A Palynological Study of the Liabeae (Asteraceae).

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ABSTRACT

Robinson, Harold, and Clodomiro Marticorena. A Palynological Study of the Liabeae (Asteraceae). *Smithsonian Contributions to Botany,* number 64, 50 pages, 208 figures, 1986.—Surface features and internal structure of the spines in the pollen of the Liabeae are illustrated by scanning electron microscopy and drawings made from oil immersion light microscopy. Observations are presented for all 16 genera of the tribe, *Paranephelius* and *Pseudonoseris* of the Paranephelinae, *Astroliabum, Bishopanthus, Cacosmia, Chionopappus, Ferreyranthus, Liabellum, Liabum, Microliabum, Oligactis,* and *Sinclairia* of the Liabinae, and *Chrysactinium, Erato, Munnozia* and *Philoglossa* of the Munnoziinae. No examples of echinolophate pollen are found in the tribe, but irregular groupings of spines are found to be characteristic of all but *Munnozia* and *Chrysactinium* in the Munnoziinae and *Paranephelius* and *Pseudonoseris* in the Paranepheliinae. The distribution of caveate forms in the Liabeae is clarified. The presence of a large cavus-like space interrupted by thin basal columuellae is confirmed in the genus *Paranephelius,* correcting early observations showing the genus as an exception to the basic uniformity of exine structure in the tribe. However, subcaveate forms have been discovered in the tribe in the genus *Munnozia.* SEM study of broken tecta in the genus *Munnozia* show previously unsuspected great potential for variation between closely related species and species groups. The structure of the exine supports views derived from floral structures regarding relationships with other tribes. No support is seen for a phyletic position near the Senecioneae, and closest similarity is seen to the Vernonieae. A basic difference is discovered in the arrangement of the basal columellae between the Liabeae and the Vernonieae, being clustered or forming a hollow cylinder under each spine in the former but forming a single solid basal columella under each spine in the most nearly comparable members of the latter. Genera of the Vernonieae shown for comparison include the non-lophate *Blanchetia, Pseudostifftia,* and *Vernonia,* and the lophate *Bishopalea, Heterocypsela,* and *Phyllocephalum.*

Contents

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Introduction

A recent series of studies (Robinson and Brettell, 1973a, 1974; Robinson, 1978, 1983a) has explored the taxonomy and evolution of the geographically restricted neotropical tribe Liabeae, using mostly macroscopic and some microscopic structural features. Most recently the chromosome numbers of the tribe have been reviewed (Robinson et al., 1985). The present study of the pollen continues the effort to improve understanding of this previously most poorly understood tribe of the Asteraceae whose members were neither placed together nor recognized at the tribal level in the traditional treatments of the family. A summary of the pollen characters of the tribe is given based on examination of over half the species by at least oil immersion light microscopy. Generic patterns are noted, and detailed taxonomically significant variations in exine structure in closely related species groups are documented. The views presented in the recent studies by the senior author regarding relationships and distinctions between the Liabeae and other tribes such as the Senecioneae and Vernonieae are extended by knowledge of the pollen structure.

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The Liabeae was not recognized at the tribal level or properly placed together in a related group until this century (Rydberg, 1927; Blake, 1935; Sandwith, 1956; Cabrera, 1954; Robinson and Brettell, 1973a, 1974; Robinson, 1978, 1983a). In the earliest classifications the members of the tribe with a capillary pappus were placed in the Vernonieae (Cassini, 1828). Later these were placed in the Senecioneae (Bentham and Hooker, 1873) while genera with reduced or plumose pappus forms were described in various other tribes such as the Heliantheae, Helenieae, and Mutisieae. The history of the tribe is dealt with more completely by Robinson (1983a).

The restricted neotropical distribution of the Liabeae and the failure to treat the group as taxonomically distinct resulted in their omission from the earliest palynological studies of the Asteraceae. It was in the study by Stix (1960) that the group was first included with observations on 14 species that are presently considered members of the genera *Liabum, Austroliabum, Liabellum, Munnozia, Sinclairia,* and *Paranephelius.* The study by Stix cited some variation in internal structure of the tectum in the pollen of the tribe. In 1966, the pollen of *Cacosmia* was described and compared with that of *Liabum* by Skvarla and Turner. Light microscope oil immersion observations of thick sections of *Chionopappus* pollen were used by Marticorena and Parra (1974) to confirm the relationship of that

genus to *Liabum*. Regularity of spine distribution and some variation in size of grains were mentioned by Robinson and Brettell (1974). The results of transmission electron microscope studies were included in the review of the family by Skvarla et al. (1977) where apparent variations between non-caveate forms with basal columellae and forms without basal columellae were noted in the tribe. The apparently anomalous *Paranephelius* was shown to possess thin basal columellae by Feuer and Dillon in an oral presentation (1982). It remains for the present study to broaden the survey of the tribe to include all 16 genera, introduce results of scanning electron microscope observations of whole and broken pollen grains, and to compare the results with conclusions from the simultaneous phyletic studies of the tribe (Robinson, 1983a).

Materials and Methods

A variety of techniques have been used for the study of pollen of the Liabeae. Many initial observations have been made of material mounted in Hoyer's solution (50 cm³ distilled water; 30 grams Gum Arabic, U.S.P. Flake; 200 grams Chloral hydrate; 20 cm³ Glycerin). The medium is regarded as temporary, eventually altering the index of refraction and making the exine essentially invisible. Whole grains have also been mounted in glycerin jelly. Paraffin sections have been prepared by Marticorena. All the above material was viewed with the light microscope with ×40 or oil immersion objectives. Results were comparable in detail to those by Stix (1960). The sections, which are often fragmentary and folded, have been used in the present study primarily for reference and only one photograph of a section of *Chionopappus* prepared during the study of Marticorena and Parra (1974), is presented herein. The slides of whole grains were used by Marticorena to produce ink drawings representing the internal spine structure in vertical view of over 100 species. These were grouped to show a range of columellar variation under different spines in grains from single col-

lections. Representatives (Figures 1–40), redrawn from the Marticorena camera lucida drawings, are included herein to provide the reader with a more convenient survey of the variation of such structure in the tribe than is available in the SEM micrographs.

No observations have been made in this study with the transmission electron microscope, but data from previous TEM studies by Skvarla et al. (1966, 1977) and Tomb (1975) are cited. In spite of some artifacts produced by breakage, the use of broken grains has proven much superior to TEM preparations for obtaining an understanding of the three-dimensional columellar structure.

A primary effort in the present study has involved use of the scanning electron microscope (SEM). Pollen samples have been removed from herbarium material or in one case from a living plant. In a few cases the pollen was not acetolized, but most samples were acetolized according to the procedure outlined in Erdtman (1966). Acetolyzed grains were fractured by crushing with the edge of a glass slide, or more often while still in the centrifuge tube by using a needle. All samples were pipetted on to cover slips and allowed to dry. The samples on coverslips were thinly coated using an EFFA carbon coater, involving evaporation by the carbon-arc technique. They were then coated with gold-paladium using a DC sputtering unit. Specimens were examined and photographed with Cambridge Stereoscan MK IIA, Cambridge Stereoscan S4-10, or Coates and Welter field emission microscopes.

The terminology for pollen structure used in the present paper follows mostly that of Skvarla et al. (1977). Sizes of pollen grains are given over a broad range to account for variations due to method of preparation. Grains mounted in Hoyer's solution tend to swell most, those in glycerine jelly are about the same size or slightly smaller than those in Hoyer's, the grains in water are distinctly smaller, and air- or vacuum-dried material, such as that examined by SEM, is completely unexpanded and may be as small as ⅔ the Hoyer's Solution diameter. Actual overlap in

sizes in various genera should be less in any one medium than indicated by the general figures given. Measurements cited for the Liabeae pollen are of the equatorial diameters, but none of the grains of the tribe are sufficiently oblong or oblate in shape to produce a markedly different polar diameters. Since only the general sizes are mentioned for the Vernonieae the shorter polar diameters of the larger oblate grains of that tribe are not noted. Measurements in the study exclude the projecting parts of the spines. Specimens used in the study are listed in the appendix.

Pollen Structure of the Liabeae

Stix (1960) in the initial study of pollen of the Liabeae, recognized three variations in the tribe. The first or andromachioides-type has large columellae restricted to the area under the spines, and most closely agrees with the type termed "Liaboid" by Skvarla et al. (1977). The species listed with this pollen type by Stix include five species now placed in *Sinclairia*, two species now placed in *Liabellum*, two species of *Austroliabum*, and *Munnozia rusbyi*.

The second pollen type of Stix (1960), the umbellata-type, has smaller columellae under each spine and some basal columellae in the intervening parts of the exine. The three species cited by Stix include one now known as *Munnozia hastifolia* and the only two true *Liabum* species in her study. The pollen type is treated herein as a comparatively minor variation of the first type. The different examples seem to occur in species that are closely related to others of the andromachioides-type with larger columellae under the spines.

The remaining pollen type of Stix (1960), the ovatum-type, has the columellae partially to completely separate from the footlayer. The columellae have the form seen in the upper layer of the first and second types. This pollen type is cited by Stix from *Liabum ovatum*, which is a member of the genus *Paranephelius*. The type was examined by Skvarla et al. (1977) on the basis of a specimen presently determined as *P. uniflora*, and the suggestion of a cavus and the more senecoid rather than anthemoid nature was emphasized. The apparent anomaly of a senecoid pollen type in the Liabeae was partially resolved in the study by Feuer and Dillon (1982), which discovered slender columellae under the spines that connect with the foot layer.

The present understanding of the pollen structure in the Liabeae is reviewed herein according to the revised concept of the tribe with 16 genera distributed in three subtribes, Paranepheliinae, Liabinae, and Munnoziinae (Robinson, 1983a,b).

The pollen of the Liabeae (Figures 1–180) is generally characterized as follows:

Tricolporate; 25–50 μm in diameter, spherical to slightly oblate-spheroid or in some cases where colpi are closed appearing oblong; ecto-apertures meridionally elongate (Figures 41, 50, 69, 74, 104, 124) and endo-apertures transversely short-oval (Figure 121); echinate with spines often irregularly distributed and variously confluent with each other at the base (Figures 60, 62, 64, 67, 94), sometimes regularly dispersed on the intercolpar area (Figures 49, 50, 140, 141, 147, 148, 150). Internal structure basically with two levels (Figures 68, 88, 132, 179, 180) of columellae. Usually with few (Figures 1, 2, 46) to many (Figures 156, 160) large basal columellae clustered under spine bases, rarely with additional basal columellae dispersed in inter-spinal areas (Figure 118), columellae under spines sometimes coalesced into hollow cylinders (Fig-

ures 175, 176); basal columellae sometimes reduced or separated from foot layer (Figures 162–167) with partial to complete development of cavus; upper layer of columellae usually regular, short, dense, with upper ends forming a perforate tectum, and covered below by unsupported or partially supported internal tecta forming a somewhat undulating or papillose surface in interspinal areas.

Pollen size and spine distribution show variation in the Liabeae. The generic pair of *Liabum* and *Oligactis* has the smallest average pollen size in the tribe at 25–35 μm. A number of other members of the subtribe Liabinae, such as *Cacosmia* and *Ferreyranthus,* can have pollen as small, 27–30 μm and 29–35 μm respectively, but one species of the latter ranges up to 43 μm. Still, in other Liabinae, such as *Austroliabum,* 33–40 μm, *Chionopappus,* 37–40 μm, and especially *Sinclairia,* 35–55 μm and *Liabellum,* 47–52 μm, the pollen is characteristically larger. The members of the other two subtribes are more consistent in size. Both genera of the Paranepheliinae have pollen mostly 35–45 μm in diameter. The four genera of the Munnoziinae, with rare exceptions, range from 30–40 μm in diameter. The primary exception is the typical element of *Munnozia* that ranges between 37–45 μm in diameter. For a sampling of size measurements see the appendix.

Many genera of the Liabeae have a type of uneven distribution of the spines on the pollen that seems unique in the family. In these forms the spines seem to be in groups, sometimes in pairs or in short crests of three with confluent bases. This is especially evident in SEM views of some unacetolized grains (Figures 62, 63). Such grains seem to be best characterized by the irregular placement of the spines along the lateral margins of the colpi (Figures 72, 74). This pollen form is found throughout the subtribe Liabinae and in *Erato* and *Philoglossa* of the Munnoziinae, but it is lacking in *Munnozia* and *Chrysactinium* of the Munnoziinae and in the Paranepheliinae. The distribution in the tribe suggests that is the plesiomorphic condition in the tribe. It is correlated rather closely in its distribution in the tribe

with the apparent plesiomorphic condition of the basal columellae under the spines.

The spines are more evenly disposed on the surfaces of the pollen in two pairs of genera in two separate, comparatively derived groups, *Munnozia* and *Chrysactinium* in the Munnoziinae, and *Paranephelius* and *Pseudonoseris* in the Paranepheliinae. This arrangement is reflected in the regularly aligned spines along the lateral margins of the colpi (Figures 41, 50). The pattern is more evident in a preparation of unacetolized grains of *Paranephelius* (Figure 49), where the depressions between the bases of each of the spines are equal in spite of some displacement seen in the spines. The character can be observed under the light microscope. The separate and derived nature of the regular spine pattern in the two groups is indicated by the retention of the irregular pattern in two of the genera of the Munnoziinae and by the slight evidence of irregularity that survives along the margin of the colpus in *Paranephelius.*

There is greater variation in the Liabeae in the internal structures of the pollen than in external features. The variations between many species of *Munnozia* are perhaps the greatest thus far known for internal exine structure of pollen in any such closely related group. Variations include tendencies toward the caveate condition seen in the Paranepheliinae, *Philoglossa,* and *Munnozia,* the fusion of columellae into hollow cylinders in *Chrysactinium* and *Munnozia,* and the production of an anomalous inner series of columellae seen in *Munnozia* subgenus *Kastnera.* These and other details of pollen structure in the Liabeae are best reviewed in each subtribe individually. The subtribes are treated herein in the following order: Paranepheliinae, Liabinae, and Munnoziinae.

