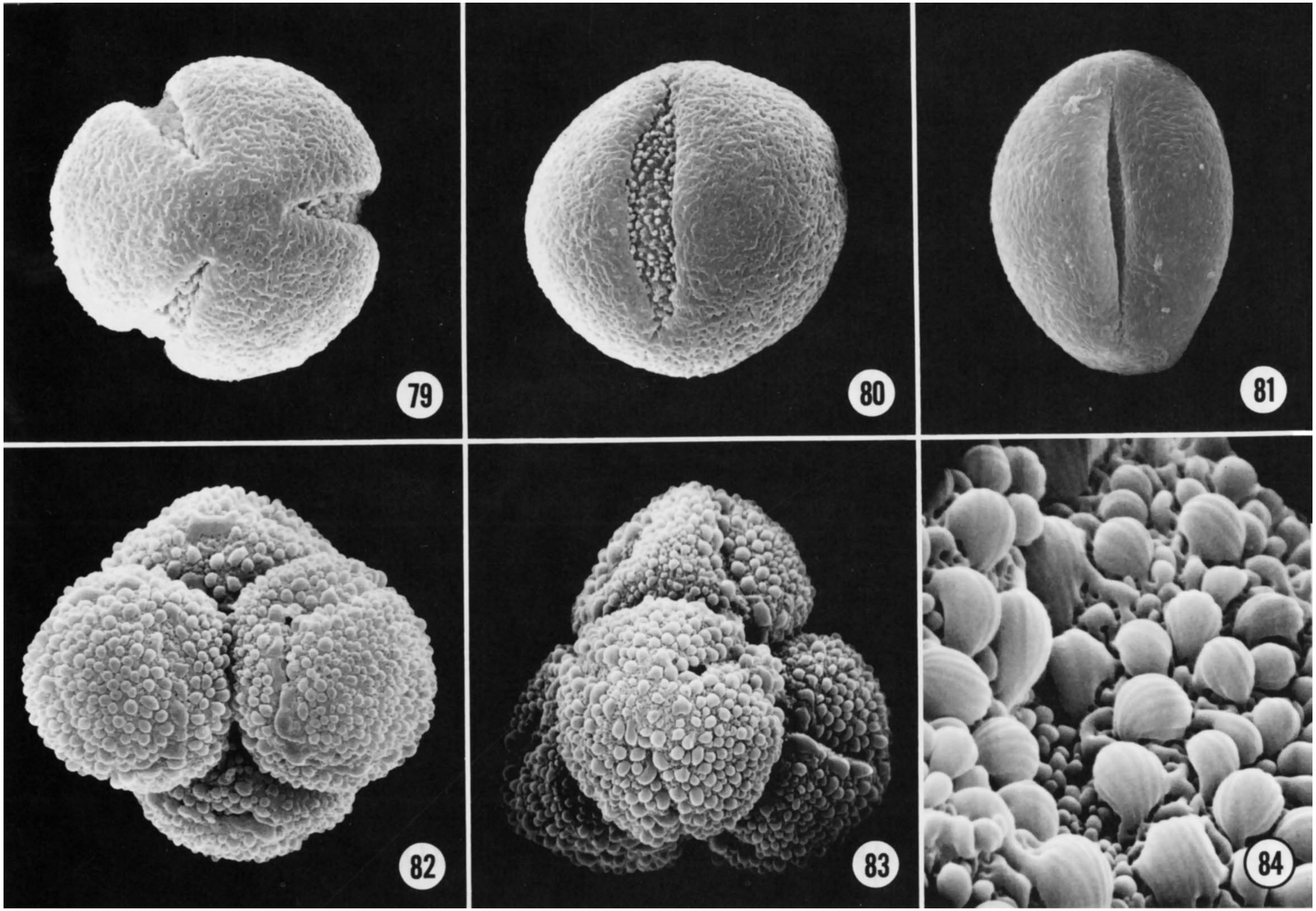
FIGURES 61–66.—Berberidaceae, *Leontice* pollen, SEM: 61, *L. altaica* Pallas, 3-colpate, equatorial view, × 1920 (Anon. 597803 US, U.S.S.R.); 62, *L. altaica*, ektexine surface, × 7500 (same collection); 63, *L. odessana* Rogowicz, 3-colpate, equatorial view, × 2000 (A. Dojcz s.n. 5 Apr 08 MO, U.S.S.R.); 64, *L. odessana*, ektexine surface, × 7500 (same collection); 65, *L. armenaica* Boivin, 3-colpate, equatorial view, × 1700 (Koelz 14701 US, Iran); 66, *L. armenaica*, ektexine surface, × 7480 (same collection). (Micrographs reduced to 77%.)



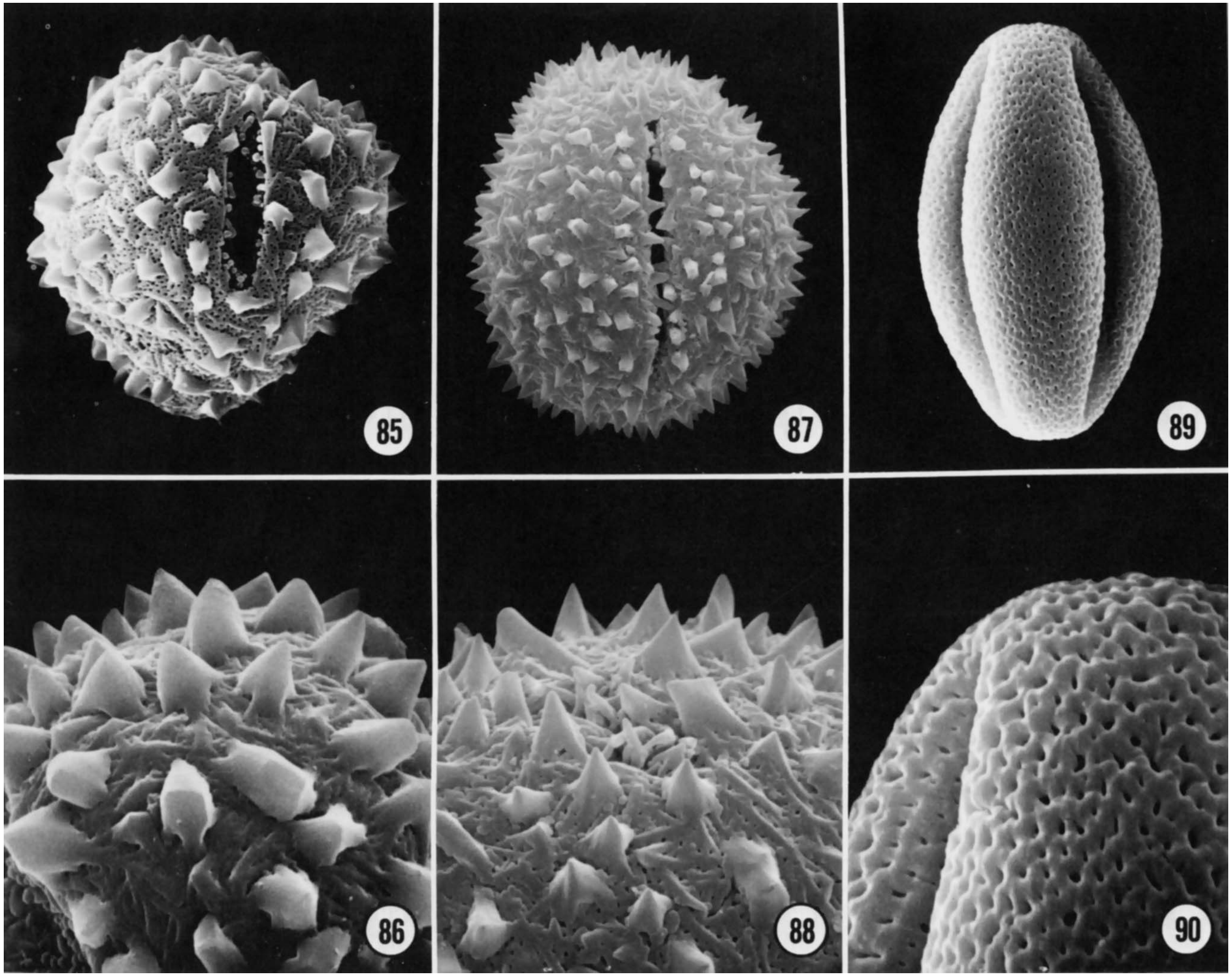
FIGURES 67–72.—Berberidaceae, *Bongardia* and *Leontice* pollen, SEM: 67, *Bongardia chrysogonum* (L.) Spach, 3-colpate, equatorial view, × 1670 (Sintenis 35 US, U.S.S.R.); 68, *B. chrysogonum*, ektexine surface, × 7500 (same collection); 69, *Leontice leontopetalum* L., 3-colpate, equatorial view, × 1800 (Gillett & Rawi 10275 US, Iraq); 70, *L. leontopetalum*, ektexine surface, × 7500 (same collection); 71, *L. eversmannii* Bunge, 3-colpate, equatorial view, × 2300 (Sintenis 121 MO, U.S.S.R.); 72, *L. eversamannii*, ektexine surface, × 7500 (same collection). (Micrographs reduced to 77%.)



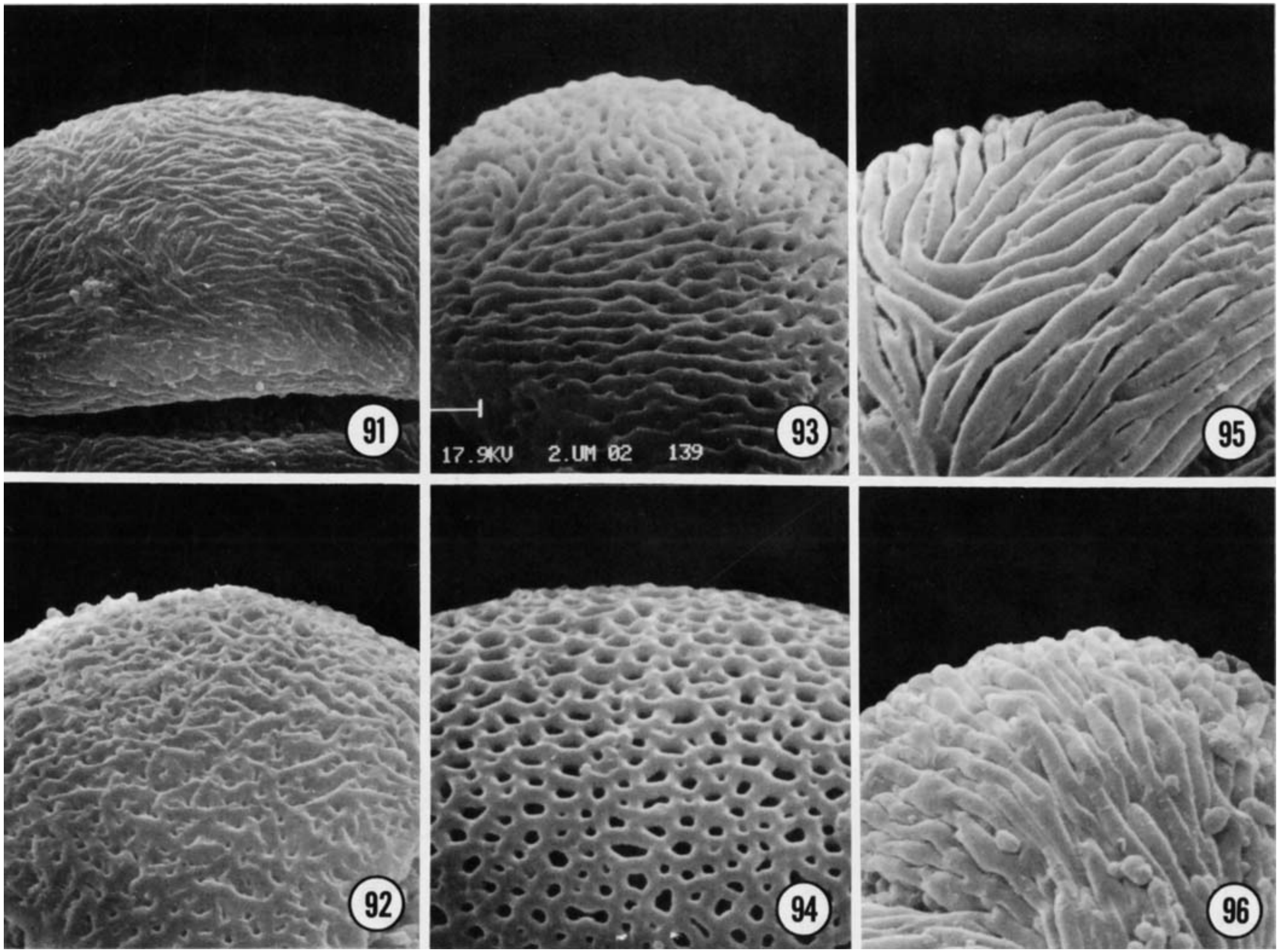
FIGURES 73–78.—Berberidaceae, *Podophyllum peltatum* pollen, SEM: 73, 3-colpate, equatorial view, × 2500 (Rowell, York & Tharp 47171 US, Texas); 74, ektexine surface, × 7530 (same collection); 75, 3-colpate, equatorial view, × 2910 (McDougall 1231 US, Mississippi); 76, ektexine surface, × 7500 (same collection); 77, 3-colpate, equatorial view, × 2600 (Crampton 76 US, Illinois); 78, ektexine surface, × 7500 (same collection). (Micrographs reduced to 79%.)