PARANEPHELIINAE.—The subtribe contains two genera that share long style branches, pale anthers, elongate raphids in the achene wall, narrow disk corollas, and leaves mostly in basal rosettes. The inflorescence has few heads and in the type-genus the heads are sessile in the rosette of leaves. The two genera, *Paranephelius* (Figures

1, 2, 41–49) and *Pseudonoseris* (Figures 50–53), have pollen structure that supports their status as a related pair. Both have grains that appear caveate, with spines rather evenly distributed over the intercolpar regions. The illustrations of *Paranephelius* (as *Liabum ovatum*) by both Stix (1960, Abb. 11) and Skvarla et al. (1977, pl. 15: fig. F) are equivocal regarding complete separation of the outer exine from the footlayer, and their preparations seem to have a columellate layer of the exine tightly contracted against the footlayer. A point in the TEM of Skvarla et al. (1977, pl. 15: fig. F) seems to show many columellae closely appressed against the foot layer and at least one clear example of a basal attachment. However, closer examination of the most obvious basally attached element shows that it is not directly attached to the overlying tectum. Preparations in Hoyer's Solution, thick sections viewed with the light microscope, and SEMs of broken grains indicate that the columellate exine is normally less close to the foot-layer, and that a cavus-like area is present in the intercolpar parts of the grain. Studies of *Paranephelius* with oil immersion (Figures 1, 2) and SEM (Feuer and Dillon, 1982; Figures 45–48) show that the grains are not strictly caveate. They have a few narrow basal columellae under the spines that reach the foot layer. The SEM also shows occasional short pegs on the foot layer, but it is most likely that the basally attached structure seen in the TEM photo of Skvarla et al. (1977) is part of one of the slender columellae that has been bent and cut.

Broken pollen grains of *Pseudonoseris* have not been examined with the SEM, and oil immersion study does not show columellae of the type found in *Paranephelius*. If basal columellae are present in *Pseudonoseris*, they are more reduced than those of *Paranephelius*, which can by seen by light microscopy. The two genera, nevertheless, both show a tendency for great reduction in the basal columellae in pollen grains of comparatively large size.

In its vegetative or floral characters, *Pseudonoseris* seems less specialized than *Paranephelius*,

but the pollen seems more specialized. It is *Paranephelius* rather than *Pseudonoseris* that retains some irregularity of spine position and has more obvious remnants of basal columellae under the spines.

The presence of slender basal columellae under the spines of *Paranephelius* pollen conforms to the anthemoid pattern of typical Liabeae and eliminates doubts about the senecioid pollen patterns or Senecionean relationships of the tribe. Nevertheless, the extremely slender form of the basal columellae represents a trend toward cavus development that is interpreted herein as apomorphic within the tribe. The trend toward cavus development here and in some Munnoziinae indicates at least two separate instances of reduction in basal columellae in the Liabeae.

Similarities between the pollen of the Paranepheliinae and Munnoziinae might indicate close relationship between the two, but this is not supported by other evidence. In fact, on the basis of such characters as style form, anther color, endothecial cells, and raphids of the achene wall, the two subtribes are at opposite extremes in the tribe. The surviving slight irregularity of spine distribution along the margin of the colpus that is evident in *Paranephelius* (Figure 41) supports the idea that the regularly disposed spine pattern of the Paranepheliinae arose from members of the tribe with more irregularly disposed spines on the pollen within the immediate relationship, and separately from that of the Munnoziinae.

LIABINAE.—Members of the subtribe share pale anthers with fringed bases, narrow bases on the disk corolla throats, and leaves rarely or never in rosettes. The heads are often on short peduncles in crowded inflorescences. The style branches and the raphids in the achene wall may be long or short. The subtribe consists of ten genera, *Austroliabum* (Figures 3, 69–73), *Bishopanthus* (Figures 54–57), *Cacosmia* (Figures 4, 58–63), *Chionopappus* (Figures 5, 64–68), *Ferreyranthus* (Figures 6, 7, 78–82), *Liabellum* (Figures 11, 94–98), *Liabum* (Figures 12–20, 108–123), *Microliabum* (Figures 74–77), *Oligactis* (Figures 21–23, 99–107), and *Sinclairia* (Figures 8–10,

83–93), ranging north to central Mexico and the Greater Antilles and south to northern Argentina. In all these genera the spines are unevenly distributed in small subgroups on the pollen surface (Figures 60, 62–65, 67, 69, 70). As far as known, this type of arrangement is unique to the Liabeae but apparently plesiomorphic in the tribe. The pattern is reflected in cross-sections (Figure 68; Skvarla et al., 1977) by the irregular thickness of the intercolpar exine and by the confluence between the bases of the adjacent spines. Size of the pollen grains, in contrast, is highly variable in the subtribe (Appendix). Size of pollen grains seems to be reflected in the subtribe in the size of the columellae, smallest in *Liabum* and *Oligactis* (Figures 12–23), and largest in *Sinclairia* and *Liabellum* (Figures 8, 10, 11). The two closely related genera with the smallest pollen grains, *Liabum* and *Oligactis* (25–35 μm), are also distinctive in the shorter stouter tips of the spines. This is evident in both the Andean (Figures 99–107) and West Indian (Figures 108–111) material.

The SEMs of broken pollen in *Austroliabum, Ferreyranthus, Liabum,* and *Sinclairia,* and sectioned grains of *Chionopappus* (Marticorena and Parra, 1974), all indicate a distinct group of large basal columellae under the spines. Nevertheless, oil immersion studies by Marticorena (Figures 3, 7, 11) show variations toward a fused hollow cylinder in each of these genera. The fusion might be the result of poorer resolution or of the vertical direction of the observation in the oil immersion studies. Still, the pollen in one SEM preparation of *Microliabum* (Figure 77), which is closely related to *Austroliabum,* may be interpreted as an example of a fused hollow cylinder. There is no other SEM evidence of the trait in the subtribe.

The pollen form called the umbellatum-type by Stix (1960) has been examined in *Liabum* (Figures 12, 13, 18, 20, 118, 123) using SEM preparations. The pollen type differs from the more common form in the tribe by the basal columellae being somewhat smaller and more numerous, and extending into the areas between the spines. Although named after *Liabum umbellatum* (L.) Schultz-Bipontinus of Jamaica, the character does not occur in that species. The character does occur in species in Hispaniola that have sometimes been included in a broader concept of *L. umbellatum.* Two species from Hispaniola have been examined. In *L. subacaule* Rydberg the columellae under the spines become narrower distally while those between the spines are often constricted at the base (Figure 118). There are also a few projections from the under surface of the internal tectum among the interspinal columellae. In *L. barahonense* Urban the supposed columellae between the spines are seen to be mostly projections from the under surface of the internal tectum and they are not connected to the foot-layer (Figures 122, 123). From the evidence, the umbellatum-type pollen in West Indian *Liabum* has columellae of basically different structure in the interspinal areas from those under the spines. This particular design of columellae is probably restricted to the genus *Liabum.* The umbellatum-type pollen was also credited to *Munnozia hastifolia* by Stix (1960, as *Liabum*), but the latter seems to be different in the details of its structure.

Most of the remaining genera of the subtribe have massive columellae clustered under the spines, but the survey of material under oil immersion by Marticorena has revealed a variant in *Sinclairia deamii* (B.L. Robinson and Bartlett) Rydberg having only small columellae (Figure 9). Examination with the SEM shows these columellae to be further distinguished by their common failure to reach the foot-layer (Figures 91, 92). The variant seems to represent an extreme reduction of a type that is rare in the subtribe Liabinae, though it does occur commonly in the Munnoziinae. As interpreted herein on the basis of the exposed unbroken basal columellar surface, the SEM photograph of *Microliabum* (Figure 77) represents another example in the subtribe of basal columellae that are incompletely fused to the foot-layer.

MUNNOZIINAE.—The subtribe contains four genera, *Erato, Philoglossa, Chrysactinium,* and

Munnozia that share short style branches, black anthers, quadrate raphids in the achene wall, somewhat expanded bases in the throats of the disk corollas, and a tendency for long-pedunculate heads. Nevertheless, for purposes of discussion of the pollen, the subtribe falls into two distinct subgroups consisting of two genera apiece. On the basis of pollen alone, the two subgroups would not be considered closely related.

Erato (Figures 24, 124–133) and *Philoglossa* (Figures 25, 26, 134–139) both have the irregularly clustered pattern of spines on the pollen surface (Figures 124–127, 134–136) that is characteristic of the larger subtribe Liabinae. Thick sections and whole grains examined with oil immersion, and broken grains viewed with the SEM, show that *Erato* further resembles the Liabinae by the large clustered basal columellae under each spine (Figures 24, 129, 131, 132, 133), all firmly attached to the foot layer. The presence of such pollen in *Erato* in the subtribe Munnoziinae strongly indicates that the form is plesiomorphic in the tribe.

In *Philoglossa* the pollen is externally the same as *Erato;* however, oil immersion and SEM studies show that the basal columellae under the spines are reduced in size and number. Such reduction is independent of the size of the grain that is the same size as in *Erato*. The oil immersion and SEM studies show that basal columellae are present (Figures 25, 26, 138, 139), a fact demonstrated also by Feuer and Dillon (1982). Still, the SEM preparations indicate that the columellae are weakly attached to the foot-layer and that a near-caveate condition exists (Figures 138, 139). The broken grains show a large expanse of papillose foot-layer with little evidence of columellar scars. *Philoglossa* is the only member of the tribe characteristically combining such reduction of the basal columellae with an irregular disposition of spines on the surface.

The remaining two genera of the subtribe, *Chrysactinium* (Figures 27, 28, 140–146) and *Munnozia* (Figures 29–40, 147–180) have spines regularly distributed on the surface of the pollen

with no merging of spine bases. Internally the columellae show a strong tendency for reduction, although a number of species (Figures 151–160) including the type of the genus, *M. lanceolata,* show the massive type seen in *Erato* and the Liabinae. Nevertheless, partial or complete columellae are clearly present in all members of the two genera that have been examined by light microscope or SEM. In this respect the pollen differs from that found in the Paranepheliinae. As seen in SEMs, however, there is a capacity in *Munnozia* for the most complete separation of the columellae from the foot-layer and thus the most technically complete cavus development in the tribe.

In the *Chrysactinium-Munnozia* complex, the detailed structure of the columellae and tecta shows great variation, and the variations seem to correlate well with taxonomic groups within a genus. As such, the variations are of more taxonomic value than variations in other parts of the tribe. In *Chrysactinium*, according to oil immersion studies (Figures 27, 28), the basal columellae vary from separate strands to a single hollow cylinder, but they are rather small and regularly arranged. An SEM view shows that the columellae connect with the foot-layer (Figures 144, 145). The examples seen in the SEM preparation are all fused, with the hollow center evident in one view (Figure 146). The form of the columellae in the genus is not precisely matched in size, symmetry, attachment to the foot-layer, or variable dissection in any member of *Munnozia*.

Munnozia itself has many different subgroups that can be distinguished by the internal structure of the pollen walls. The type-species, *Munnozia lanceolata* Ruiz and Pavon (Robinson and Brettell, 1974), and a series of close relatives, *M. cardenasii, M. foliosa, M. olearioides, M. peruensis,* and *M. rusbyi,* all having rather coriaceous leaves, appear to have a characteristic cluster of large, separate, basal columellae in a ring under each spine (Figures 29, 33, 151–155). No members of the group have the columellae completely fused into a hollow cylinder. In this typical group, the

columellae, as observed in thick section and SEM, are attached to the foot-layer. A singularly distinctive species, *M. perfoliata*, also has columellae grouped and unfused under the spines (Figure 156), but these columellae are less massive and are sometimes mixed with smaller columellae inside the circle. The even smaller circle of columellae in *M. lyrata*, as seen with oil immersion and SEM, seems to be unique to that distinctive species, with the enlarged proximal ends that do not reach the foot-layer (Figures 34, 161–165). The foot-layer characteristically bears a small peg under each spine below the hollow center.

The dissected pattern of columellae in *Munnozia lyrata* is in sharp contrast to the fused cylinder, which is mostly separated from the foot-layer, and seems to be characteristic of the subgenus *Kastnera* (Figures 39, 40, 172–180), *M. senecionidis* (Figure 35), and the latter's relatives, *M. affinis*, *M. angusta*, *M. convencionensis*, *M. corymbosa*, *M. glandulosa*, *M. longifolia*, *M. oxyphylla*, *M. pinnulosa*, *M. silphioides* (Figure 36), and *M. venosissima* (Figure 38). These fused columellae seem usually eccentric, and as seen by SEM, the eccentric form in *M. senecionidis* may be associated with partial eccentric attachment to the foot-layer (Figure 166, 167). It is evident, on the basis of pollen, that the *M. senecionidis* group is more closely related to the subgenus *Kastnera* (Figures 39, 40) than to typical *Munnozia* (Figures 29, 33).

According to Stix (1960), and as seen in this study in thick sections examined under the light microscope and in some broken grains under SEM, *Munnozia hastifolia* has columellae in the interspinal areas of the pollen wall. For this reason, the species was included in the umbellatum-type pollen by Stix (1960). Such a design seems anomalous in the group, because the two most closely related species, *M. maronii* and *M. subviridis*, have columellae of the *Kastnera-M. senecionidis*-type according to oil immersion studies (Figure 37).

One additional distinctive pollen type is found in *Munnozia jussieui*. As observed under oil im-

mersion by Marticorena (Figures 30–32) the columellae under the spines are of two forms, with numerous smaller ones surrounding a large central mass. The central mass seems to be solid, but on the basis of the outline of many samples, the central mass seems to consist of several large basal columellae that may be slightly separated. It seems unlikely that the species would be the only member of the tribe lacking a hollow or open space under the center of the spine. SEMs of broken grains (Figures 157–160) show that all the basal columellae are completely fused at the bases to the foot-layer.