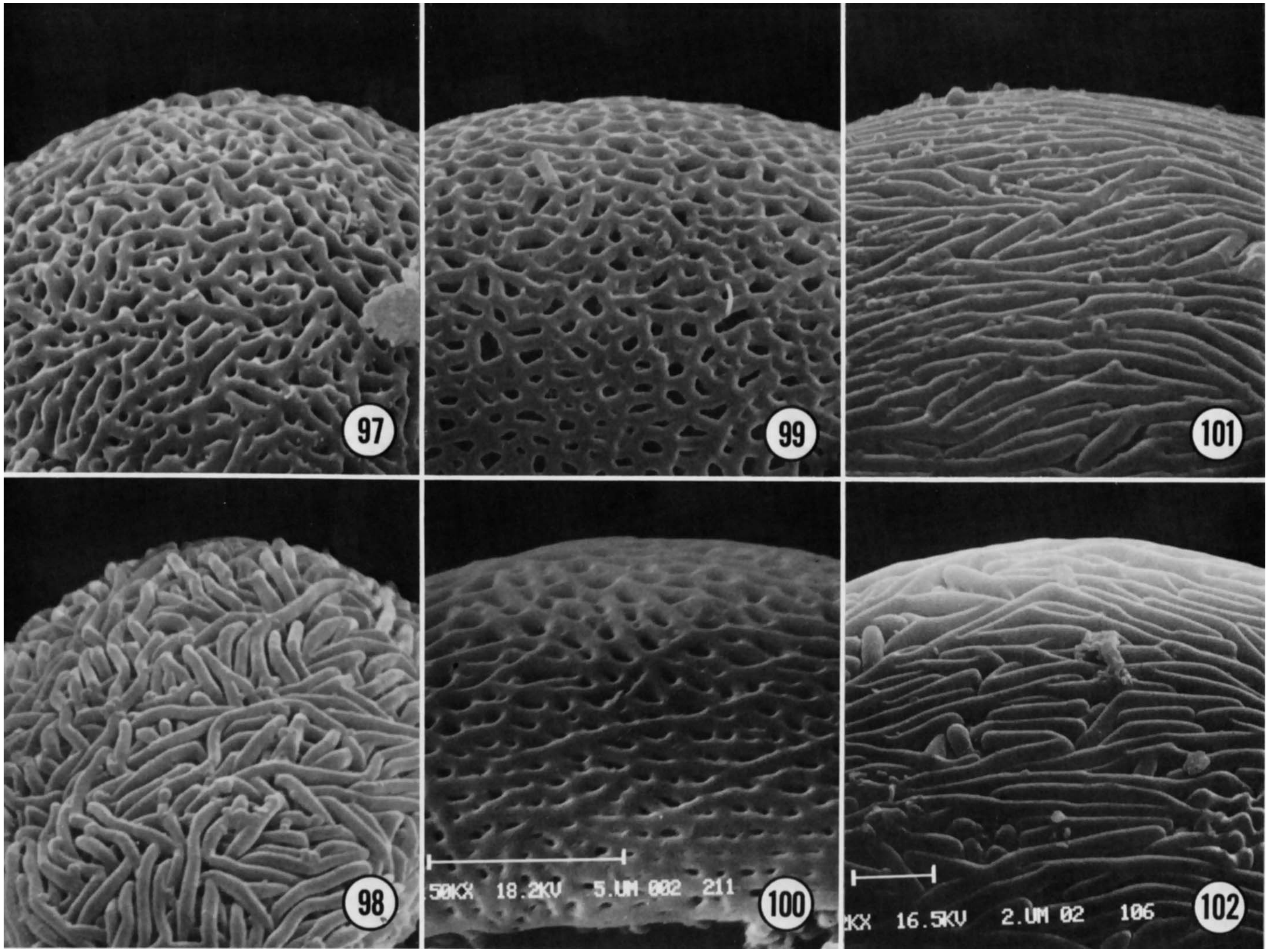
FIGURES 79–84.—Berberidaceae, *Dysosma* and *Podophyllum* pollen, SEM: 79, *Dysosma pleiantha* (Hance) R. E. Woodson, 3-colpate, polar view, × 2000 (Steward & Cheo 210 GH, China); 80, *D. pleiantha*, 3-colpate, equatorial view, × 2000 (same collection); 81, *Podophyllum hispidum* Hao, 3-colpate, equatorial view, × 2000 (T. T. Yu 15977 A, China); 82, *P. hexandrum* Royale, rhomboidal tetrad, × 1500 (Rock 12424 GH, China); 83, *P. hexandrum*, tetrahedral tetrad, × 1415 (Rock 12259 US, China); 84, *P. hexandrum*, ektexine surface, × 7500 (same collection). (Micrographs reduced to 74%.)



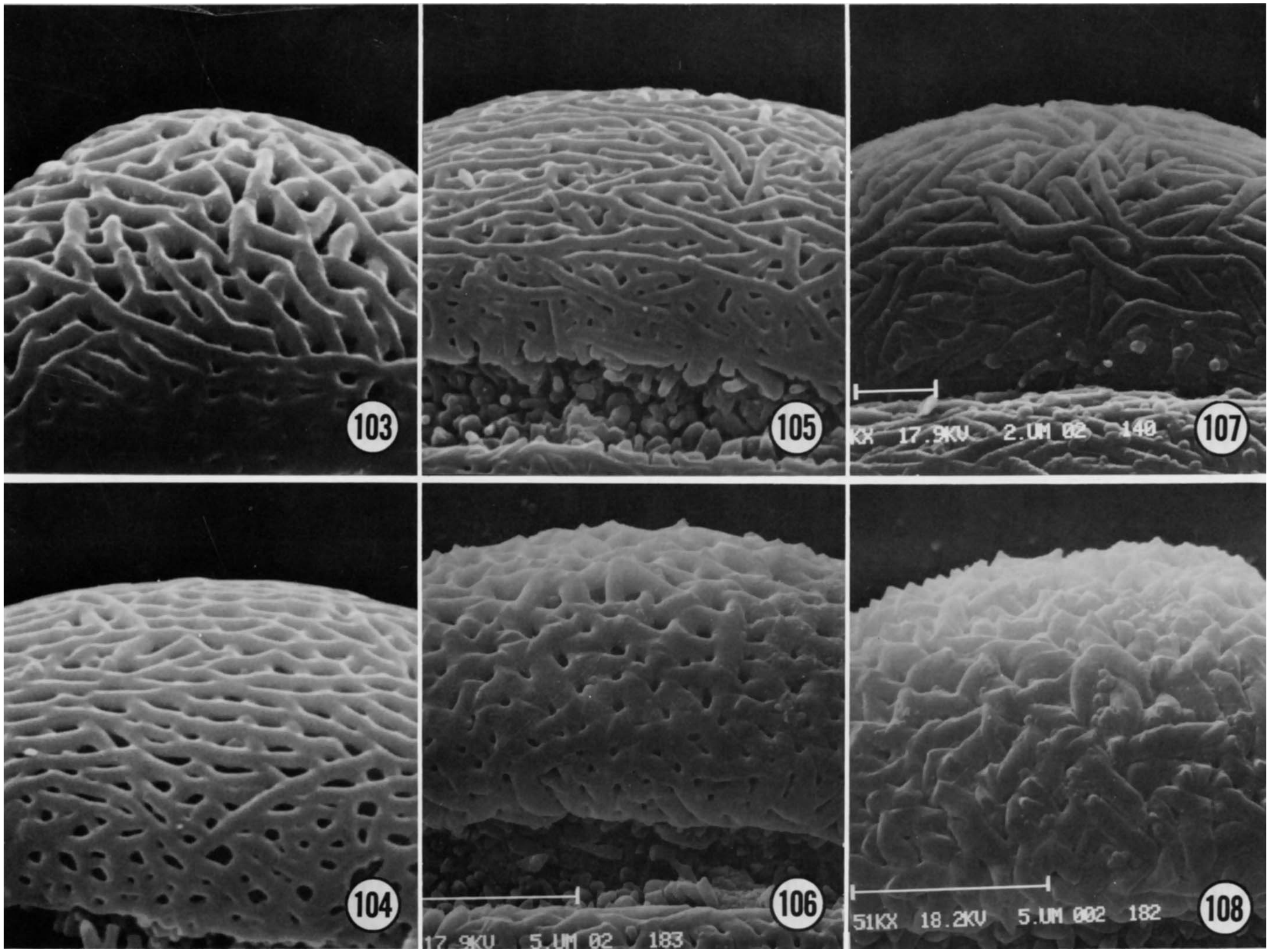
FIGURES 85–90.—Berberidaceae, *Diphylleia* and *Nandina* pollen, SEM: 85, *Diphylleia cymosa* Michaux, 3-colpate, equatorial view, × 2200 (Pollard s.n. 16 May 01 US, North Carolina); 86, *D. cymosa*, ektexine surface, × 5000 (Braun s.n. 25 Apr 27 US, Tennessee); 87, *D. sinensis* Li, 3-colpate, equatorial view, × 2250 (Rock 4230 US, China); 88, *D. sinensis*, ektexine surface, × 5300 (same collection). 89; *Nandina domestica* Thunberg, 3-colpate, equatorial view, × 2500 (Tai & Class 4034 US, China); 90, *N. domestica*, ektexine surface, × 8400 (same collection). (Micrographs reduced to 73%.)



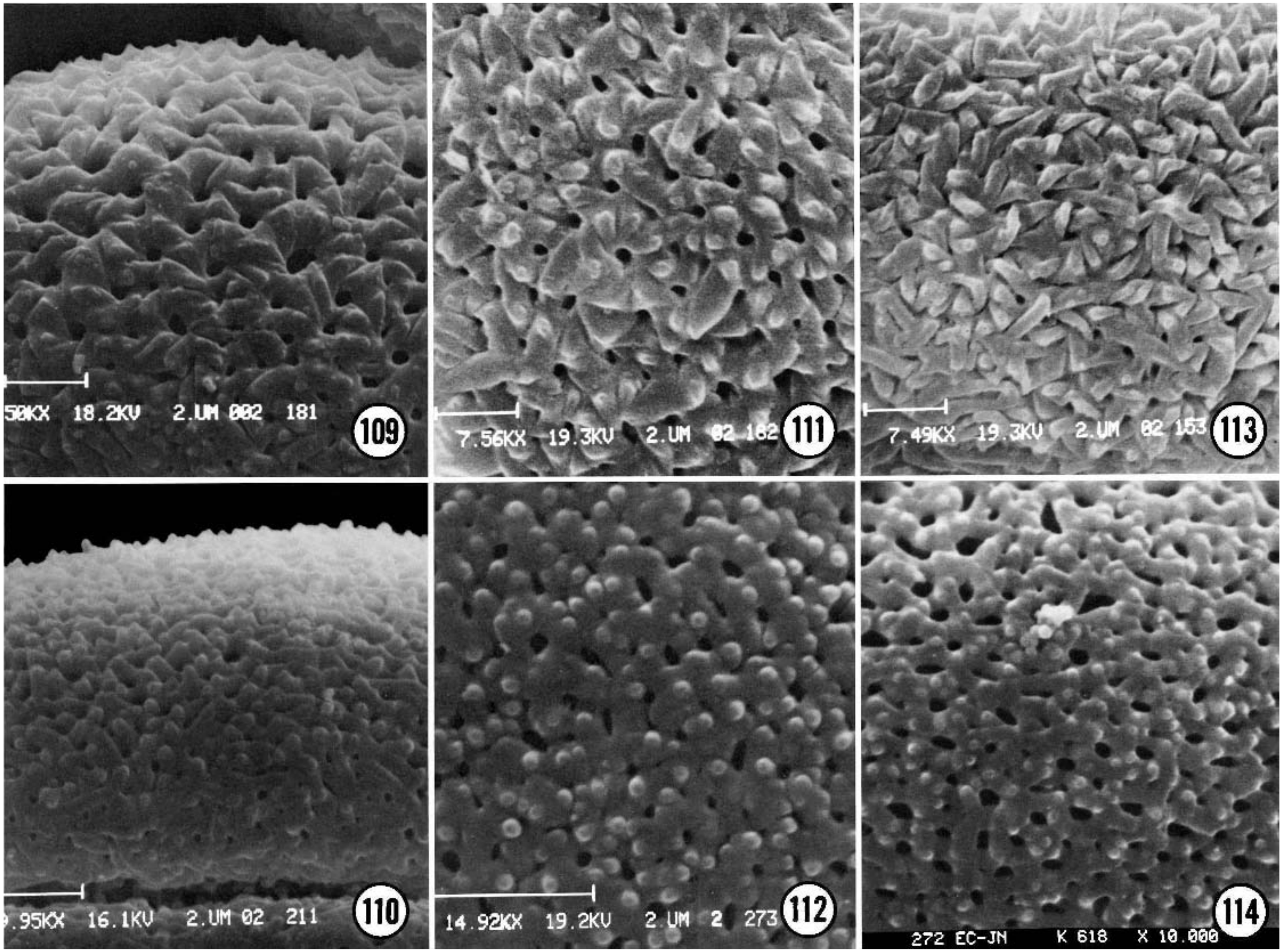
FIGURES 91–96.—Berberidaceae pollen, view of ektexine surface, SEM: 91, *Podophyllum hispidum* Hao, × 5000 (T. T. Yu 15977 A, China); 92, *Dysosma pleiantha* (Hance) R. E. Woodson, × 5000 (Steward & Cheo 210 GH, China); 93, *Jeffersonia dubia* (Maximowicz) Bentham & Hooker, × 7520 (Mrs. R. K. Smith s.n. 30 May 38 US, Korea); 94, *Epimedium membranaceum* K. Meyer, × 7500 (Forrest 25471 US, China); 95, *Jeffersonia dubia* (Maximowicz) Bentham & Hooker, × 7500 (Palczevsky 3616 US, U.S.S.R.); 96, *Achlys triphylla* (Smith) De Candolle, × 7500 (Evert s.n. 1920 US, Washington). (Micrographs reduced to 75%.)



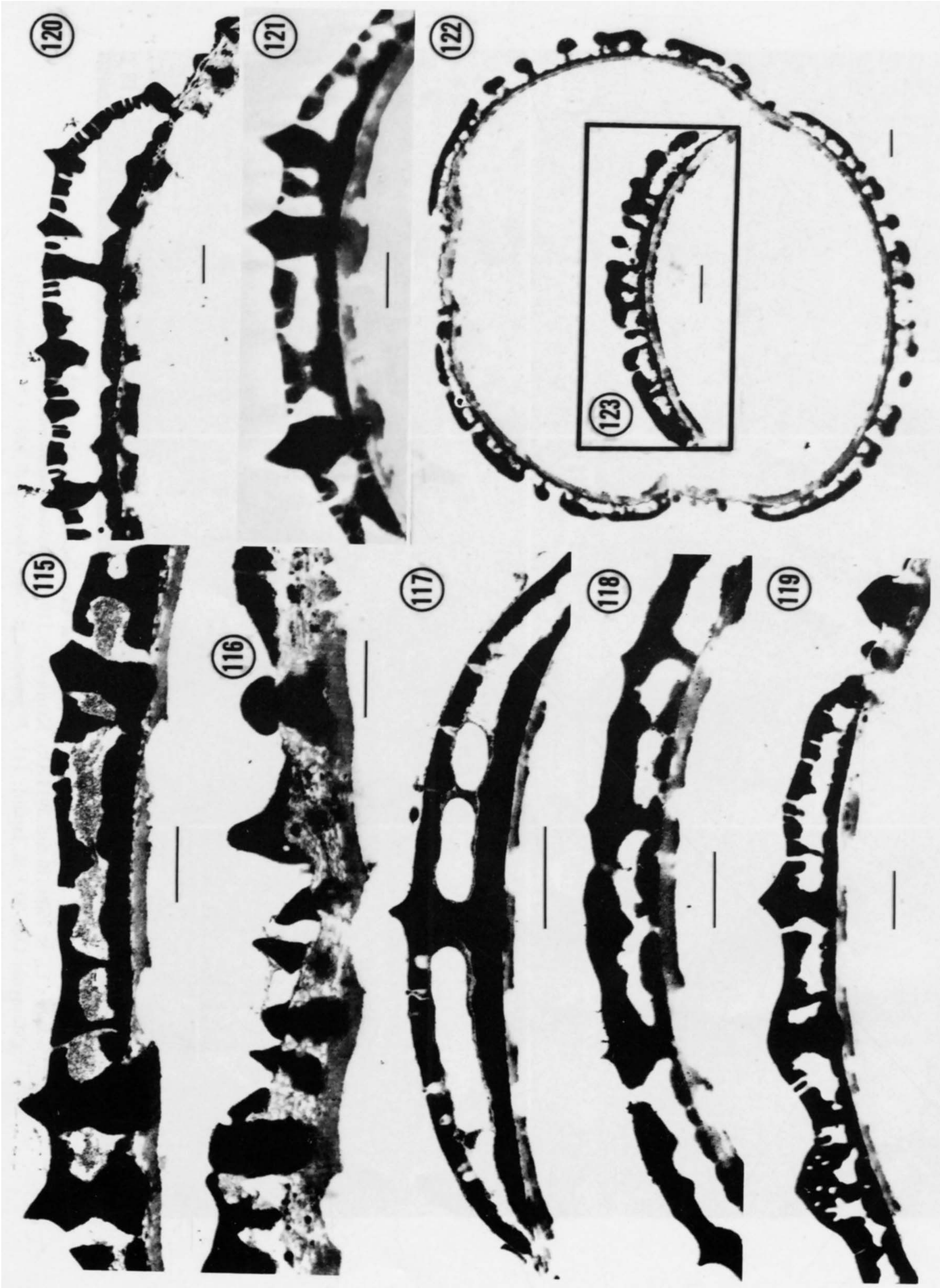
FIGURES 97–102.—Berberidaceae pollen, view of ektexine surface, SEM: 97, *Vancouveria chrysantha* Greene, × 7500 (Thompson 4605 US, Oregon); 98, *Jeffersonia diphylla* (L.) Persoon, × 7500 (Shafer & Miller 180a US, Pennsylvania); 99, *Epimedium sagittatum* (Siebold & Zuccarini) Maximowicz, × 7500 (Anon. 1314880 US, Japan); 100, *Vancouveria hexandra* Morren & Decaisne, × 7500 (Ebert s.n. Aug 1920 US, Washington); 101, *V. planipetala* Calloni, × 7500 (Constance 2514 US, California); 102, *V. planipetala*, × 7520 (Hoover 5046 US, California). (Micrographs reduced to 77%.)



FIGURES 103 108.—Berberidaceae and *Hydrastis* pollen, view of ektexine surface, SEM: 103, *Hydrastis canadensis* L., × 10,000 (Hardin 610 US, Arkansas); 104, *Epimedium alpinum* L., × 7500 (Porta s.n. Jun 1894 US, Italy); 105, *E. brevicornu* Maximowicz, × 7500 (Rock 12302 US, China); 106, *Podophyllum peltatum* L., × 7530 (Rowell, York & Tharp 47171 US, Texas); 107, *Jeffersonia diphylla* (L.) Persoon, × 7500 (Baxter s.n. 15 Apr 11 US, New York); 108, *P. peltatum* L., × 7510 (McDougall 1231 US, Mississippi). (Micrographs reduced to 77%.)



FIGURES 109–114.—Berberidaceae pollen, view of ektexine surface, SEM: 109, *Podophyllum peltatum* L., × 7500 (Braun 3911 US, Kentucky); 110, *Epimedium sempervirens* Nakai, × 10,000 (Masayuki Oue 33 US, Japan); 111, *P. peltatum*, × 7560 (McDougall 1231 US, Mississippi); 112, *E. grandiflorum* Morren, × 14,920 (Togasi 1031 US, Japan); 113, *P. peltatum*, × 7490 (Crampton 76 US, Illinois); 114, *E. cremeum* Nakai, × 10,000 (Kirino 618 US, Japan). (Micrographs reduced to 79%.)



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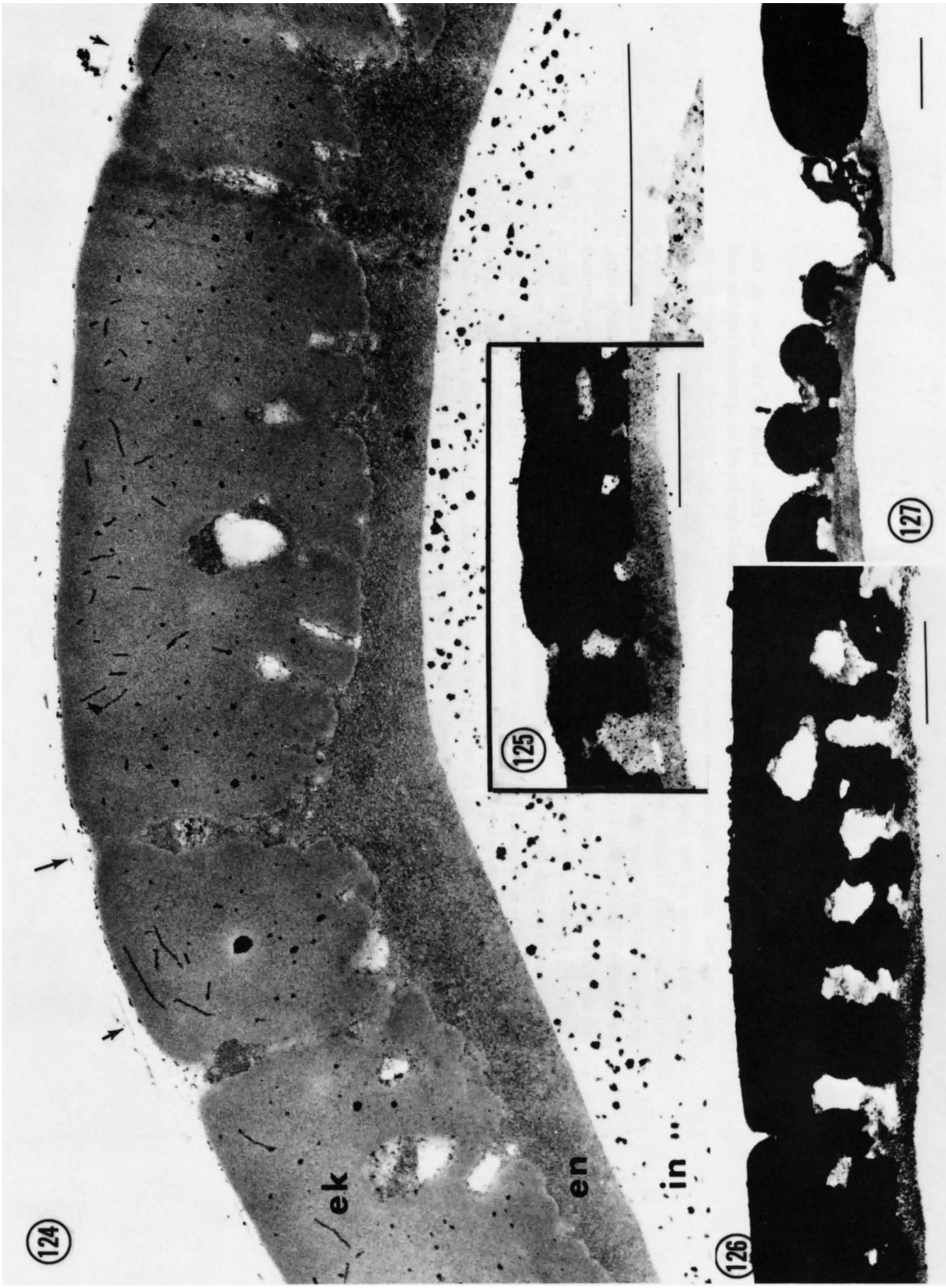
FIGURES 115–123.—Ranunculaceae and *Hydrastis* pollen, TEM. Most of the taxa in the Ranunculacae were similar in thin section: an endexine well developed in aperture regions and disrupted but still conspicuous in non-aperture regions; foot layer relatively uniform in the sense that none of the taxa examined had very thin or very thick foot layers; prominent columellae, which in some taxa appear to penetrate the endexine in the apertures (see discussion in text as well as Figure 149 of *Epimedium diphyllum*, Figure 154 of *E. cremeum*, Figure 155 of *E. grandiflorum*, Figure 159 of *Vancourveria*, Figure 161 of *V. hexandra* and Figure 169 of *V. planipetala*); tectum uniform or average in thickness, but with perforations and spines, the latter sometimes large. 115, *Ranunculus oreophytus*, the massive columellae appear to be continuous with foot layer and tectum, the endexine is well represented but somewhat disrupted, note acetolysis-resistant spongy material in the area between foot layer and tectum, × 12,760; 116, *R. oreophytus*, section through the colpus showing highly lamellate endexine and aperture columellae, which appear to penetrate the endexine, × 12,760; 117, *Clematis heracleifolia*, section through mesopore, note acetolysis resistant material between foot layer and tectum as shown in Figure 115, × 16,240; 118, *Glaucidium palmatum*, an example of this family with reduced columellae, × 12,650; 119, *Batrachium aquatile*, typical Ranunculaceae structure, × 9900; 120, *Hepatica transsilvanica*, the tectum is commonly channeled-perforate, a portion of the colpus (at the right) contains aperture columellae as described in Figure 116 (see also right side of Figure 119), × 6120; 121, *Hamadryas magellanica*, typical Ranunculaceae structure (compare with Figures 115, 119), × 9570; 122, *Hydrastis canadensis*, low magnification, median section more or less, as discussed in text note the lack of similarity to other Ranunculaceae pollen grains (Figures 115–121) and general overall similarity to *Jeffersonia dubia*, Figure 173, and *Vancouveria hexandra*, Figure 163, × 4100; 123, *H. canadensis*, see legend comments to Figure 122, × 6120. (Scales equal 1 μm.)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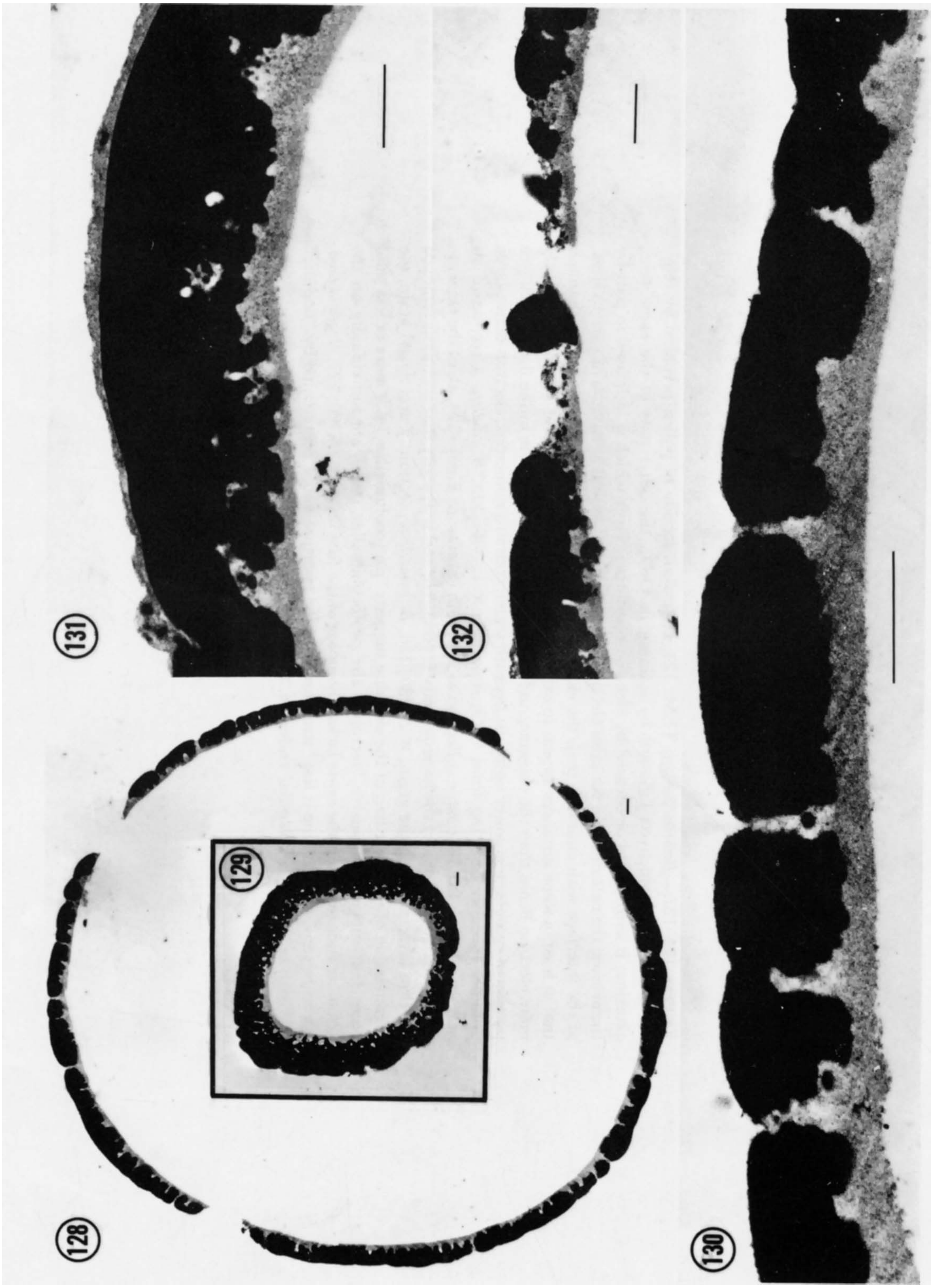