In *Munnozia tenera* of the subgenus *Kastnera*, there is, as usual, an outer layer of short uniform columellae, but there also is a second inner layer of similar short uniform columellae between the spines and adjacent to the foot-layer (Figures 172–180). Close examination shows that the proximal ends of the short columellae in both series are narrow and not, or only weakly, attached to the structure below them. Thus, the inner layer is not, or only weakly, attached to the foot-layer, and more surprisingly the outer layer is not, or only weakly, attached to the "internal tectum" that caps the inner layer of short columellae. This differs from the structure of the "internal tectum" seen in other members of the tribe and described by Skvarla et al. (1977:156), which is attached to, or gives rise to, the outer layer of columellae. The inner layer of columellae is at a level equivalent to that occupied under the spines in most Liabeae by the larger basal columellae attached to the foot-layer. In *M. tenera*, it is notable that the cylindrical structure formed by the basal columellae under the spines is like the smaller columellae in not being attached to the foot-layer. The character may be more widely distributed in the subgenus *Kastnera*, but it is not found in *M. senecionidis*, which is the closest relative outside of the subgenus that has been examined under SEM in this study (Figures 166, 167).

Key to Types of Liabeae Pollen

1. Pollen with spines arranged in irregular groups on the surface, not evenly aligned along margin of colpus, with bases of spines variably confluent 2

    2. Exine nearly or truly caveate, with only slender basal columellae present under the spines . . . .*Philoglossa*

    2. Exine not caveate, with stout or numerous basal columellae present under the spines 3

        3. Pollen 25–35 μm in diameter; spines short with stout tips. 4

            4. With small numerous basal columellae under both the spines and areas between the spines (umbellata-type of Stix, 1960) . . . *Liabum barahonense* and some other *Liabum* species from Hispaniola

            4. With large columellae restricted to area under the spines . . . . *Oligactis* and most *Liabum;*

        3. Pollen mostly 30–50 μm in diameter; spines with narrow tips. 5

            5. Pollen less than 40 μm in diameter. . . . . *Austroliabum, Cacosmia, Chionopappus, Erato, Ferreyranthus,* and *Microliabum*

            5. Pollen mostly 40–50 μm in diameter . . . . *Liabellum, Sinclairia,* and one *Ferreyranthus* species

1. Pollen with spines regularly arranged on surface of intercolpar area and mostly aligned along sides of colpus, each spine separated to equal depth on all sides 6

    6. Pollen 35–45 μm in diameter, with no or only very slender basal columellae under the spines 7

        7. Spines regularly aligned along sides of colpi; basal columellae not visible under the spines using light microscopy . . . . *Pseudonoseris*

        7. Spines slightly unaligned along sides of the colpi; a few slender basal columellae present under the spines . . . . *Paranephelius*

    6. Pollen 27–45 μm in diameter, with basal columellae forming clusters, rings, or fused cylinders under the spines 8

        8. Basal columellae under the spines completely or almost completely separated from foot-layer at the base 9

            9. Pollen 40–42 μm in diameter; basal columellae in a circular unfused cluster under each spine. . . . . *Munnozia lyrata*

            9. Pollen 27–37 μm in diameter; basal columellae under each spine usually fused into a single unit 10

                10. With two layers of short, dense columellae in interspinal areas of tectum . . . . *Munnozia* subgenus *Kastnera*

                10. With only one layer of short dense columellae in interspinal area of tectum . . . . *Munnozia senecionidis*

        8. Basal columellae under the spines attached at bases to foot-layer 11

            11. Basal columellae under each spine in small single symmetrical series about 2 μm in diameter . . . . *Chrysactinium*

            11. With at least some massive basal columellae under each spine, the clusters mostly 3–4 μm in diameter 12

12. Basal columellae under the spines of two types, many small peripheral colu-
mellae surrounding a central, massive, fused column . . . .
. . . . *Munnozia jussieui*
12. A simple cluster of mostly large basal columellae under each spine 13
    13. Pollen 28–30 μm in diameter; with basal columellae in both interspinal
    and spinal areas of tectum . . . . **Munnozia hastifolia**
    13. Pollen 37–45 μm in diameter; with basal columellae only under the
    spines 14
        14. Cluster under each spine with individual basal columellae often
        2–3 μm in diameter . . . .
        . . . . typical **Munnozia, M. lanceolata** and its relatives
        14. Cluster under each spine with individual columellae not more than
        1.5 μm in diameter . . . . **Munnozia perfoliata**

Palynological Evidence on the Relationships of the Liabeae in the Asteraceae

The pollen structure in the Liabeae reinforces recent conclusions regarding the two conflicting placements of the group in the family by various authors. Cassini (1828), Robinson and Brettell (1973b), Nordenstam (1977), Jansen and Stuessy (1980), and Robinson (1983a) have placed the genera of the Liabeae in or near the Vernonieae. In contrast, Bentham and Hooker (1873) followed by Hoffmann (1894) and Cronquist (1955) have placed the broadly interpreted genus *Liabum* in the Senecioneae. The two tribes involved have the distinction of belonging to two different subfamilies of the Asteraceae as interpreted by Carlquist (1976) and Robinson (1977). The Vernonieae share most characters with the Arctoteae, Eremothamneae, Echinopsideae, Cynareae, Mutisieae, and Lactuceae in a group best recognized as the subfamily Cichorioideae, while the Senecioneae belong with the Eupatorieae, Heliantheae, Inuleae, Calenduleae, Astereae, and Anthemideae in a group best recognized as the Asteroideae. For comparisons of characters see Robinson and Brettell (1973b), Wagenitz (1976), Carlquist (1976), and Robinson (1977). As such the two tribes with which the Liabeae have been placed are not closely related, and there are many structural features by which the closest relationships of the tribe can be tested. Results of evidence from floral anatomy have most recently indicated that the Liabeae are close to the Vernonieae and other members of the Cichorioideae (Robinson and Brettell, 1973b; Nordenstam,

1977; Robinson, 1983a). Pollen evidence should reflect a similar relationship.

A general trend has been noticed by Robinson and Brettell (1973b) where all pollen surfaces that depart from an evenly distributed echinate pattern seem to belong to the subfamily Cichorioideae. These variations include some distinctive lophate and oblong psilate types, but also include most members of the Vernonieae having less obvious sublophate forms in which the spines are only arranged around depressed areoles rather than restricted to well-defined ridges.

The pollen in the Liabeae is echinate without obvious lophate or psilate variations, but the spines of most Liabeae are not evenly distributed on the surface of the grains. In all genera of the Liabeae except *Chrysactinium, Munnozia, Paranephelius,* and *Pseudonoseris,* the spines tend to be grouped in small series or crests with somewhat confluent bases. The gaps within the series are slightly but distinctly smaller than those between the series. The grouping of spines in these Liabeae is unlike the variations seen in any other tribe of the Asteraceae, but by its irregularity it would seem to be excluded from the subfamily Asterioideae, and would fall into the Cichorioideae.

Internal structure of the pollen wall shows more characters that can indicate relationship in the Asteraceae. Skvarla et al. (1966, 1977) have described features they termed a "cavus," "internal foramina," and "internal tecta," and on the basis of these structures they have recognized four basic pollen types in the family: helianthoid, senecioid, arctotoid, and anthemoid. Each of

these types shows some broad systematic correlations in the family and furnish a useful basis for comparison with the Liabeae.

The Liabeae do not have "internal foramina" in the pollen wall and therefore do not fall into the helianthoid classifiaction of Skvarla et al. (1977) that is defined by the presence of internal foramina with a cavus. The character is almost restricted to the subfamily Asteroideae, occurring especially in such tribes as the Eupatorieae and Heliantheae, which have never been considered close relatives of the Liabeae. Internal foramina are notably undeveloped in a few of the most highly evolved members of the Asteroideae, such as most true Senecioneae, the Anthemideae, and most Ambrosiinae of the Heliantheae. The fact that there are no internal foramina in the Liabeae conforms with placement in the Cichorioideae but does not in itself preclude relation to some Senecioneae.

The Liabeae seem to lack a "cavus" in the pollen wall in their plesiomorphic form. The lack of the cavus provides a further basis for excluding the Liabeae from the helianthoid grouping of Skvarla et al. (1977). The cavus is also characteristic of two of the other major pollen wall patterns described by Skvarla et al. (1966, 1977), the senecoid, and arctotoid. A cavus extends through most members of the subfamily Asteroideae including the Senecioneae and is the best character after that of spine distribution for excluding the Liabeae from the Senecioneae and the Asteroideae. The "lack" of a cavus is, in fact, the same as the "presence" of basal columellae connecting the outer exine to the foot layer in the intercolpar area, and this is the principal characteristic of the fourth or anthemoid pollen wall pattern of Skvarla et al. (1977).

The distribution of the non-caveate or anthemoid pollen of the type found in the Liabeae is of considerable interest, especially since it is the type found in most members of the subfamily Cichorioideae excluding the Arctoteae. Of the various pollen types, it is the one that most nearly aligns with the presently accepted subfamily classification of the Asteraceae. There are important exceptions in the distribution of the anthemoid pollen type, however, including its presence in the Anthemideae of the Asteroideae and its absence in various Cichorioideae such as the Arctoteae.

In one way, it is unfortunate that the non-caveate pollen type has been called anthemoid by Skvarla et al. (1977), because the type is much more characteristic of members of the subfamily Cichorioideae. The Anthemideae is the one major group in the Asteroideae in which the anthemoid pattern occurs. It should be emphasized further that the Anthemideae is not primitive within the subfamily Asteroideae and is not close to the Cichorioideae (Robinson, 1981). Caveate pollen, the type predominant in the Asteroideae, is found even in what seems to be a primitive element of the Anthemideae, in *Ursinia* (Robinson and Brettell, 1973b; Skvarla et al., 1977). One could conclude from foregoing evidence that the non-caveate pollen of the Anthemideae represents a development of basal columellae in the intercolpar area from ancestral caveate types that did not have such columellae. The anthemoid pollen pattern thus would have at least two separate origins in the Asteraceae.

In the subfamily Cichorioideae, where the anthemoid pollen pattern predominates, there are some caveate forms such as those within the arctotoid pattern, some Lactuceae having an interrupted cavus, and a few Mutisieae such as *Dasyphyllum* (which is caveate along the colpar margins). Bolick (1978) cites caveate pollen in *Ethulia, Hoplophyllum,* and *Corymbium* of the Vernonieae and *Centaurea* in the Cynareae, and indicates that the Arctoteae is approximately equally divided between caveate and non-caveate types. To these examples may be added those now known from the Liabeae. In these cases, the caveate pollen seems to be derived from non-caveate ancestors, and it has evidently been derived more than once. Apparently, the two subfamilies of the Asteraceae have the two different types of pollen as basic, but each type, caveate and non-caveate, seems able to give rise to the other. The fact that the anthemoid pollen wall type occurs in the one specialized tribe of the Asteroideae, in the absence of any other supporting characters, does not particularly favor the idea of asterioid relationships for the Liabeae.

In addition to the cavus, the presence of an

"internal tectum" is used as a basis for differentiating the arctotoid pollen pattern within the subfamily Cichorioideae (Skvarla et al., 1977). This involves the most characteristic form of internal tecta that almost equally divides the region of solid columellae. The arctotoid pollen is also claimed in *Eremothamnus* (Liens, 1970) of the tribe Eremothamneae (Robinson and Brettell, 1973c), but this should be checked. Illustrations of Skvarla et al. (1977, pl. 24: fig. F, H) suggest an arctotoid pattern in some Lactuceae such as *Rafinesquia* and *Lapsana*. Internal tecta of this type occur in pollen of other Cichorioideae, seeming to be most highly developed in the tribes Cynareae and Mutiseae. The latter two tribes show relationship to the Arctoteae in the form of the style, but they differ and are excluded from the arctotoid type by Skvarla et al. (1977) because of the lack of a "cavus." The Liabeae and Vernonieae lack the elaborate internal tecta of the arctotoid type or the Cynareae and Mutisieae type, but enlargements at the proximal ends of the short outer columellae form a layer at the lower limit of the outer columellae that is also referred to as an internal tectum by Skvarla et al. (1977:156). The latter layer is often prominent in the areas between the spines where there may be no basal columellae, and the structure thus appears very different from the structure referred to by the same name in the Arctoteae and is structurally equivalent to the layer below the internal tectum of the Arctoteae. Nevertheless, the two structures are formed in the same manner and no other better term seems to have been provided as yet.

Within the anthemoid pollen pattern Skvarla et al. (1977) have described a modified pattern they termed "Liaboid." It is distinguished by the basal columellae being much broader (Figures 68, 89, 90, 113, 114, 120) than those noted for the typical anthemoid pollen pattern. The pattern is cited from *"Liabum,"* *Cacosmia,* and the Vernonieae and is cited elsewhere by Skvarla et al. only in *Scolymus* of the Cichorioid Lactuceae on the basis of TEM studies by Tomb (1975). Observation during the present study show that *Gundelia,* of the prospective Cichorioid tribe Gundelieae, has similar massive columellar structure under the spines, but these do not reach the foot-layer. The limitation of the liaboid pollen pattern to members of the subfamily Cichorioideae seems to provide confirmation of the placement of the Liabeae in that subfamily. The distribution of the liaboid pattern within the subfamily seems to parallel evidence of stylar form in suggesting closest relationship of the Liabeae to the Vernonieae and Lactuceae, especially the former.

Of the tribes that appear to be most closely related to the Liabeae, the pollen of the Lactuceae can be distinguished by various characters such as lophate surfaces or more complex internal tecta. In the cases where Tomb (1975) and Skvarla et al. (1977) show internal structure more like that of the Vernonieae and Liabeae the structure is under the ridges of specialized echinolophate grains. Among the non-lophate members of the Lactuceae, there seem to be cavus-like areas periodically interrupted by columellae reaching the foot layer, a form seen in comparatively few derived members of the Liabeae.