FIGURES 124–127.—*Berberis* pollen, TEM: 124, *B. fendleri*, section of pollen prepared by rehydration in glutaraldehyde followed by staining in OsO_4, the outer part of the exine (viz., ektexine) is surrounded or encased by electron-translucent layer which is indicated in part by the arrows; the ektexine (ek) contains electron-dense material as well as cavities of various sizes; at the interface with endexine (en), the ektexine is very irregular and contains deep channels that at least in some instances appear to extend to the surface; the endexine is granular, slightly more electron dense than the ektexine, and has a smooth inner wall; the intine (in) is thick (see portion of cytoplasm at lower right just beneath scale), contains numerous, electron-dense, large granules (possibly resulting from OsO_4 staining), × 12,120; 125, *B. fendleri*, a section of an acetolyzed grain from the same collection as above, in contrast to Figure 124, all of the ektexine is very electron dense and the heterogeneity is obscured, and it appears that acetolysis removed the thin layer encasing the grain, × 21,280; 126, *B. grandiflora*, section of acetolyzed grain, the organization of the inner half of the ektexine suggests "protocolumellae," the more or less solid outer half suggests a massive "tectum," the protocolumellae terminate individually on the granular endexine, thus the exine lacks a homolog of the foot layer, × 16,720; 127, *B. grandiflora*, aperture view, the ektexine is less "structured" in the aperture and is represented by "nodules" or "islands" above the granular endexine, × 11,890. (Scales equal 1 μm.)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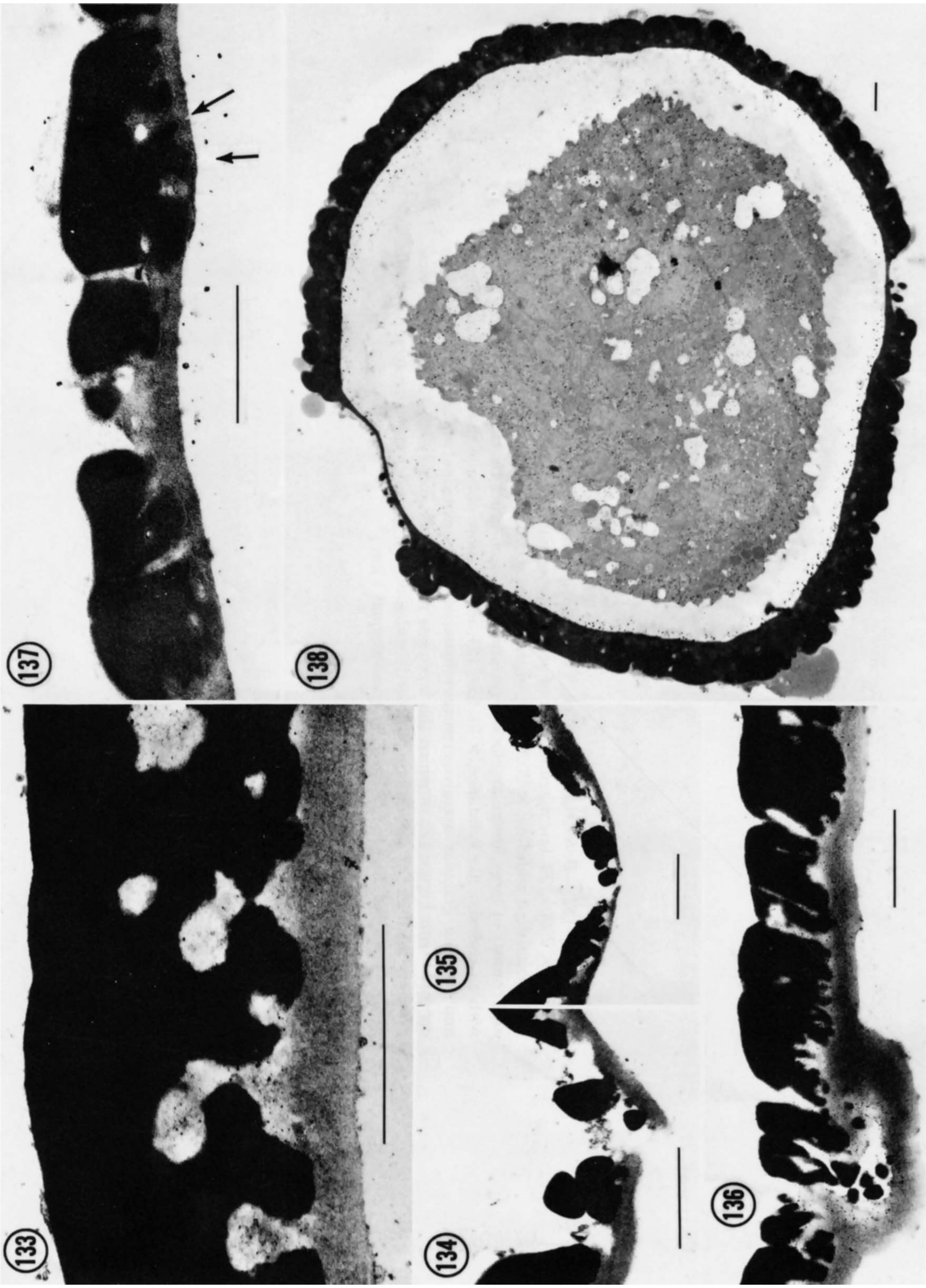
FIGURES 128–132.—*Berberis ilicifolia* pollen, TEM: 128, low magnification of entire grain, median section, × 2590; 129, low magnification of very oblique section enhancing a massive ektexine and a consistent endexine, × 2000; 130, in this radial section, the ektexine is not continuous and consists of large, irregular blocks separated from each other by channels partially filled with an endexine-like substance, × 21,460; 131, section more oblique than in previous figure and showing granular acetolysis-resistant material above ektexine surface, × 13,340 (this contrasts with Figure 125 in which the layer was removed by acetolysis); 132, aperture view showing "nodules" of ektexine on and partly embedded in, granular endexine (compare with *Berberis grandiflora*, Figure 127), × 9180. (Scales equal 1 μm.)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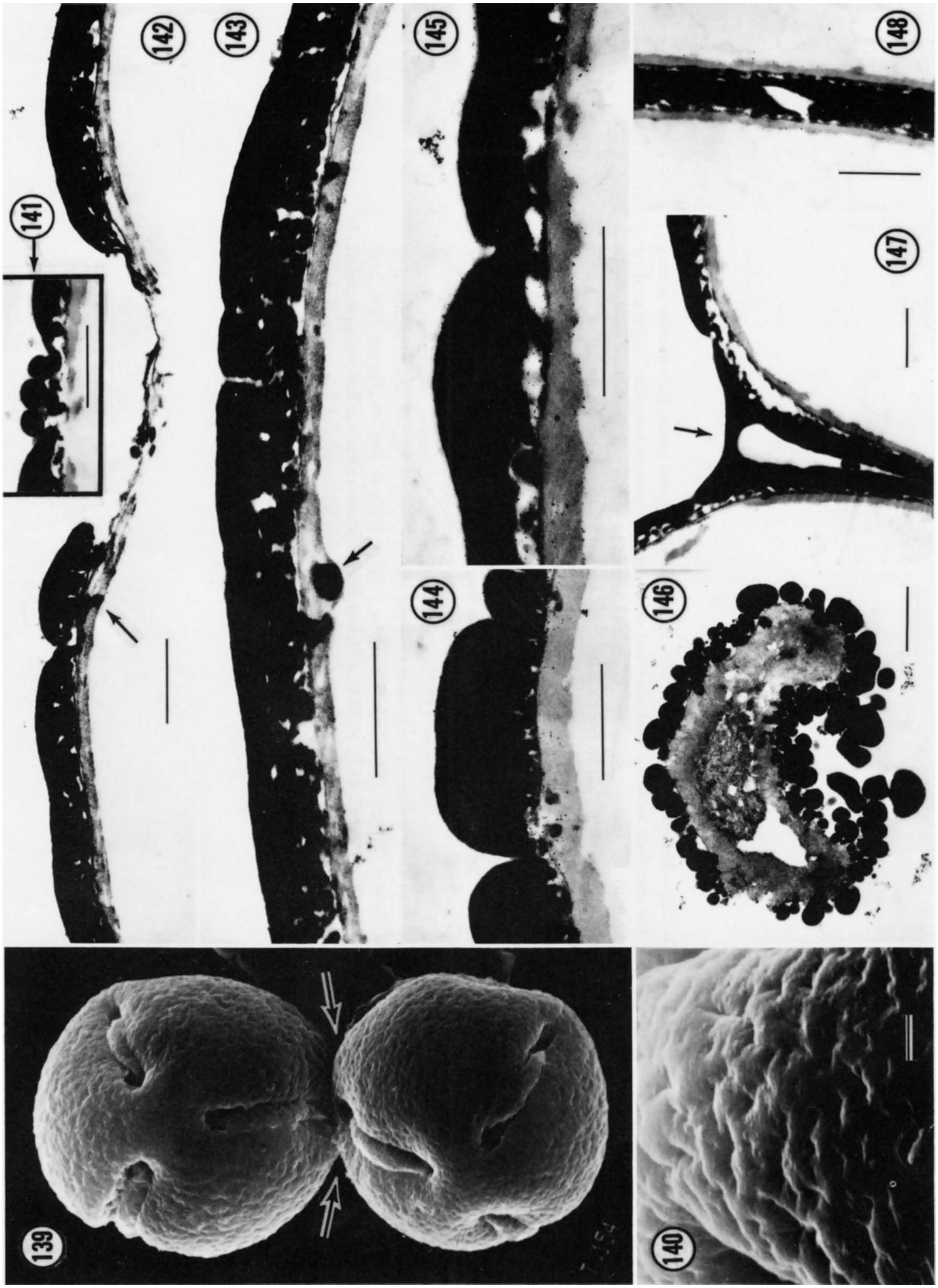
FIGURES 133–138.—*Mahonia* pollen, TEM: 133, *M. nervosa*, acetolyzed grain, the ektexine is very irregular at the interface with the endexine but does suggest "protocolumellae" separated by cavities filled with an endexine-like material; the endexine proper is granular, uniform in electron density (relative to that in the cavities), and very smooth on the inner wall, × 35,340; 134 and 135, *M. nervosa*, views of apertures showing granular endexine supporting "islands" of ektexine (compare with Figure 127 of *Berberis grandiflora*, Figure 132 of *B. ilicifolia*, and Figure 141 of *Ranzania japonica*), 134: × 16,740, 135: × 10,620; 136, *M. oiwakensis*, the ektexine is commonly fragmented by channels (compare with Figure 130 of *Berberis ilicifolia*), short, irregularly shaped "protocolumellae" are evident at base of ektexine (see legend to Figure 133), × 15,580; 137 and 138, *M. oiwakensis*, rehydrated pollen grains (as described for *Berberis fendleri* in legend to Figure 124), in Figure 137 the "protocolumellae" (arrows), while less clearly differentiated than after acetolysis treatment (compare with Figure 136), are nearly identical to section of *M. nervosa* (Figure 133), *Berberis ilicifolia* (Figure 130), *B. fendleri* (Figure 125), and *Ranzania japonica* (Figures 142, 143), × 3800; 138, low magnification near median view prepared as discussed immediately above, it is noteworthy that the combination of low magnification and lack of acetolysis imparts a nearly amorphous appearance to the exine, × 4900. (Scales equal 1 μm.)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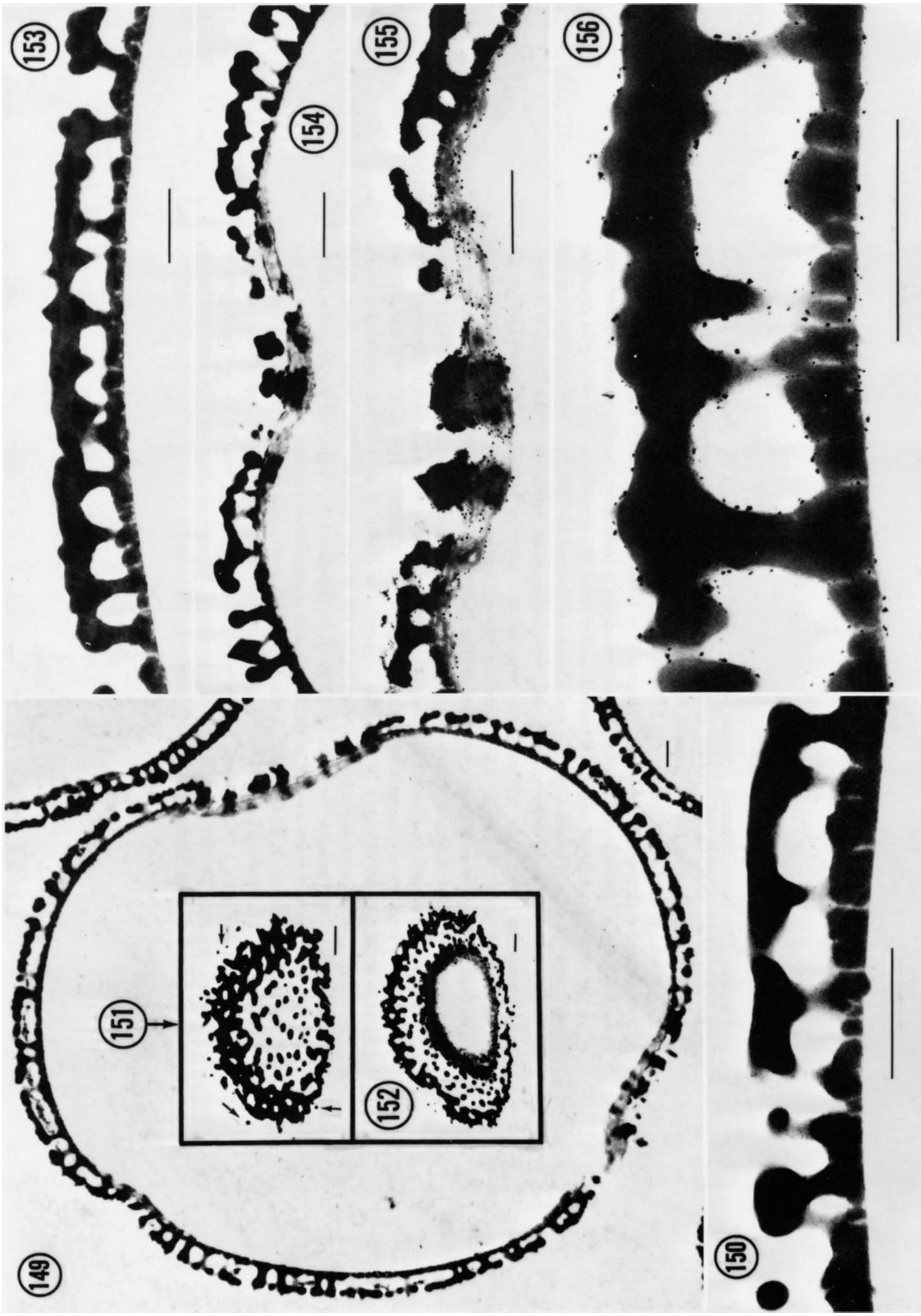
FIGURES 139–148.—*Ranzania japonica* pollen, SEM and TEM: 139, (*Terabayashi 154* KYO, Japan), SEM showing two pollen grains that appear attached (arrows) as dyads, × 1450; 140, (*Terabayashi 154* KYO, Japan), SEM showing psilate-punctate exine surface, × 7500; 141, (Cult. 12 Apr 47 K, England), TEM in colpus showing three granules of ektexine above a disrupted endexine, × 13,650; 142, (Epstein s.n. Cult. US, New York), TEM through colpus and adjacent mesocolpus, the endexine in the colpus is both more lamellate and reduced than in the mesocolpal areas, where it is smooth and regular, the ektexine is very similar in structure to that of *Berberis* (Figures 124–132) and *Mahonia* (Figures 133–138), foot layer, columellae, and tectum are not clearly differentiated, the arrow indicates an extension of the ektexine through the endexine, note that a "foot layer equivalent" appears lamellate or sheet-like in the mesocolpal areas, × 13,630; 143 (same collection), section through mesocolpus, the arrow indicates a free exine globule embedded in the endexine, free exine globules were frequently observed in TEM of *Ranzania* and although not further illustrated in this group of figures they commonly occurred in clusters on the surface of the exine, to left of globule (arrow) is an ektexine extension as discussed in legend to Figure 142, × 21,280; 144, (Cult. K), the massive ektexine and endexine may be, at least in part, the result of an oblique angle of section, × 18,620; 145, (same collection), the ektexine has a very narrow "foot layer," short, thick "columellae" and massive "tectum," × 27,950; 146, (Epstein US), tangential section, illustrating granular nature of exine as well as thick endexine (cytoplasmic remains are also present in the center of the exine), × 10,640; 147, (Cult. K), section is through adjacent exines of a dyad (see Figure 139) and shows a bridge-like connection (arrow) in the distal region (equivalent to region of arrows in Figure 139), note the free exines show a morphology similar to that described for Figure 145, × 9280; 148, (same collection), section of opposed internal walls of dyad indicating a fusion of ektexine surfaces, × 13,650. (Scales equal 1 μm.)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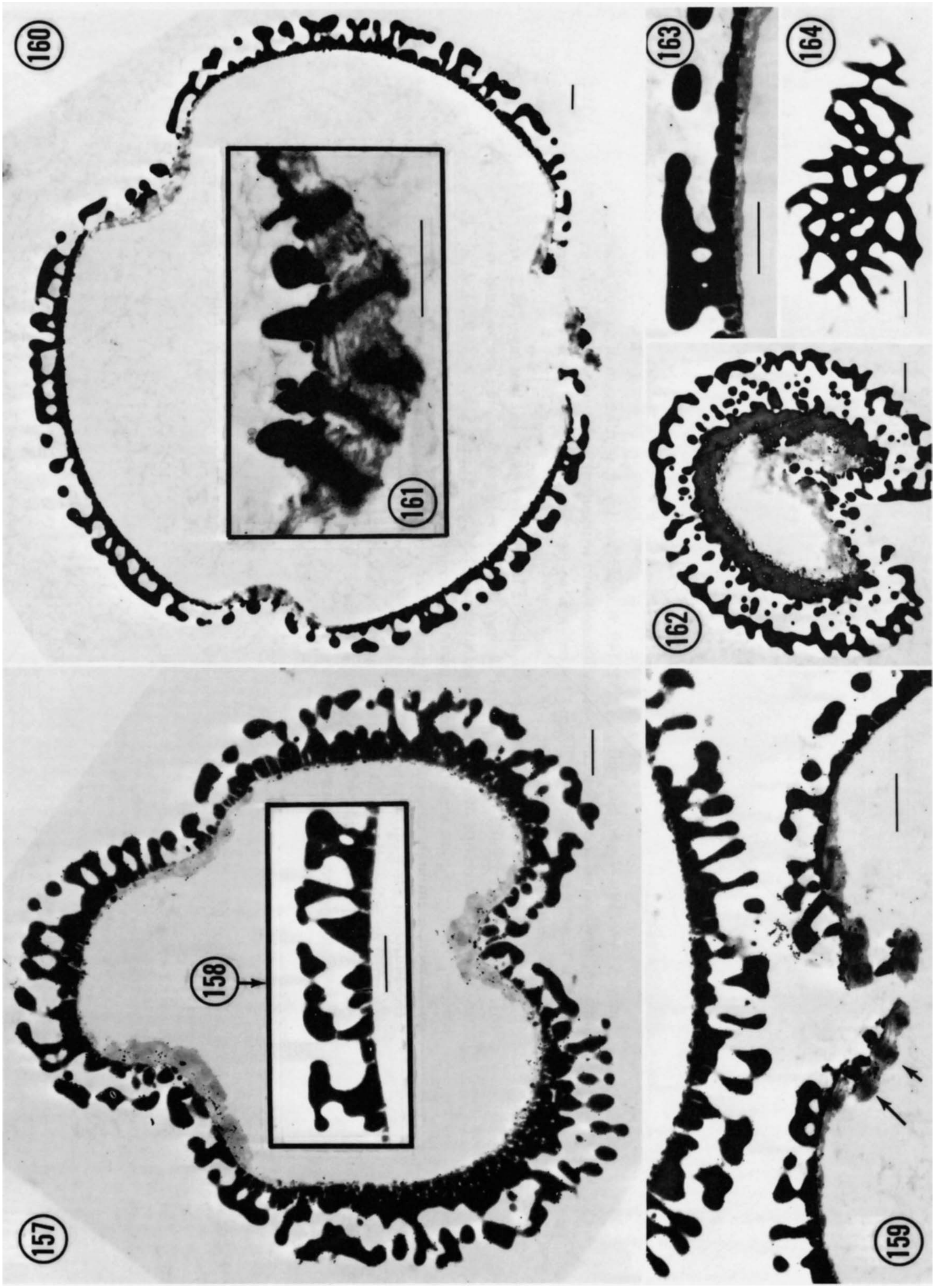
FIGURES 149–156.—*Epimedium* pollen, TEM: 149, *E. diphyllum*, low magnification of section near median, mesocolpus shows foot layer with channels and without an endexine while the colpus shows a lamellate endexine penetrated by columellae (see also *Vancouveria chrysantha*, Figure 159, *V. hexandra*, Figures 160, 161, and *V. planipetala*, Figure 169), × 4400; 150, *E. brevicornu*, section through mesocolpus illustrating highly channeled foot layer, × 3800; 151, *E. cremeum*, tangential section at and slightly beneath exine surface, the arrows indicate cross sections of free tips of tectal rods illustrated by SEM (see Figure 114), × 4930; 152, *E. cremeum*, oblique section including endexine in mesocolpal region, × 3060; 153, *E. cremeum*, radial section through mesocolpus, small peak in tectum probably represents longitudinal section through a free tip of a rod, × 12,880; 154, *E. cremeum*, colpus showing lamellate endexine perforated by columellae, × 10,080; 155, *E. grandiflorum*, colpus similar to Figure 154, × 13,340; 156, *E. grandiflorum*, section of mesocolpus with same structure as in Figures 150 and 153, × 36,400. (Scales equal 1 μm.)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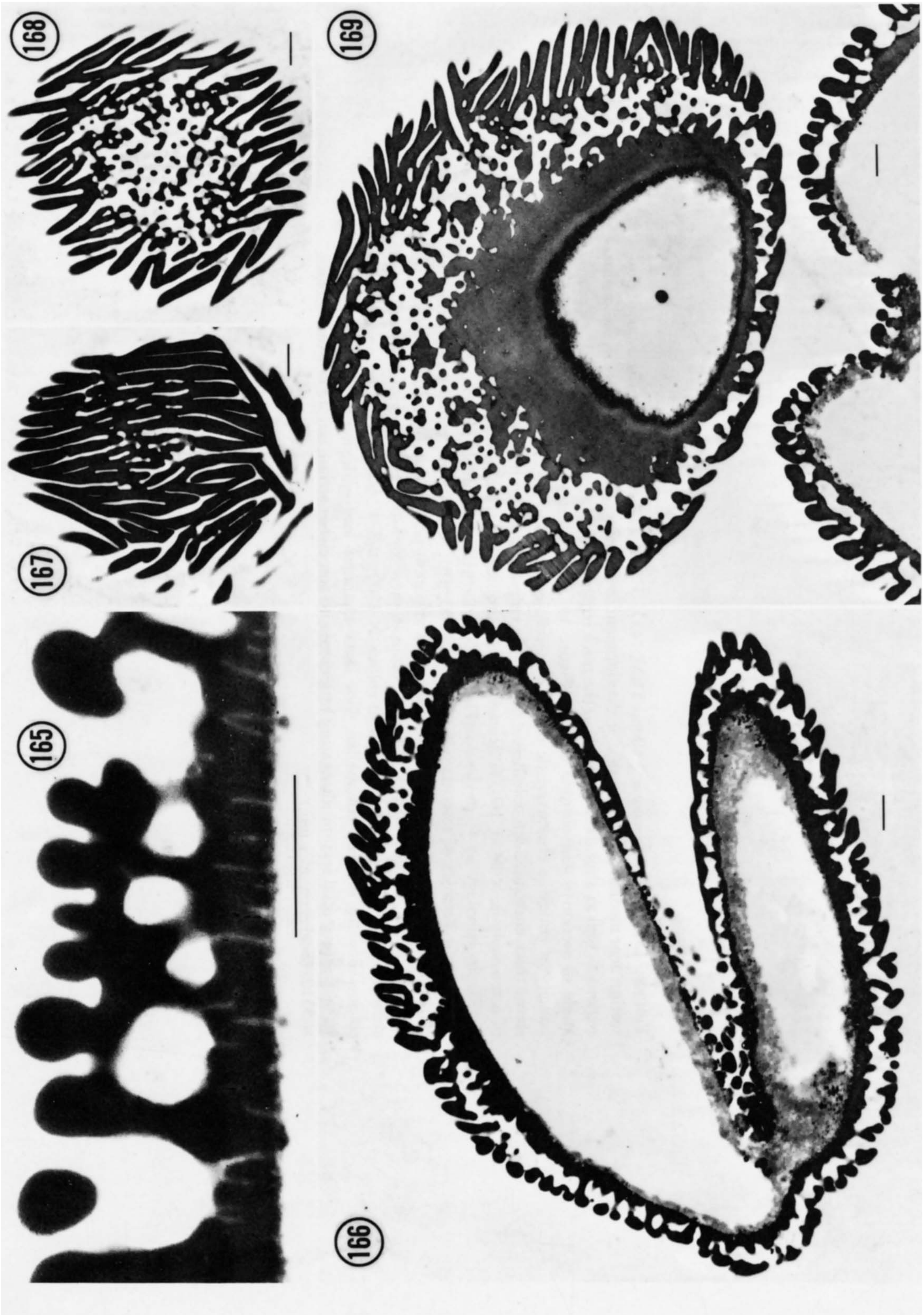