The Vernonieae is regarded here as the probable closest relatives of the Liabeae, and the two tribes have been combined by some recent authors (Nash, 1976; Turner and Powell, 1977; Jansen and Stuessy, 1980). The two groups were placed adjacent to each other in the pollen study by Stix (1960) because of their similar wall structure. It is of interest, therefore, that the pollen of the Vernonieae and Liabeae is in fact distinguishable, and almost without exception the tribes show totally different trends in the details of their anthemoid structure.

Surface features alone could be used to distinguish most Vernonieae from the Liabeae. Only the recently described *Pseudostifftia* (Robinson, 1979) in the Vernonieae appears to have no trace of a lophate surface pattern (Figures 181, 182). The remainder of the Vernonieae have various degrees of areole formation (Keeley and Jones, 1979). Most members of the tribe have a form termed the Lychnophora-type by Stix (1960), where the tectum is continuous between the

colpi, but where slight areolae are present (Figures 190–192). The polygonal areolae are more obvious under the light microscope where the columellae are visible to accentuate the pattern. The ridges in some genera, such as *Bishopalea*, are more obvious with the tectum still continuous across the areolae (Figures 200–202). More strongly lophate pollen forms in the tribe, such as *Heterocypsela*, have regularly arranged ridges with a restricted tectum (Figures 203, 204). The extreme form of lophate grain in the tribe has little or no tectum and has the columellae visible from a lateral view of the ridges. This is seen in *Elephantopus* and its relatives, as well as in some Paleo-tropical elements of the subtribe Vernoniinae, such as *Cyanthillium* and *Phyllocephalum* (Figures 205–208; Skvarla et al., 1977; Keeley and Jones, 1979; Jones, 1981; Kirkman, 1981). The trend toward a lophate pollen surface seems basic to the Vernonieae, but is absent from the Liabeae.

Size of pollen grains alone offers some distinction between the tribes. Pollen of the Liabeae is mostly 25–40 μm in diameter with some up to 50 μm. The pollen of the Vernonieae is usually 40 μm in diameter or more, and it is often over 50 μm.

Based on a limited sample, Skvarla et al. (1977) indicated some differences in the detailed internal structure of the liaboid pattern in the Vernonieae and Liabeae. On page 156 they stated the following.

In *Liabum* the lateral branches of the distal ends of the columellae (sic basal columellae) form a uniform internal tectum. From this internal tectum a short, uniform set of columellae arise which in turn are capped by a perforate tectum. Commonly, the tectum areas between the large columellae show gentle undulations. In the Vernonieae the major distinction from *Liabum* is that the lateral branches are frequently (but not always) a thick network of solid rods or tubules with complex anastomosing patterns.

The distinction is evident to some degree in the examples of broken pollen grains seen in the present study. Many Vernonieae, including *Blan-*

chetia (Figures 197–199) and *Pseudostifftia* (Figures 184–189), show a branching pattern that completely fills the inter-spinal areas, while *Vernonia fuertesii* shows that even an unsupported internal tectum in the tribe does not bear a layer of regular short columellae as in the Liabeae (Figures 193–195).

The most important difference in the internal structure of the pollen wall was first noted by Stix (1960) and has been confirmed in the present study by the light microscope and SEM views of broken grains. In the Vernonieae with well-developed spines, each spine seems to have a single solid basal columella centered under the spine, which is continuous with the apex of the spine (Figures 193–195, 197–199). The only exception seems to be *Pseudostifftia* with basal columellae distributed more randomly throughout the spinal and interspinal areas with branches of more than one basal columella contributing to each spine (Figures 184–189). Though unlike any other Vernonieae, *Pseudostifftia* is not like any Liabeae. In the Liabeae, the basal columellae are either grouped under the spines (Figures 12–16, 29, 46, 89, 163–165) or are coalesced into a single hollow cylinder (Figures 40, 145, 146, 166, 167, 174–176). The coalesced form, which seems continuous with the apex of the spine, resembles the single columella of the Vernonieae except for the hollow center. Single solid columellae centered under the spines do not seem to occur in the Liabeae except possibly in a specialized form seen in *Munnozia jussieui*. In the latter case the oil immersion studies (Figures 30–32) suggest a characteristically higher degree of coalescence than any other member of the tribe, but the SEM seems to show narrow separation (Figures 157–160) that was overlooked at the lower magnification. The difference between the basal columellae in the two tribes is regarded herein as fundamental, and observation of the range of variation in the Liabeae indicates that the cluster of separate columellae is plesiomorphic in the tribe. The form most resembling the Vernonieae is apparently an isolated derivative.

Appendix

List of specimens examined palynologically in the study with figures in which they appear and with measurements (in μm) of pollen in glycerine mounts and Hoyer's (H) mounts.

<div align="center">LIABEAE</div>

Austroliabum
  A. candidum (Grisebach) H. Robinson & Brettell
    O. Kuntze s/n, Argentina, Figures 69–72
  A. eremophyllum (Cabrera) H. Robinson & Brettell
    Venturi 6580, Argentina   H 38–40
  A. polymnioides (R.E. Fries) H. Robinson & Brettell
    Pflanz 4102, Bolivia, Figure 3   H 33–37
    Venturi 5280, Argentina   35–37
    Wall & Sparre 622, Argentina, Figure 73   33–37

Bishopanthus
  B. soliceps H. Robinson
    King 9280, Peru, Figures 54–57   30(–35), H 35

Cacosmia
  C. rugosa Humboldt, Bonpland, & Kunth
    Barclay & Juajibioy 8305, Ecuador
    Barclay & Juajibioy 8339, Ecuador   H 27–30
    Wurdack 1016, Peru, Figures 4, 58–61   H 27

Chionopappus
  C. benthamii (Bentham) Blake
    Asplund 10996, Peru, Figures 5, 64–67
    Ferreyra 7663, Peru   H 40
    Ferreyra 11078, Peru
    Macbride & Featherstone 162, Peru   H 35–37
    Pennell 14480, Peru

Chrysactinium
  C. acaule (Humboldt, Bonpland, & Kunth) Weddell
    Camp E-2231, Ecuador, Figures 27, 144–146   30
    Haught 3261, Ecuador, Figures 140–143
  C. amphothrix (Blake) H. Robinson & Brettell
    Ferreyra 9481, Peru
  C. caulescens (Hieronymus) H. Robinson & Brettell
    Jameson s/n, Ecuador, type of *Liabum bicolor* Blake   H 40
    Wurdack 764, Peru
  C. hieracioides (Humboldt, Bonpland, & Kunth) H. Robinson & Brettell
    Wurdack 1113, Peru, Figure 28   30–32
  C. longiradiatum (Hieronymus) H. Robinson & Brettell
    Fagerlind & Wibon 1563, Ecuador   30–34
    Haught 3261, Ecuador   H 35–37
    Holmgren 560, Ecuador

Erato
  E. polymnioides DeCandolle
    Ferreyra 8168, Peru   H 35–37

<div align="center">14</div>

Valeur 994, Dominican Republic

L. eggersii Hieronymus
  Camp E-3196, Ecuador 27–30
  Fagerlind & Wibon 290, Ecuador, Figure 15
  Haught 3446, Peru .... H 30–32

L. falcatum Rusby
  Smith 2012, Colombia, type, Figure 16 .... H 27

L. ferreyrii H. Robinson
  Hutchison, Wright & Straw 5948, Peru

L. floribundum Lessing
  Camp E-3196, Ecuador 24–46
  Hutchison & v. Bismark 6337, Peru

L. grandiflorum (Humbolt, Bonpland, & Kunth) Lessing
  Camp E-3123, Ecuador
  Rose, Pachano & Rose 23232, Ecuador, type of *L. amplexans* Blake

L. igniarium (Humboldt, Bonpland, & Kunth) Lessing
  Heilborn 534, Ecuador, Figures 112–117 32–35
  Lehmann 4896, Ecuador, type of *L. lehmannii* Hieronymus

L. kingii H. Robinson
  Sydow 484, Ecuador 27–30

L. melastomoides (Humboldt, Bonpland, & Kunth) Lessing
  Dryander 39172, Colombia .... H 30–32
  Humbert et al. 25795, Colombia 25–27

L. nigro-pilosum Hieronymus
  Mexia 6686, Ecuador

L. nudicaule H. Robinson
  Hutchison 1191, Peru

L. oblanceolatum Urban & Ekman
  Loigier 15402, Dominican Republic

L. ovatifolium Urban
  Ekman H-12578, Dominican Republic, type 33–35

L. polycephalum Urban
  Ekman H-5346, Haiti 33–35

L. poiteaui (Cassini) Urban
  Ekman H-3713, Haiti, Figure 17 30–33

L. sandemanii H. Robinson
  Sandeman 4420, Peru, type .... H 35

L. selleanum Urban
  Ekman H-1548, Haiti, type, Figure 18 32–35

L. solidagineum (Humboldt, Bonpland, & Kunth) Lessing
  Humbert 31002, Peru .... H 25–27
  Hutchison 1129, Peru 32, 33
  Macbride & Featherstone 1519, Peru 32–35

L. subacaule Rydberg
  Ekman H-1870, Haiti, Figure 19 30–32
  Valeur 56, Dominican Republic, Figures 20, 118–120 30–32

L. umbellatum (L.) Schultz-Bipontinus
  Maxon 277, Jamaica
  Maxon 8575, Jamaica 32–35

L. vargasii H. Robinson
  Vargas 10182, Peru, type

L. wrightii Grisebach
  Ekman 5061, Cuba 31–34
  Ekman 14745, Cuba

L. wurdackii Ferreyra

M. senecionidis Benth
  García-Barriga 12518, Colombia
  Cárdenas 3277, Bolivia
  Haught 3295, Ecuador, Figure 35
  King & Almeda 7842, Ecuador, Figures 166, 167
  Pennell 769, Colombia, type of *M. attenuata* Rusby
  Schneider 7, Colombia   27–30
  v. Sneidern 2778, Colombia   30–32
M. silphioides (Poeppig & Endlicher) H. Robinson & Brettell
  Swingle 183, Peru, Figure 36
M. subviride (Blake) H. Robinson & Brettell
  Cook & Gilbert 1365, Peru, type, Figure 37
M. venosissima Ruiz & Pavon
  Macbride 4312, Peru, type of *Liabum pulchrum* Blake, Figure 38

Munnozia subgenus *Kastnera*
  M. acostae Chung
    Asplund 9586, Ecuador   H 34–37
  M. annua (Muschler) H. Robinson & Brettell
    Hutchison & Wright 5084, Peru, Figures 39, 168–171
  M. liaboides (Lessing) H. Robinson
    Ferreyra 6968, Peru
    Haught 3294, Ecuador   H 35–37
  M. nivea (Hieronymus) H. Robinson & Brettell
    Killip & Varela 34590, Colombia, Figure 40
    Weberbauer 6022   H 33–35
  M. tenera (Schultz-Bipontinus) H. Robinson & Brettell
    Barclay & Juajibioy 5760   H 35–37
    Killip 9775, Colombia, Figures 172–180

Oligactis subgenus *Oligactis*
  O. latifolia (Hieronymus) H. Robinson & Brettell
    v. Sneidern 354, Colombia   27–30
  O. sessiliflora (Humboldt, Bonpland, & Kunth) H. Robinson & Brettell
    Allart 370, Venezuela, type of *Liabum tovarense* Badillo
    Ariste-Joseph A-257, Colombia   25–27
  O. volubilis (Humboldt, Bonpland, & Kunth) Cassini
    Cuatrecasas 12855, Colombia, Figures 99–103
    Gehringer 427, Venezuela, type of *Liabum meridense* Badillo
    Pérez-Arbelaez & Cuatrecasas 8164, Colombia, type of *Liabum boyacense*
      Cuatrecasas
    Smith 2013, Colombia, type of *Liabum biattenuatum* Rusby, Figure 21

Oligactis subgenus *Andromachiopsis*
  O. coriacea (Hieronymus) H. Robinson & Brettell
    Camp E-4190, Ecuador, Figure 22   33–37
    Mexia 7476, Ecuador
  O. ecuadoriensis (Hieronymus) H. Robinson & Brettell
    Lehmann 4897, Ecuador, type
  O. ochracea (Cuatrecasas) H. Robinson & Brettell
    Townsend A-193, Peru   H 33–35
  O. pastoensis (Cuatrecasas) H. Robinson & Brettell
    Cuatrecasas 11949, Colombia, type   H 33–35
  O. pichinchensis (Hieronymus) H. Robinson & Brettell
    Mexia 7697, Ecuador, Figures 104–107   30–32, H 35
    Sydow 605, Ecuador, Figure 23   27–30

Paranephelius
  P. asperifolius (Muschler) H. Robinson & Brettell
    Fiebrig 3538, Bolivia, type   38–40
  P. bullatus A. Gray ex Weddell
    Macbride & Featherstone 1656, Peru
    Macbride & Featherstone 2131, Peru
  P. jelskii (Hieronymus) H. Robinson & Brettell
    Wurdack 760, Peru, Figure 1   35–37
    Wurdack 1240, Peru, Figure 48
  P. ovatus Weddell
    Pennell 13363, Peru   47–50
  P. uniflorus Poeppig & Endlicher
    Cerrate 1367, Peru, Figures 45–47   36–40
    Ferreyra 5580, Peru, Figures 41–44
    Herzog 1840, Bolivia, Figure 2   42–45

Philoglossa
  P. mimuloides (Hieronymus) H. Robinson & Cuatrecasas
    Dodson & Thien 1467, Ecuador   H 35
    Firmin 52, Ecuador
    King 6633, Ecuador
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  P. peruviana DeCandolle
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  P. pterocarpa Sandwith
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    Metcalf 30531, Peru, Figures 50–53   H 37–40
  P. striata (Cuatrecasas) H. Robinson & Brettell
    Weberbauer 7107, Peru, type   H 38–40