FIGURES 157–164.—*Vancouveria* pollen, TEM: 157, *V. chrysantha*, low magnification oblique section near median showing endexine development in colpal regions and absence in mesocolpal regions as well as abundant channels in the thick irregular foot layer, × 7380; 158, *V. chrysantha*, angle of section is less oblique than in Figure 157, and illustrates foot layer channels and paucity of endexine characteristic of the mesocolpus, × 9430; 159, *V. chrysantha*, lower grain shows thick endexine with columellae (arrows) in colpus, upper grain shows an oblique section of a mesocolpus, × 9430; 160, *V. hexandra*, low magnification cross section at median showing similar morphology as *V. chrysantha* (Figure 157), foot layer channels are abundant but less conspicuous because of low magnification, × 4000; 161, *V. hexandra*, radial section through colpus showing lamellar nature of endexine and apparent penetration by columellae (also see Figure 159), × 15,580; 162, *V. hexandra*, oblique view showing cross sections of foot layer channels and endexine accumulation in colpus, × 4500; 163, *V. hexandra*, section parallel with colpus showing reduced columellae, foot layer channels and endexine, × 11,890; 164, *V. hexandra*, tangential section illustrating reticulate and somewhat striate nature of exine surface, × 5510. (Scales equal 1 μm.)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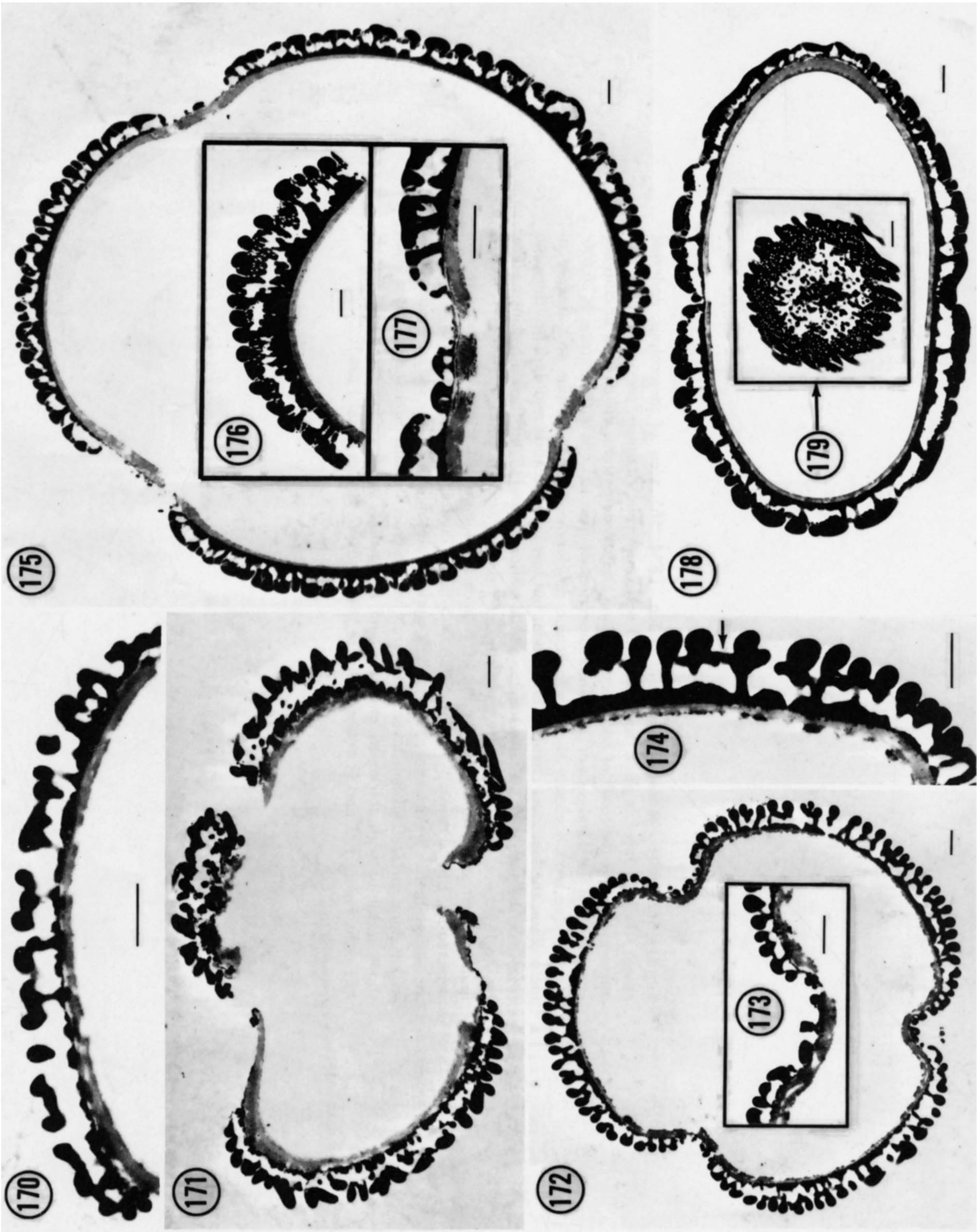
FIGURES 165–169.—*Vancouveria planipetala* pollen, TEM: 165, view of mesocolpus, endexine absent, the foot layer is thick, irregular and with numerous channels, the inconsistent and uneven tectum is the result of both section plane and striate pattern, the circular or club-like appearance of the distal ends of the columellae represent cross sections of these striae, × 26,650; 166, oblique section clearly showing endexine development in the colpus and absence in mesocolpus; the foot layer channels are present but low magnification and dark printing tend to obscure them, × 5460; 167 and 168, tangential sections at and slightly beneath exine surface, Figure 167 agrees with the mostly parallel exine striae depicted in SEM, Figures 37, 38, 101, and 102, just as the tangential section of *V. hexandra* (Figure 164) agrees with the tectum depicted in SEM, (Figures 39, 40, and 100), × 5760, in Figure 168 cross sections of columellae are surrounded by exine striae, × 5290; 169, upper grain highly oblique section emphasizing striate exine surface and foot layer with barely visible cross sections of channels; lower grain shows a colpus with thickened endexine and columellae, as described previously (see *V. chrysantha*, Figure 159, and *V. hexandra*, Figure 161), × 5460. (Scales equal 1 μm.)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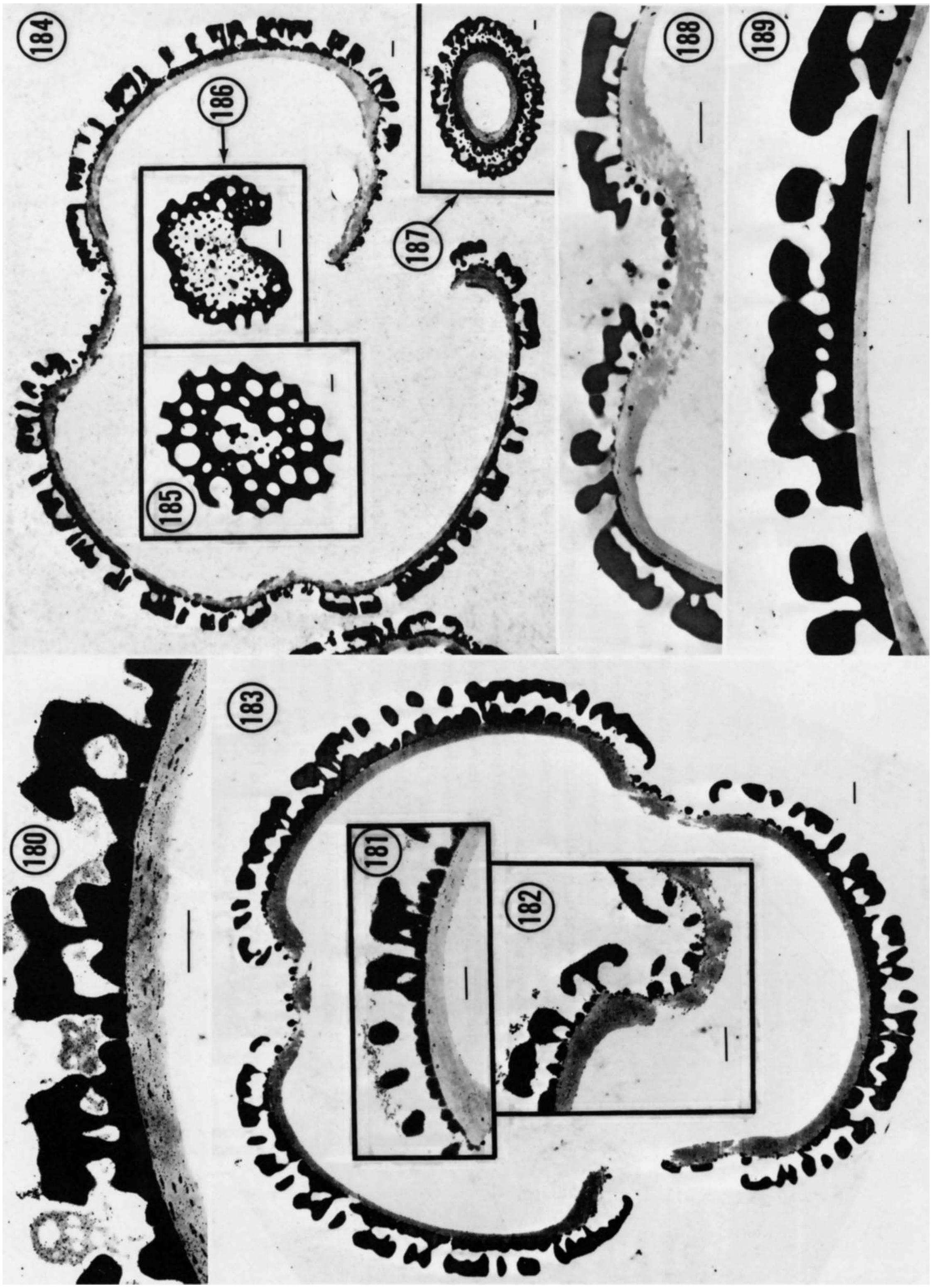
FIGURES 170–179.—*Jeffersonia* and *Achlys* pollen, TEM: 170, *J. diphylla*, mesocolpal view, note the well developed and essentially uniform endexine which contrasts with the highly irregular foot layer, × 10,080 (Shafer & Miller 180a US, Pennsylvania); 171, *J. diphylla*, low magnification view including portions of each mesocolpal region, × 5000 (same collection); 172, *J. dubia*, low magnification, median section, the endexine is present in mesocolpus but is irregular; the beaded appearance of the tectum is due to the mostly parallel striae being cut perpendicular to the long axis, × 3780 (Palczevsky 3616 US, U.S.S.R.); 173, *J. dubia*, section in colpus region indicates ektexine elements do not penetrate endexine as is commonly noted for *Epimedium* and *Vancouveria*, × 6200 (same collection); 174, *J. dubia*, mesocolpal-colpal (at bottom) view, arrow indicates "inner" striae, note the regular and consistent foot layer and endexine, × 9120 (same collection); 175, *Achlys triphylla*, low magnification median section, the endexine is very narrow in the mesocolpus and thicker in the colpus, the foot layer is thicker than the endexine and highly irregular, × 4300 (Calder & Savile 8323 US, Canada); 176, *A. triphylla*, mesocolpal section, the numerous openings in the tectum, reflect packing of striae as discussed in text, × 4600 (same collection); 177, *A. triphylla*, section in colpus showing reduced ektexine over endexine (see comments to Figure 173 above), × 8410 (same collection); 178, *A. japonica*, low magnification of a near equatorial section (approximately perpendicular to section in Figure 175), × 4000 (Terabayashi 209 KYO, Japan); 179, *A. japonica*, in this tangential view the openings (see legend to Figure 176) are abundant in the ektexine, × 4060 (same collection). (Scales equal 1 μm.)