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  S. andrieuxii (DeCandolle) H. Robinson & Brettell
    Cronquist & Sousa 10457, Mexico   H 50–52
  S. andromachioides (Lessing) Rydberg
    Pringle 5905, Mexico   H 37–42
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  S. brachypus Rydberg
    Pittier 1886, Guatemala, type
  S. caducifolia (B.L. Robinson & Bartlett) Rydberg
    King & Soderstrom 4988, Mexico
    Palmer 245, Mexico
  S. deamii (B.L. Robinson & Bartlett) Rydberg
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  S. dimidia (Blake) H. Robinson & Brettell
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S. sericolepis (Hemsley) Rydberg	
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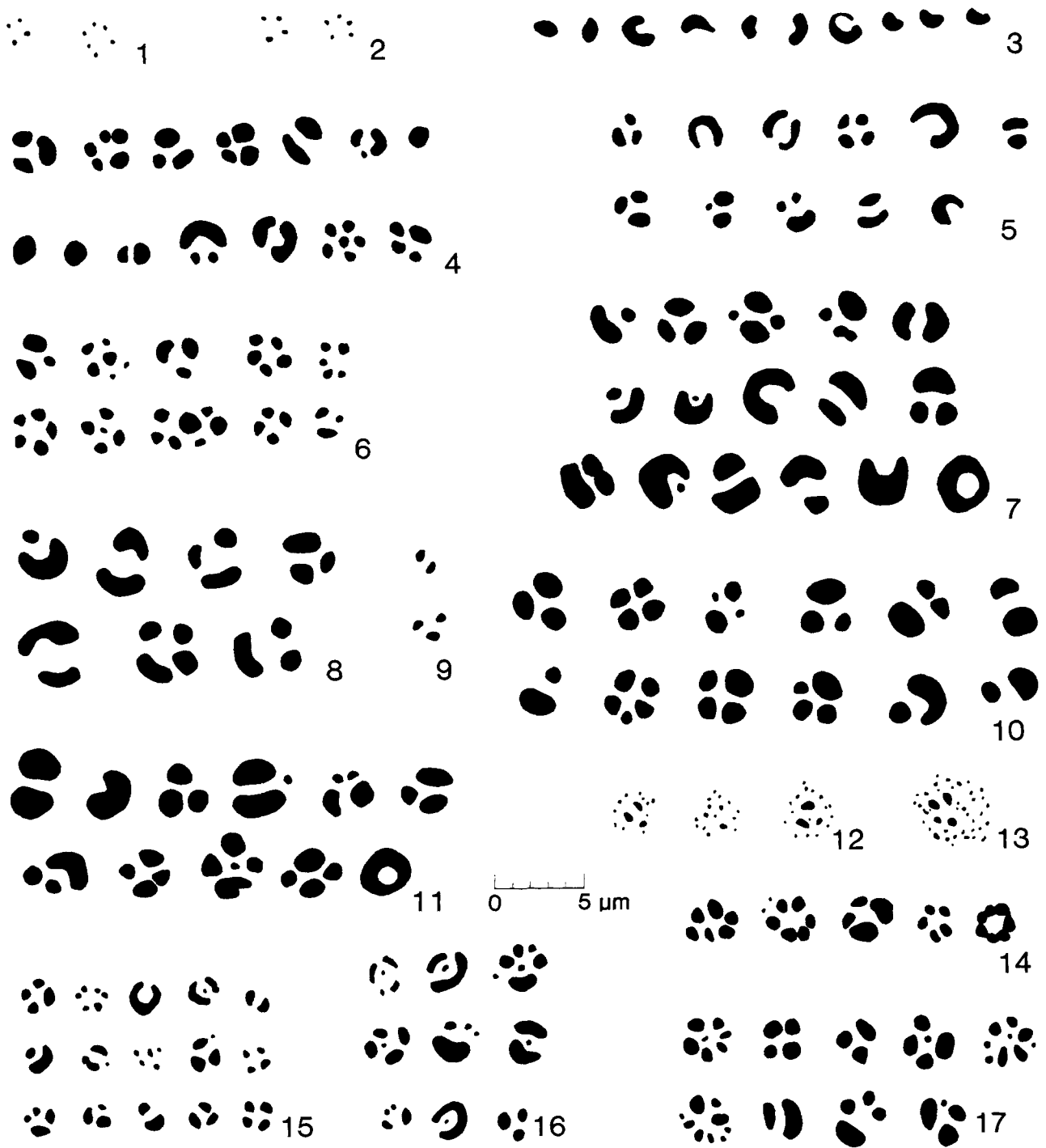