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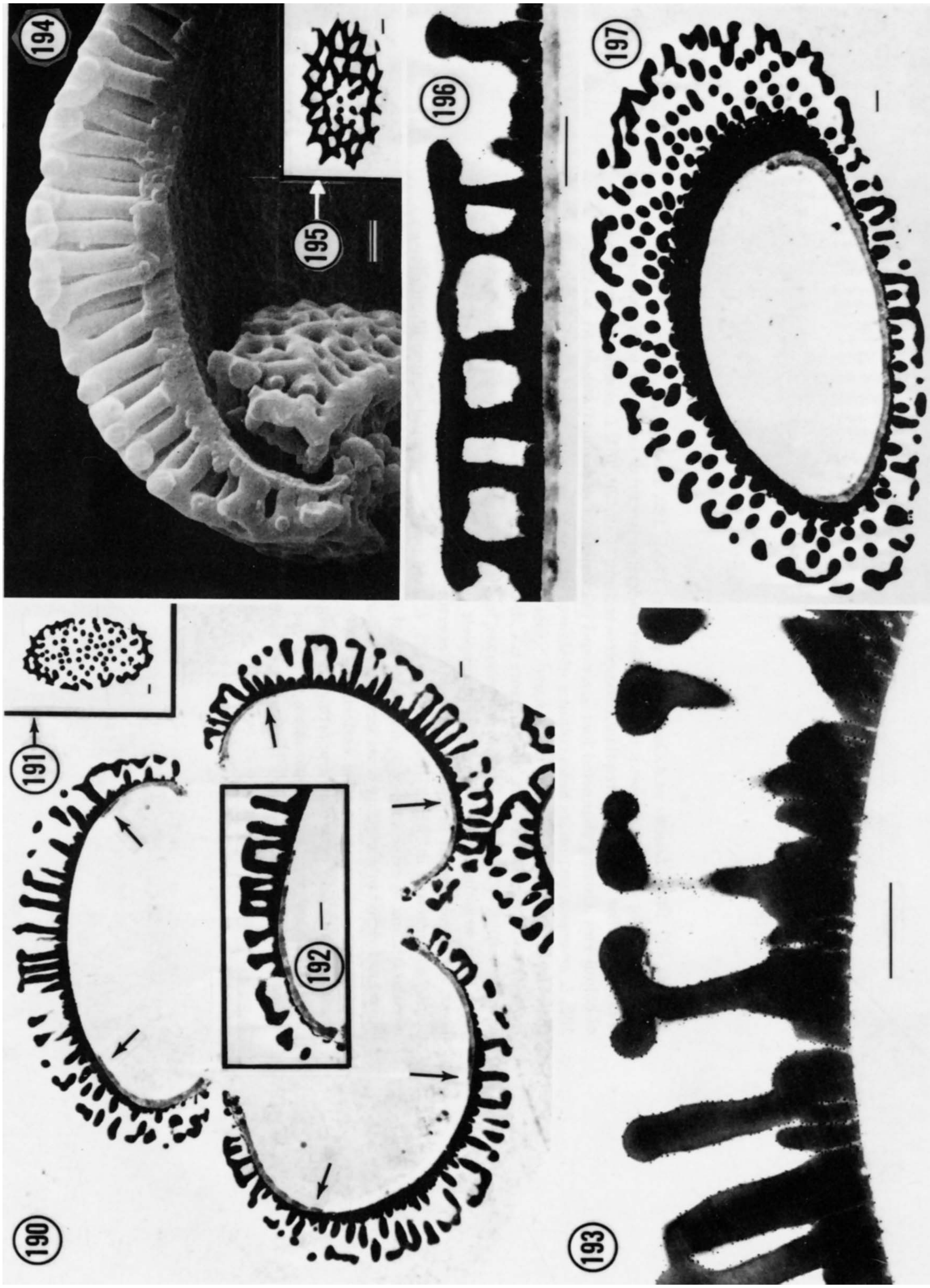
FIGURES 180–189.—*Leontice* and *Caulophyllum* pollen, TEM: 180, *L. armeniaca*, section of mesocolpus showing a thick, uniform, and lamellate endexine, irregular foot layer with channels, short columellae and thick, irregular, incomplete tectum, × 10,120; 181, *L. armeniaca*, at margin of colpus emphasizing channeled foot layer and thickening of endexine (to the left), × 5880; 182, *L. armeniaca*, section includes colpus and shows ektexine fragments on surface of endexine, these fragments appear joined by a narrow foot layer, × 5880; 183, *L. leontopetalum*, low magnification, median section, the endexine is well developed in non-apertural regions as well as in the colpus, × 3010; 184, *Caulophyllum robustum*, low magnification median section illustrating same basic structure as in Figure 183: incomplete tectum, short columellae, channels in foot layer, endexine present in non-aperture and aperture regions, note trace of foot layer across colpus as suggested in Figure 182, × 2800; 185, *C. thalictroides*, tangential section illustrating circular lumina of exine surface as shown in SEM (see Figure 60), × 2990; 186, *C. thalictroides*, tangential view but including cross sections of columellae, × 2990; 187, *C. thalictroides*, oblique cross section indicating uniform endexine, × 1400; 188, *C. thalictroides*, colpal view showing thickened lamellate endexine supporting fragments of ektexine, × 6480; 189, *C. thalictroides*, mesocolpal view similar to *L. armeniaca* in Figure 180, *L. leontopetalum* in Figure 183 and *C. robustum* in Figure 184, × 11,310. (Scales equal 1 μm.)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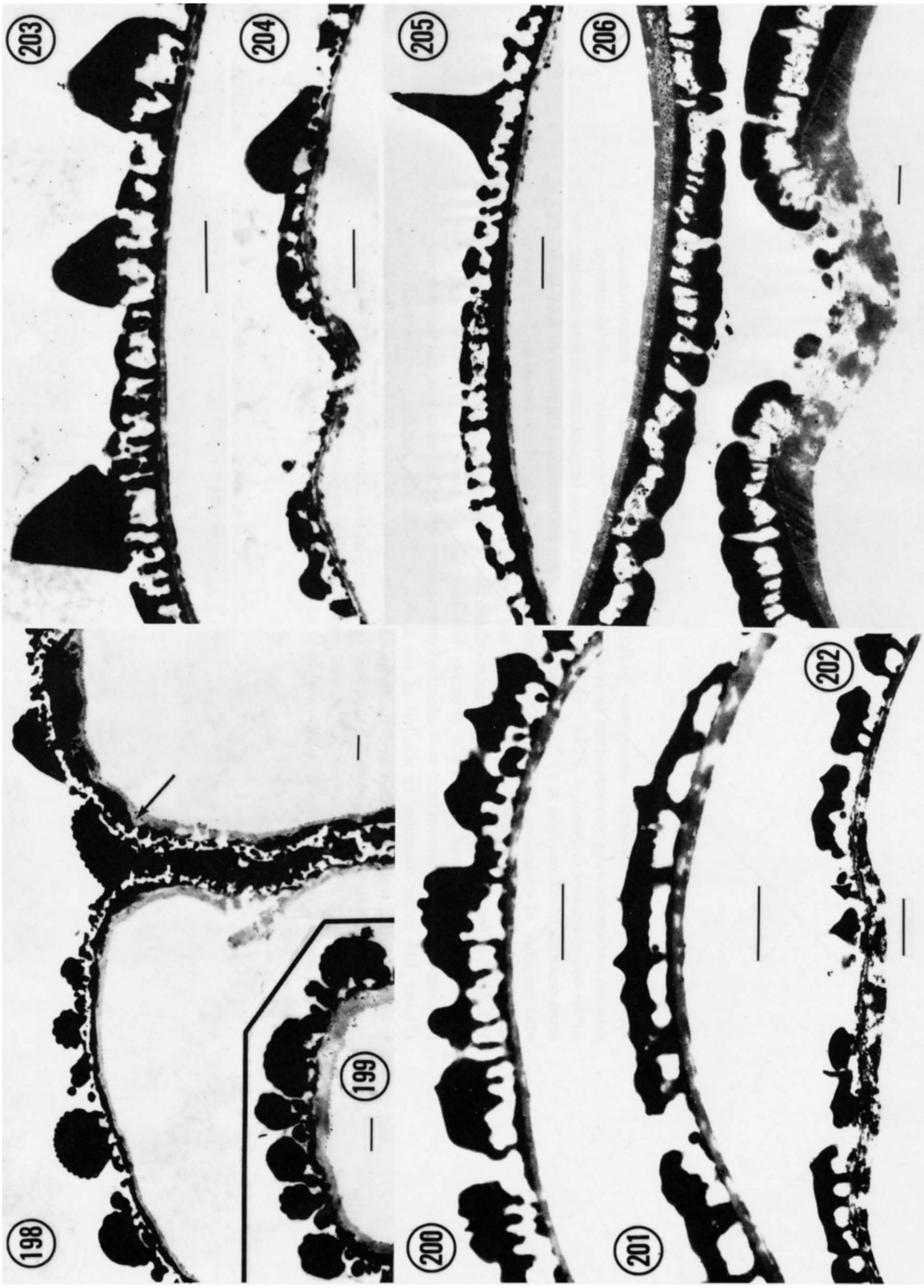
FIGURES 190–197.—*Bongardia chrysogonum* pollen, TEM and SEM: 190, low magnification median section showing portions of the three apertures, note that the endexine is only developed in the colpal regions (arrows), × 2730; 191, tangential section just beneath tectum and showing cross sections of columellae, × 1400; 192, section of colpus emphasizing thinning of foot layer and presence of endexine, × 4370; 193, mesocolpal view showing thick irregular foot layer containing numerous channels, an endexine is not present in this area of the exine, × 15,960; 194, SEM of fractured grain, the long, slender columellae in the mesocolpus and thick, irregular foot layer correlate well with TEM (Figures 190 and 193), × 6060; 195, tangential section showing reticulate exine surface, note identical correlation with SEM surface in fractured grain (Figure 194, exine fragment to the left of the scale), × 2530; 196, section parallel with the colpus showing well developed and uniform endexine, although not clearly shown the foot layer has channels (see Figure 193), note that in the colpus the columellae are reduced (as in Figures 190 and 194 which show both colpal and mesocolpal regions), × 11,310; 197, highly oblique section that includes a substantial area of a colpus (bottom half of TEM), × 3700. (Scales equal 1 μm.)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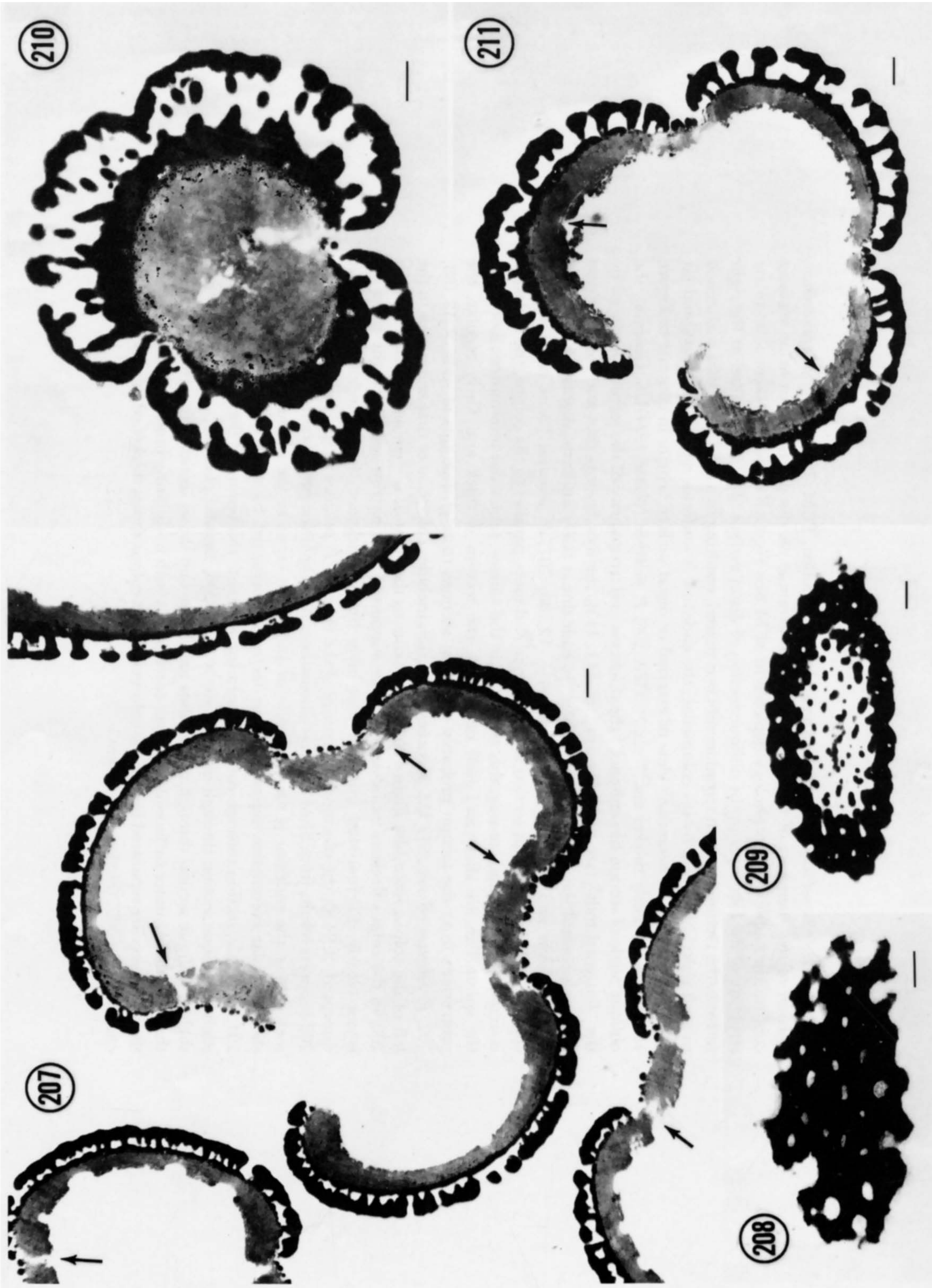