FIGURES 1–17.—Basal columellar patterns of the tribe Liabeae in vertical view (for citation of specimens see appendix): 1, *Paranephelius jelskii;* 2, *P. uniflorus;* 3, *Austroliabum polymnioides;* 4, *Cacosmia rugosa;* 5, *Chionopappus benthamii;* 6, *Ferreyranthus excelsus;* 7, *F. vernonioides;* 8, *Sinclairia klattii;* 9, 10, *S. deamii;* 11, *Liabellum angustissimum;* 12, 13, *Liabum barahonense;* 14, *L. bourgeaui;* 15, *L. eggersii;* 16, *L. falcatum;* 17, *L. poiteaui.*
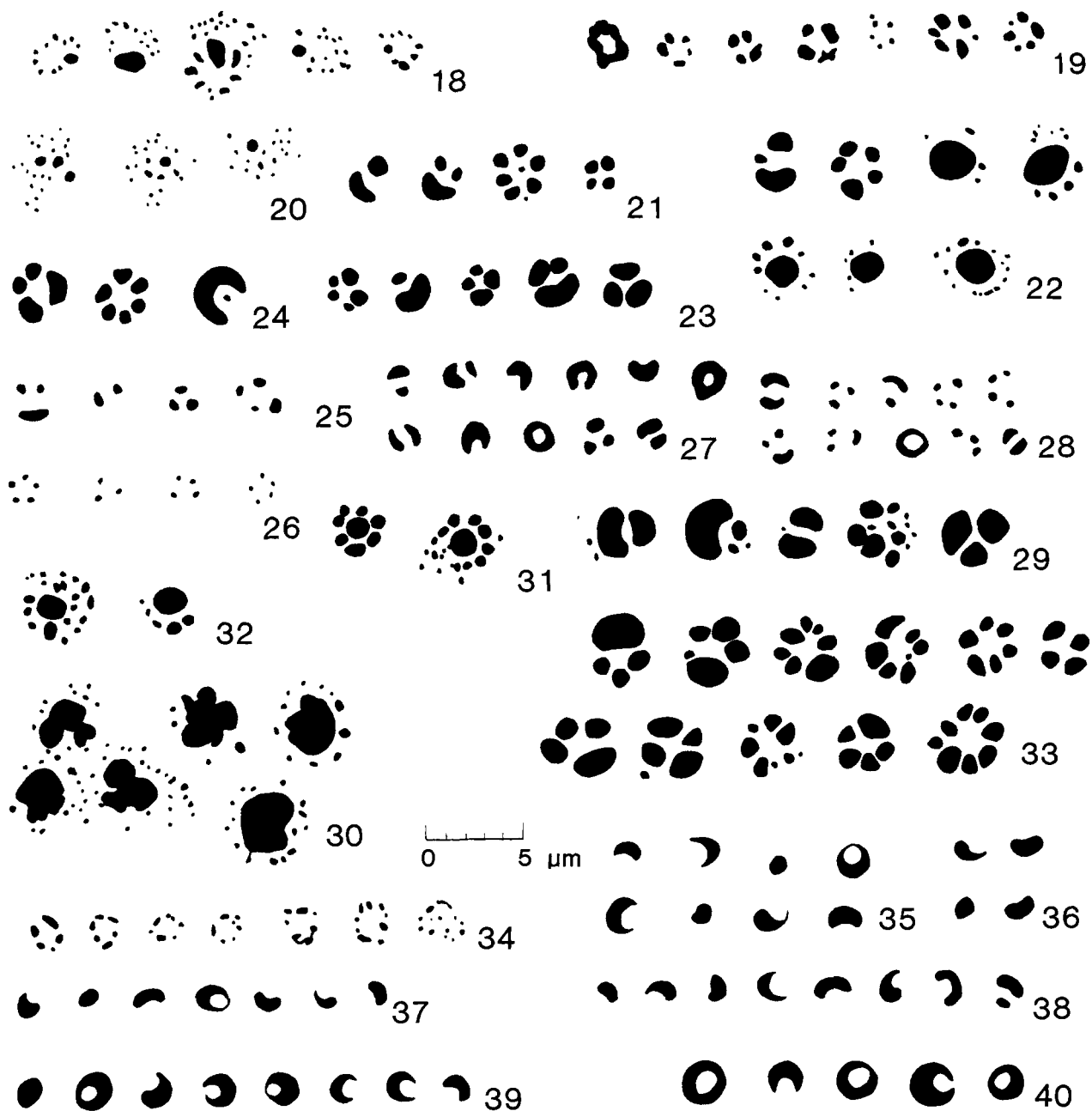
FIGURES 18-40.—Basal columellar patterns of the tribe Liabeae in vertical view: 18, *Liabum selleanum;* 19, 20, *L. subacaule;* 21, *Oligactis volubilis;* 22, *O. (Andromachiopsis) coriacea;* 23, *O. (A.) pichinchensis;* 