FIGURES 198–206.—*Podophyllum*, *Diphylleia* and *Dysosma* pollen, TEM: 198, *Podophyllum hexandrum*, portion of two members of mature tetrad, some gemmae on the distal or free exine surfaces confirm the ripple-like morphology depicted in SEM (see Figure 84), note thickened, undulate structure of the foot layer in the oblique section of distal surface of tetrad member at the right (arrow), the tectum between tetrad members is shared, resulting in a solid layer that is attached to each individual grain by it's columellae, the endexine is uniform, narrow and disrupted (at left), × 3800; 199, *P. hexandrum*, view of external or distal surface, which, in contrast to Figure 198, shows a slightly thicker endexine, × 5320; 200, *P. peltatum* (*Nunan 1914* US, Georgia), the oblique angle of section has enhanced the thickness and irregularity of the tectum produced by the "flattened rods" (see SEM Figures 109, 111, 113), the foot layer is thin and irregular and decreases toward the colpus (at the right), the endexine is fairly uniform, slightly thicker than the foot layer and increases in the colpus, × 12,180; 201, *P. peltatum* (same collection), in contrast to Figure 200 this section is less oblique and more parallel to the colpus, the endexine is smooth, uniform and considerably thicker than the narrow, somewhat intermittent foot layer, the columellae are short and well developed, the tectum is thick and fairly regular, the protrusions from the tectum probably represent sections through free tips of rods, × 12,180; 202, *P. peltatum* (*Braun 3911* US, Kentucky), section includes colpus, note that exine area to the left of the colpus resembles Figure 201 while exine to the right of the colpus resembles Figure 200, in the colpus flecks of exine appear to be supported by a narrow foot layer, the endexine is not clearly differentiated from the foot layer but is thickened, lamellate and somewhat disrupted, × 9430; the pleomorphic nature of the exine of *P. peltatum* as shown in Figures 200–202 supports results from SEM (see text discussion); 203, *Diphylleia cymosa*, radial section through mesocolpus, the endexine is narrow, uniform and about equal to the irregular foot layer; the short, regular columellae support a thin tectum interrupted by massive spines, × 11,020; 204, *D. cymosa*, section through colpus illustrating endexine thickening, × 9660; 205, *D. sinensis*, slightly oblique section through mesocolpus, × 8050; 206, *Dysosma pleiantha*, upper grain shows slightly oblique section through mesocolpus and lower one shows section through colpus, note that undulating outer surface of foot layer corresponds with undulating inner surface of tectum, the two layers are separated by narrow columellae, the colpus shows thickened, highly lamellate endexine, × 6300. (Scales equal 1 μm.)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FIGURES 207–211.—*Nandina domestica* pollen, TEM: 207, the most striking aspect of the central grain and parts of three surrounding grains is the remarkably developed endexine, which in most of these sections is thicker than the entire ektexine, a condition unparalleled for Berberidaceae pollen; the tectum is considered to be thick, but the columellae are very reduced and the foot layer thin; note traces of ektexine in the aperture as well as the gap between meso and colpial endexine (arrows), × 4200; 208 and 209, tangential sections, in Figure 208 the section is at the exine surface and shows the punctate morphology illustrated by SEM (Figures 89, 90), × 6670, in Figure 209 part of the section (i.e., the surrounding margins) shows the punctate surface morphology (as seen in Figure 208) while the central area represents the region beneath the tectum surface and distinguishes the narrow columellae depicted in Figure 207, × 4620; 210 and 211, oblique sections that include the three apertures, in Figure 210, which is highly oblique and close to a pole, the massiveness of the endexine is exaggerated, × 6300, in Figure 211, which is less oblique, the thick endexine is again emphasized and may also be somewhat lamellar (arrows), × 4900. (Scales equal 1 μm.)

FIGURE 212.—Herbarium specimen, *Ranzania japonica* (Ito) Ito, cultivated, Royal Botanic Gardens at Kew, 12 April 1947 (K).

FIGURE 213.—Herbarium specimen, *Ranzania japnoica* (Ito) Ito, *Takeda s.n.*, 27 August 1905 (K), Japan.

FIGURE 214.—Herbarium specimen, *Berberis amurensis* Ruprecht, *Korshinsky s.n.*, 22 May 1891 (US), U.S.S.R.

FIGURE 215.—Herbarium specimen, *Mohonia japonica* De Candolle *Mizushima s.n.*, 22 March 1954 (US), Japan.