24, *Erato polymnioides;* 25, *Philoglossa mimuloides* f. *sapida;* 26, *P. peruviana* DC; 27, *Chrysactinium acaule;* 28, *C. hieracioides;* 29, *Munnozia foliosa;* 30-32, *M. jussieui;* 33, *M. lanceolata;* 34, *M. lyrata;* 35, *M. senecionidis;* 36, *M. silphioides;* 37, *M. subviridis;* 38, *M. venosissima;* 39, *M. (Kastnera) annua;* 40, *M. (K.) nivea.*
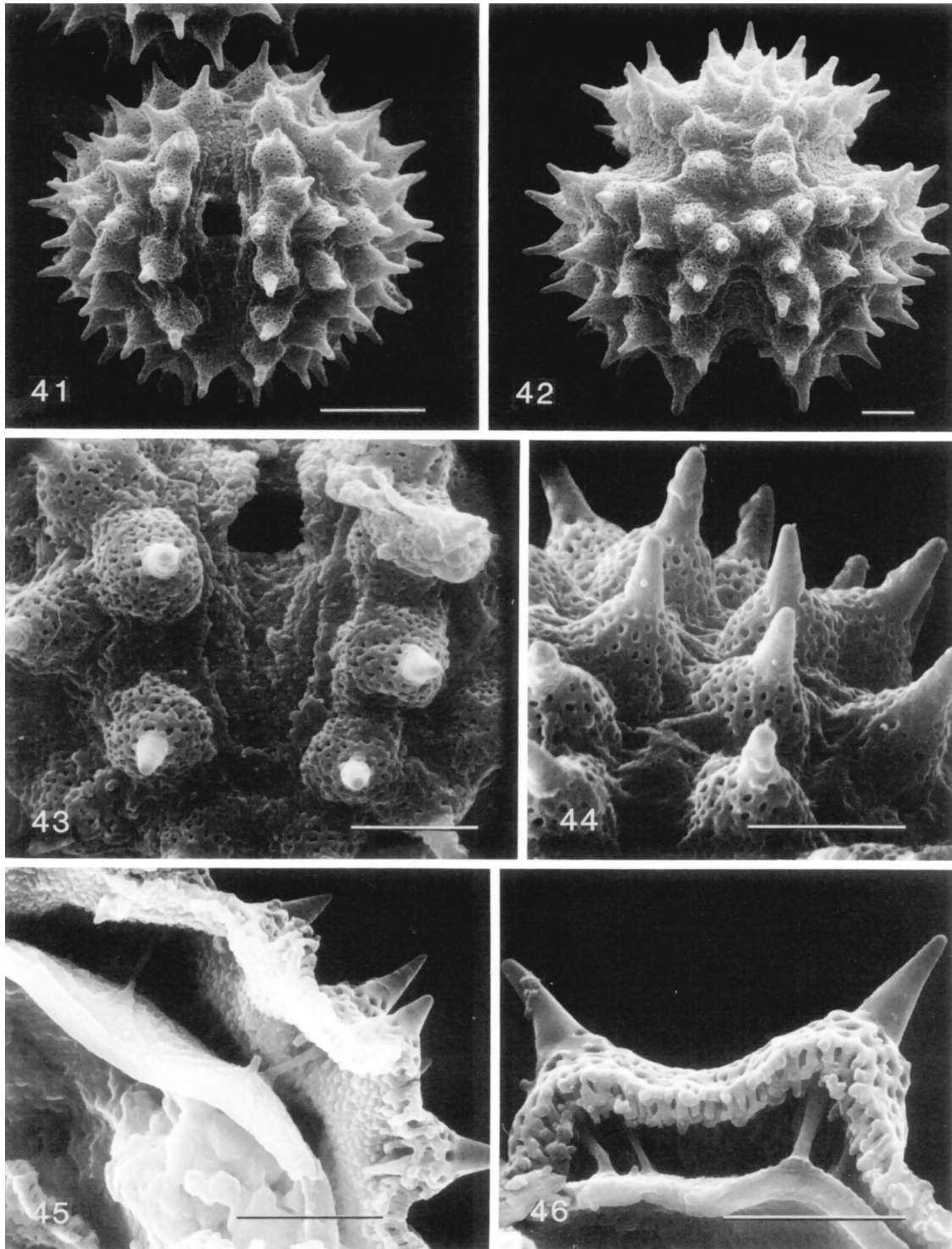
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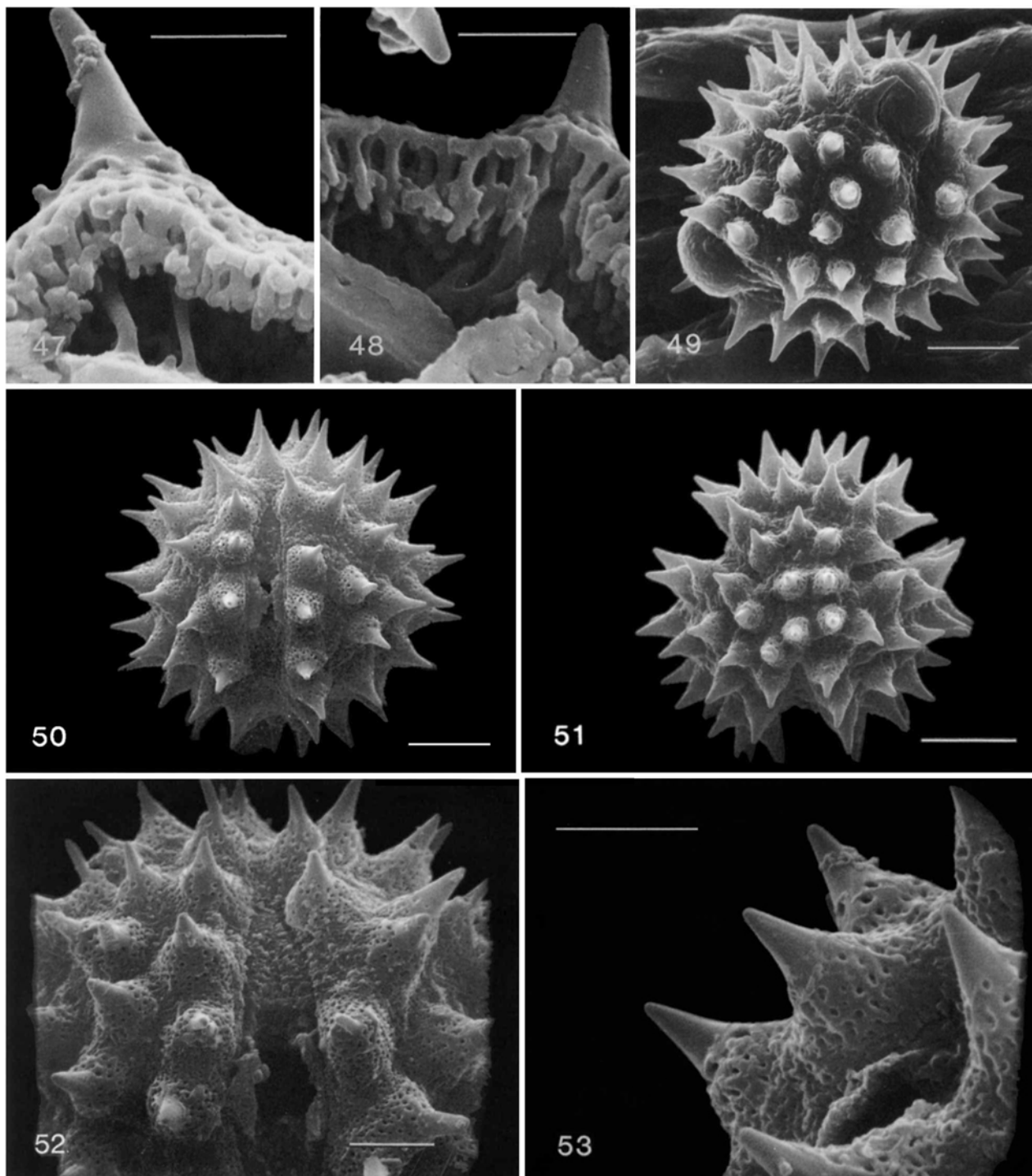
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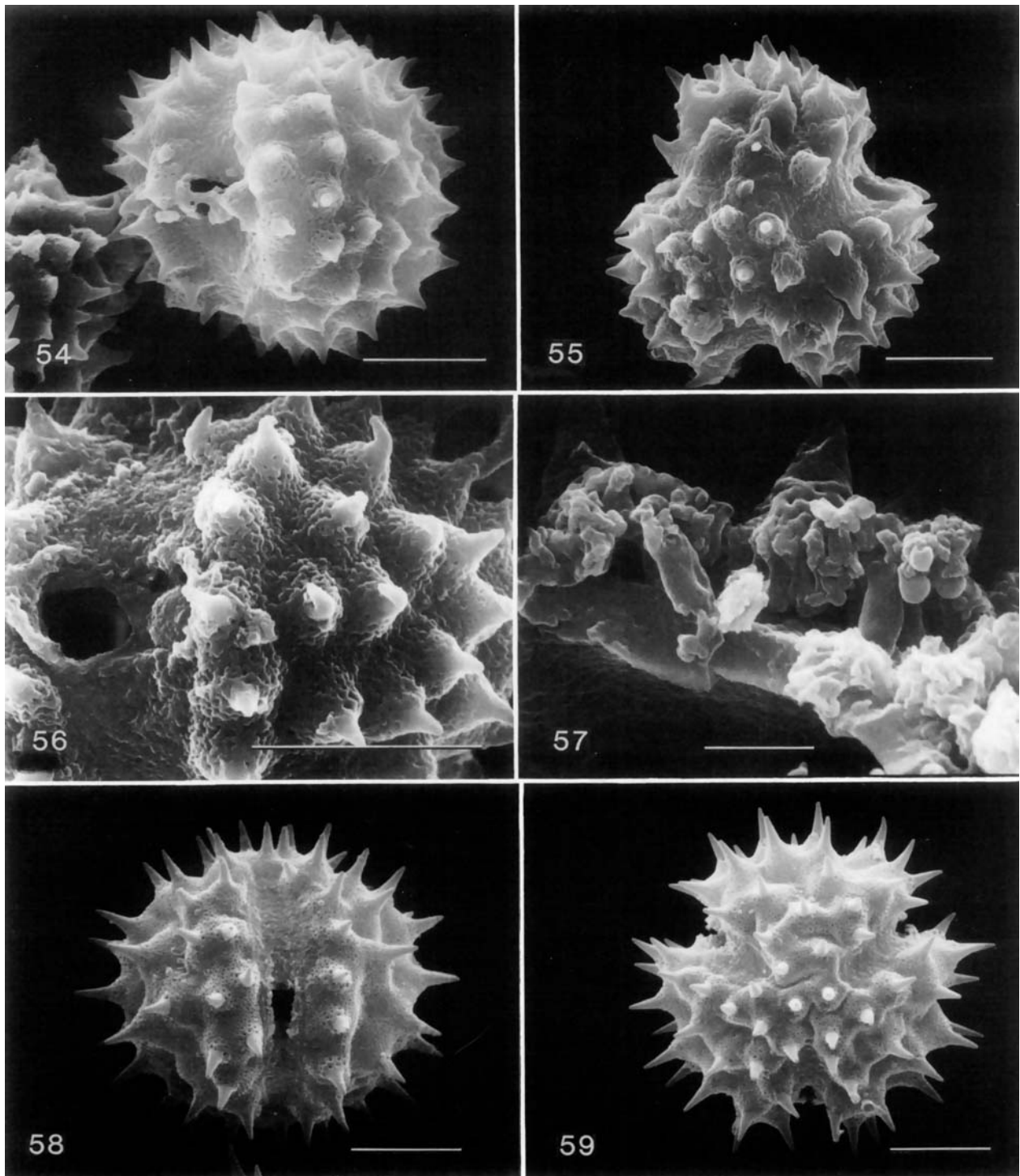
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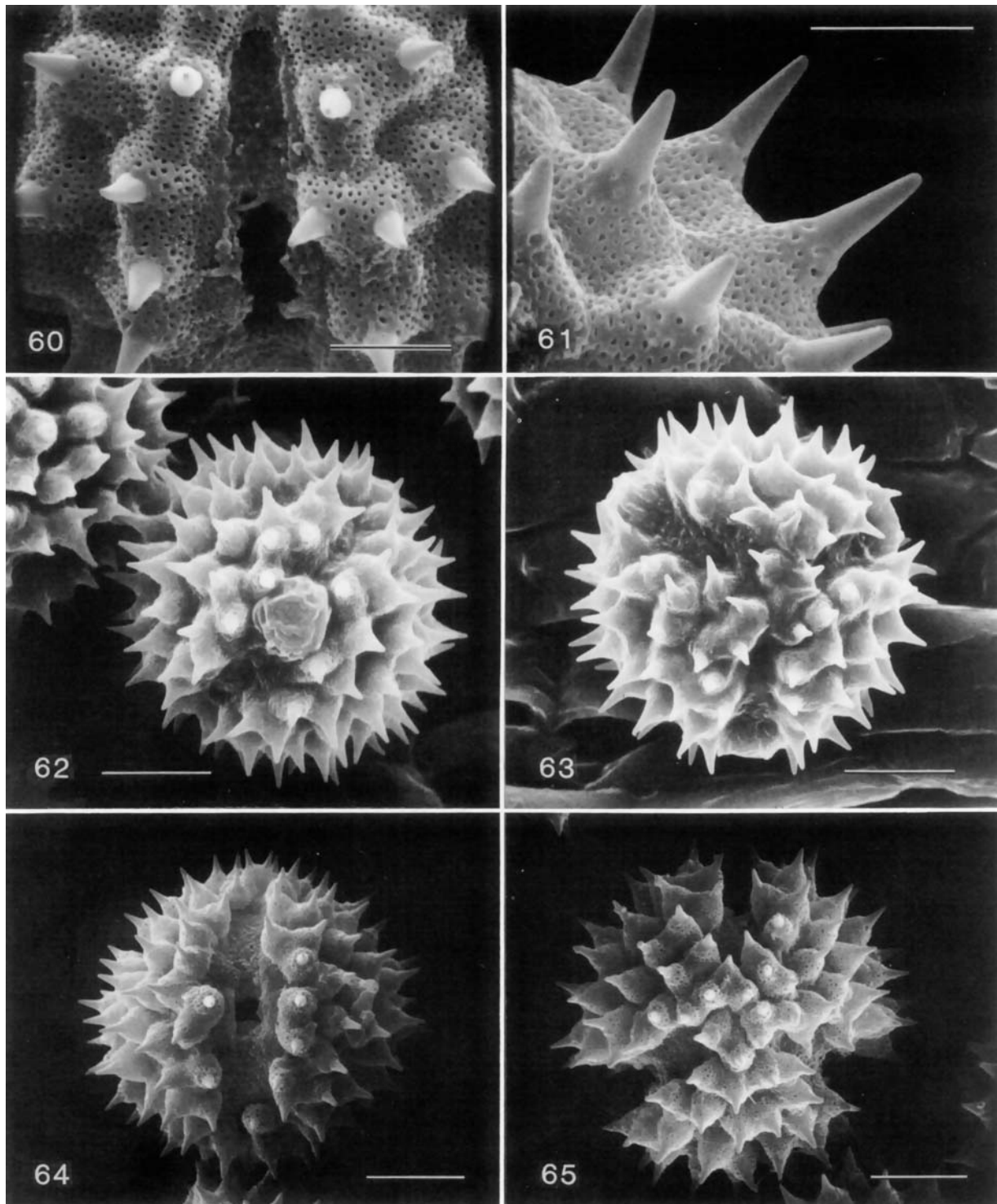
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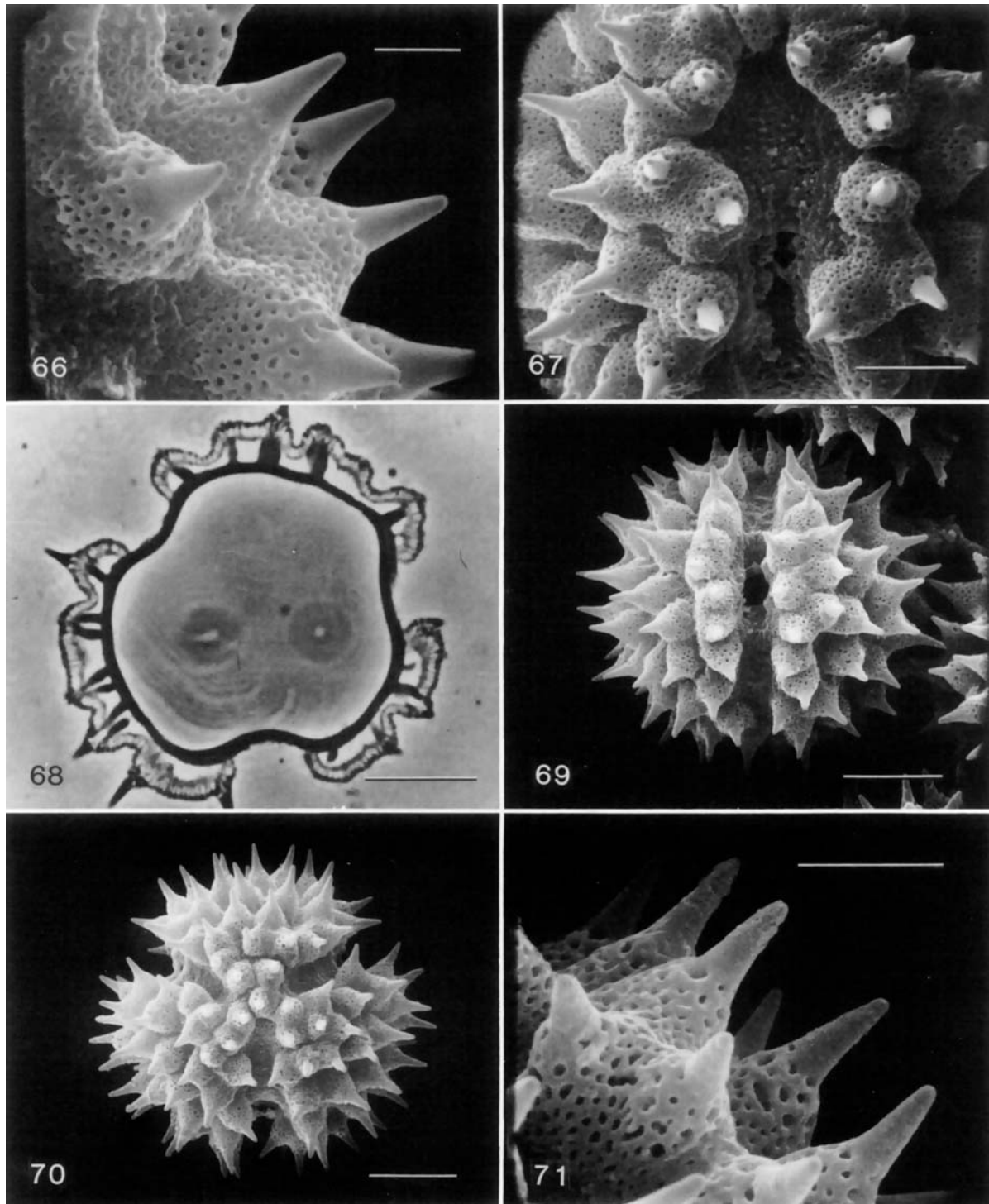
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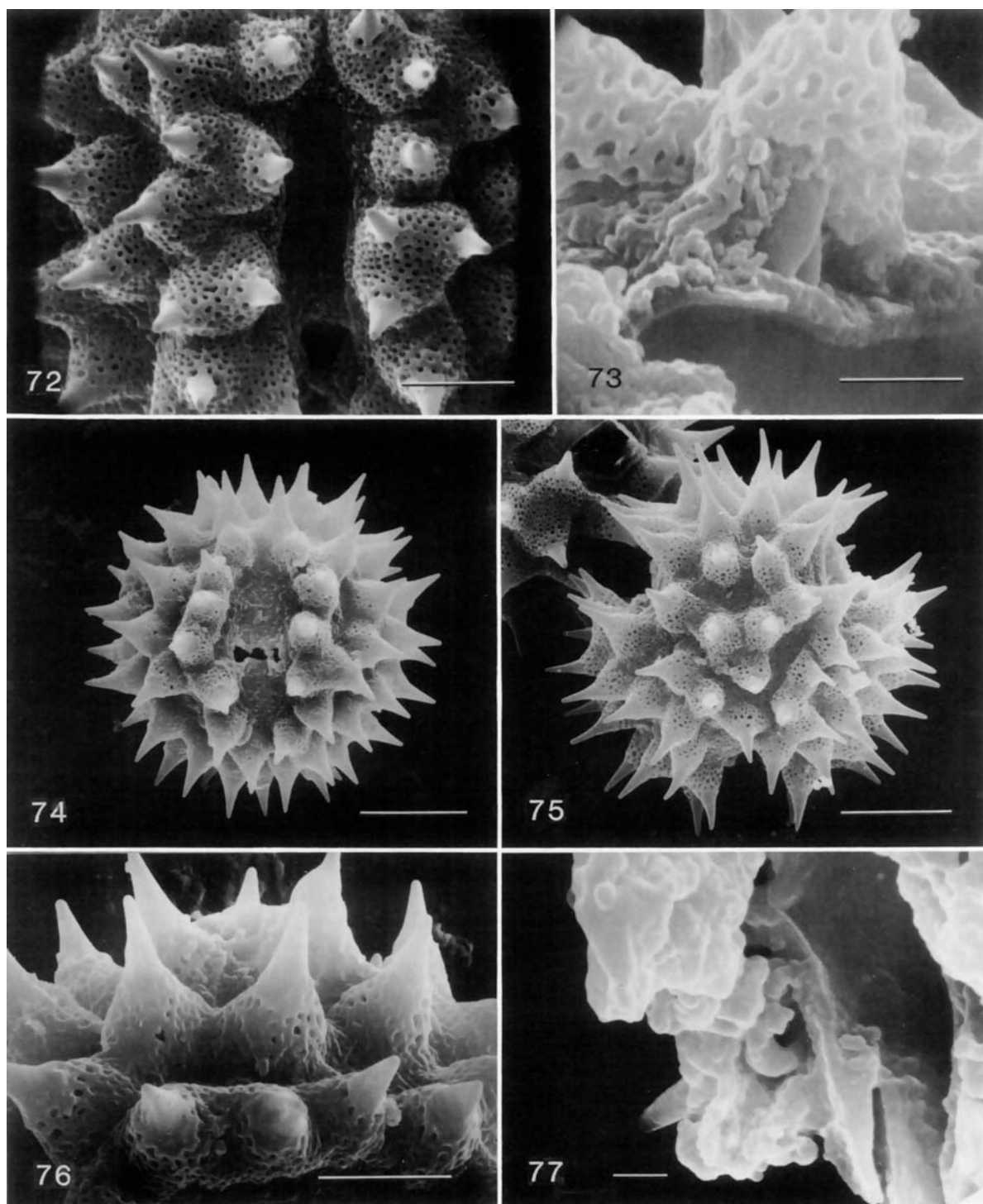
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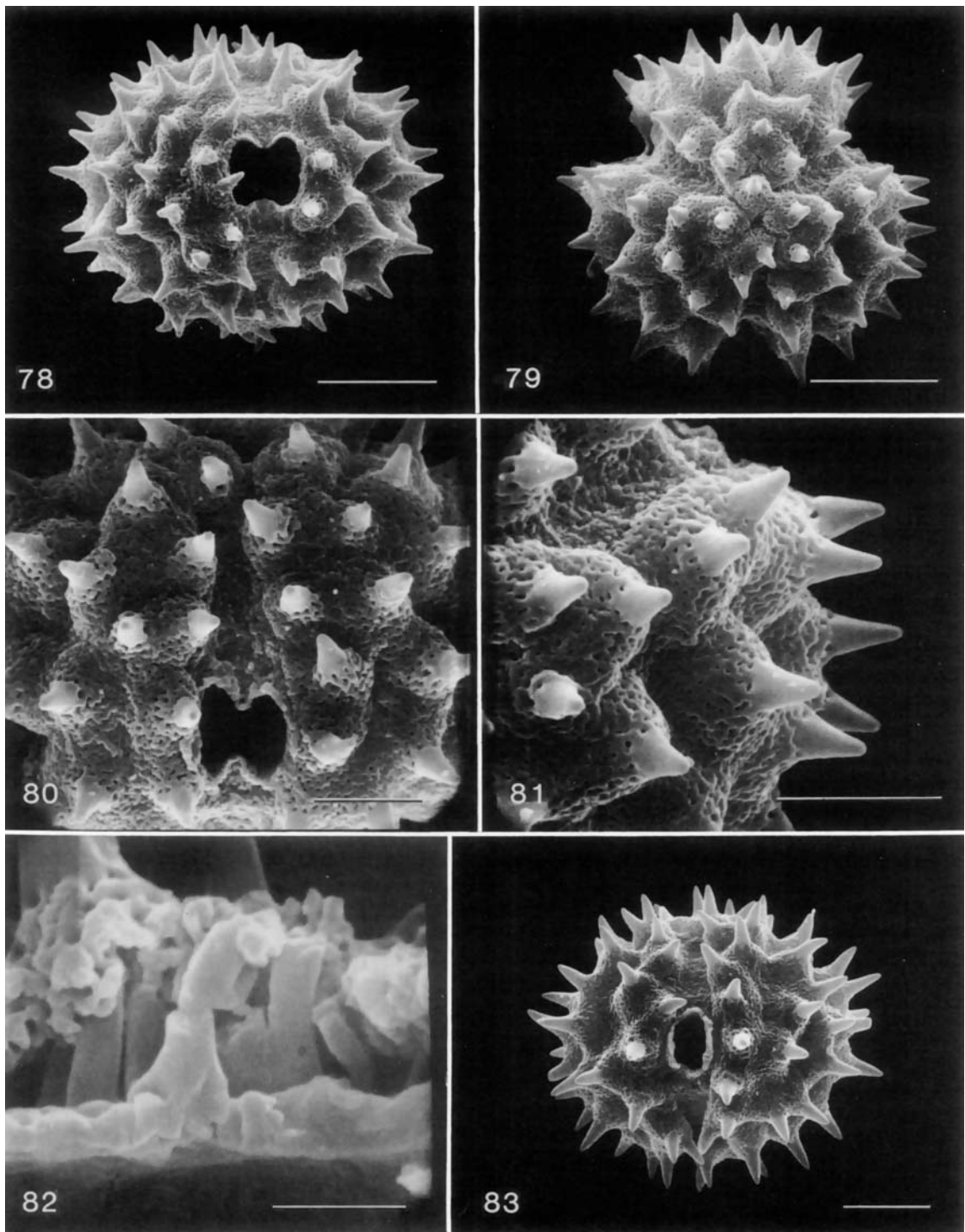
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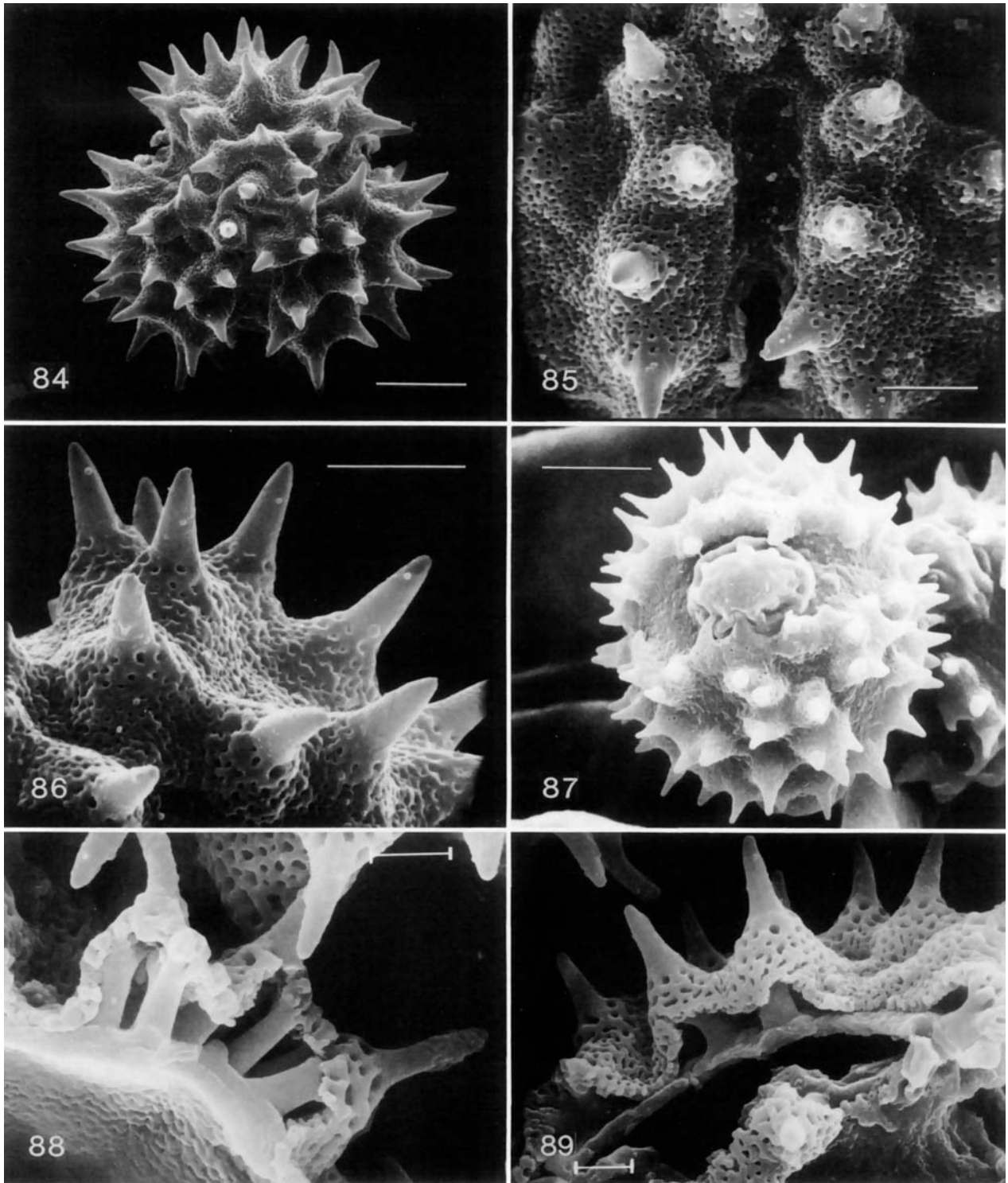
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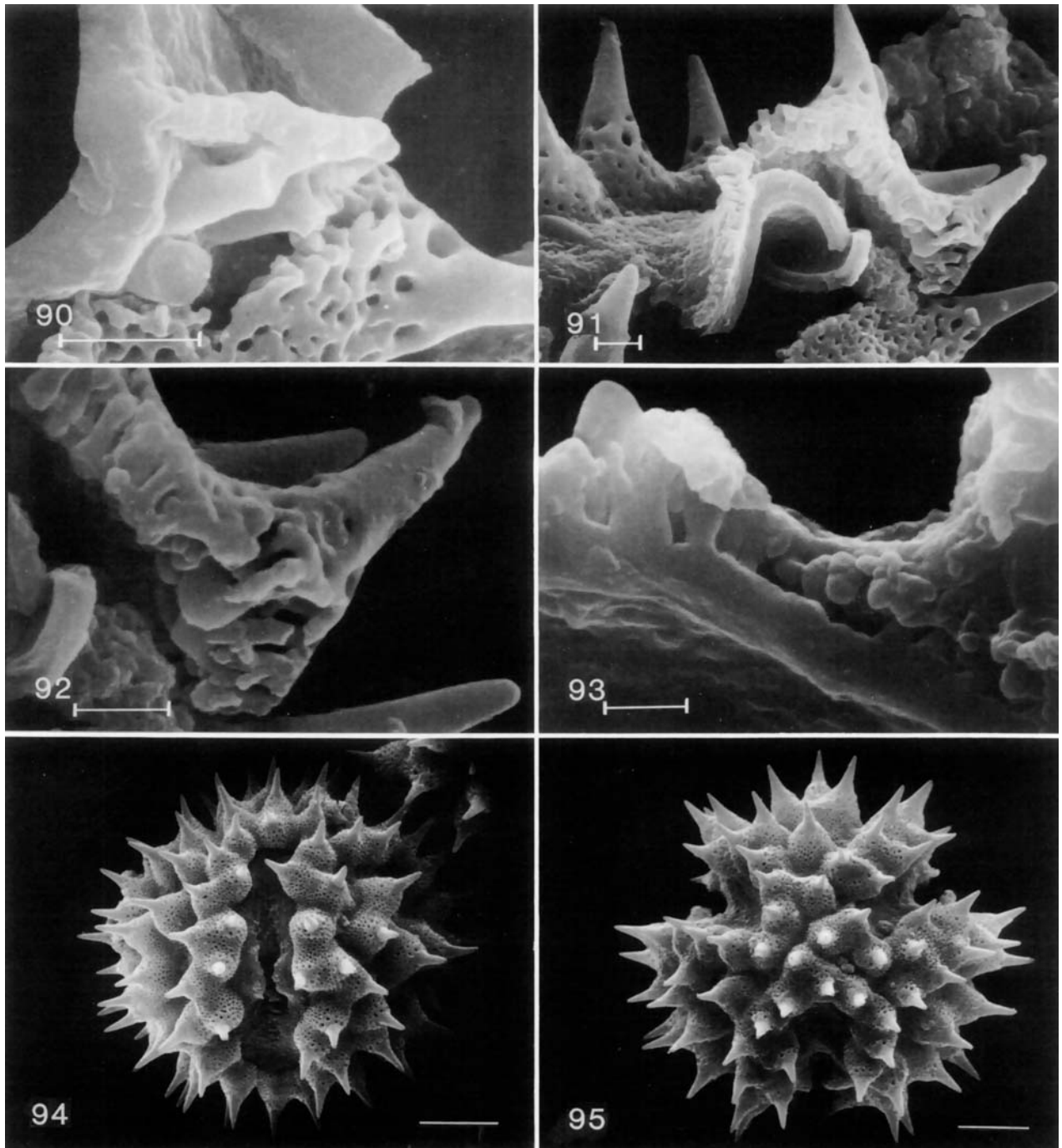
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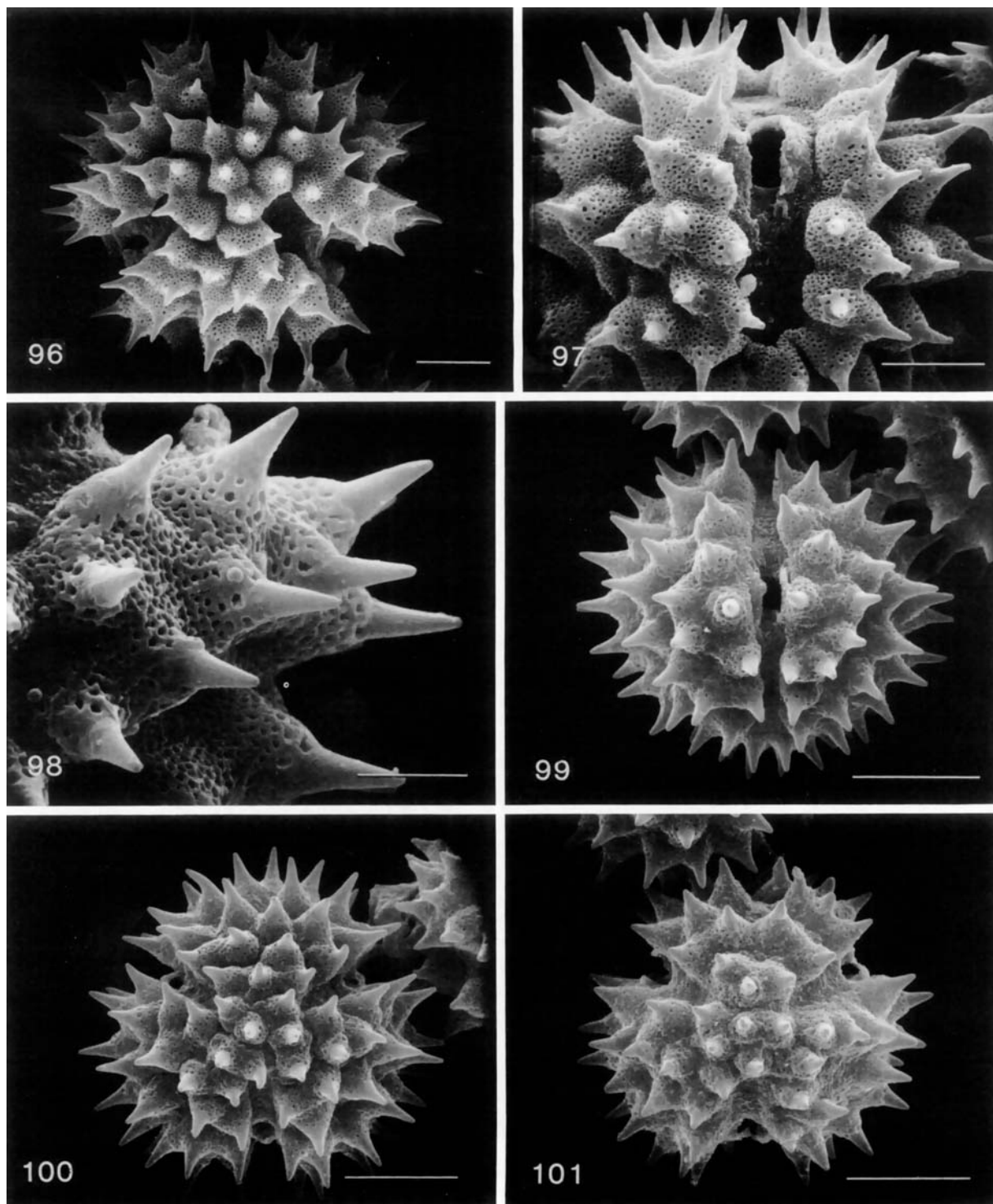
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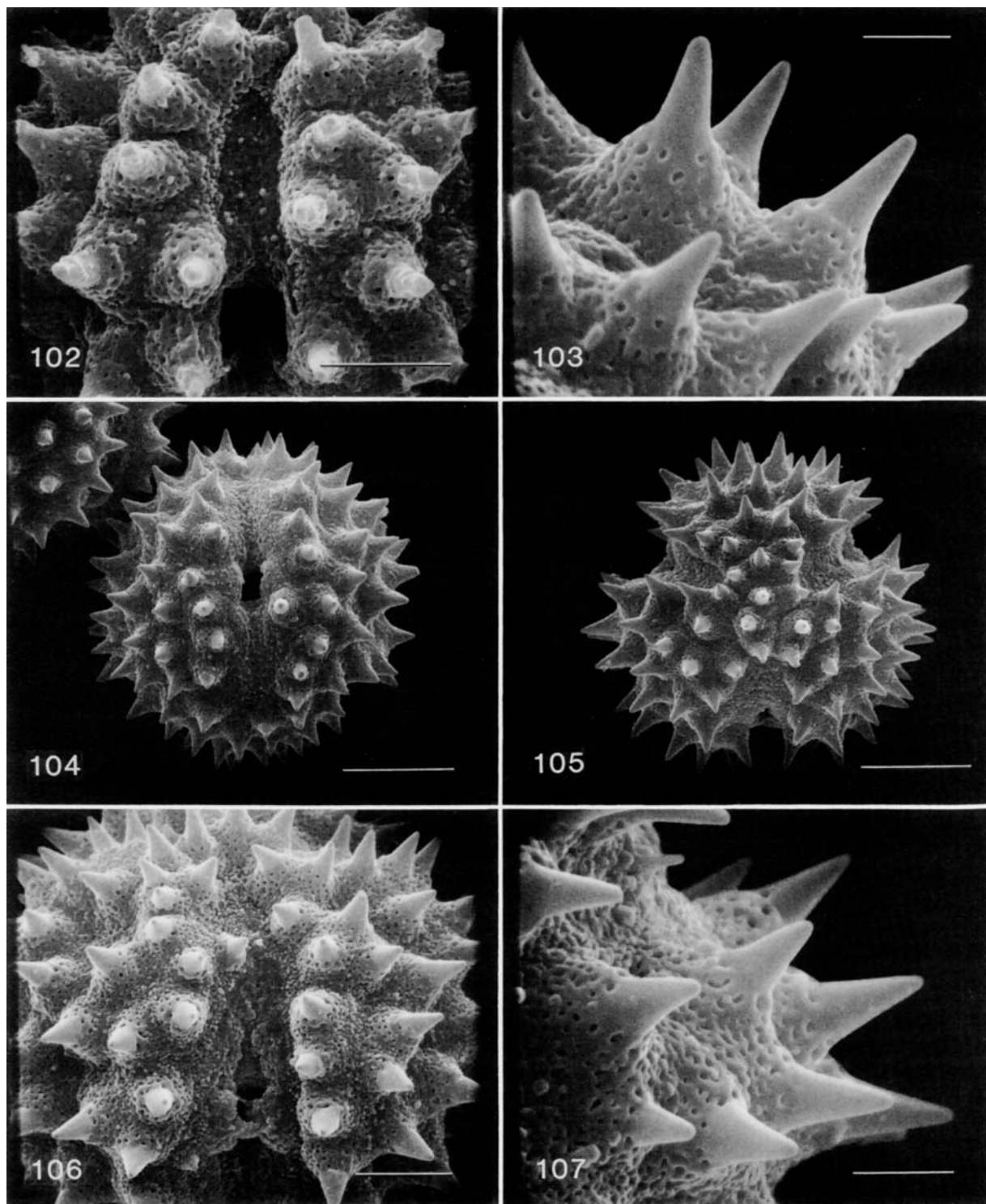
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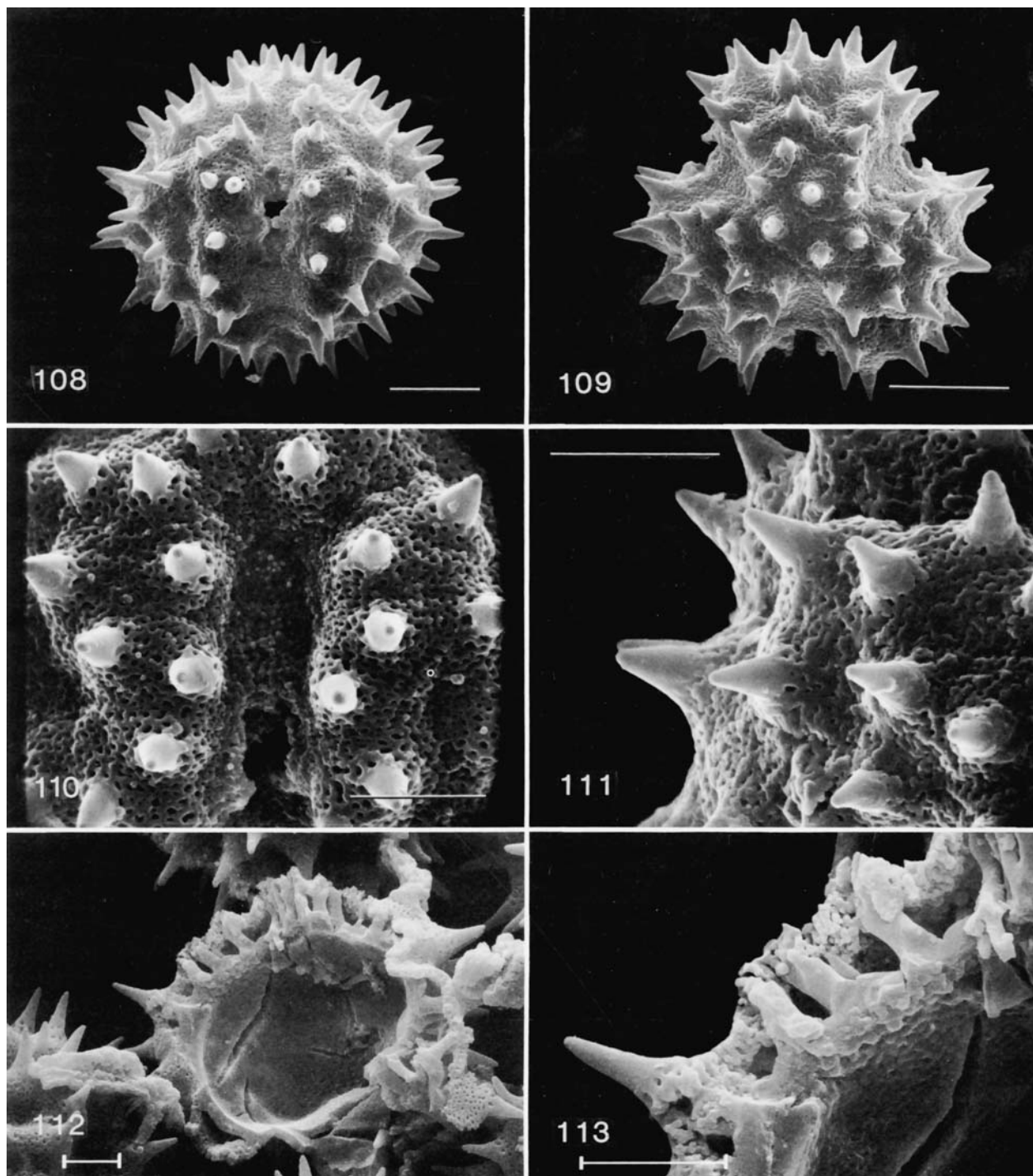
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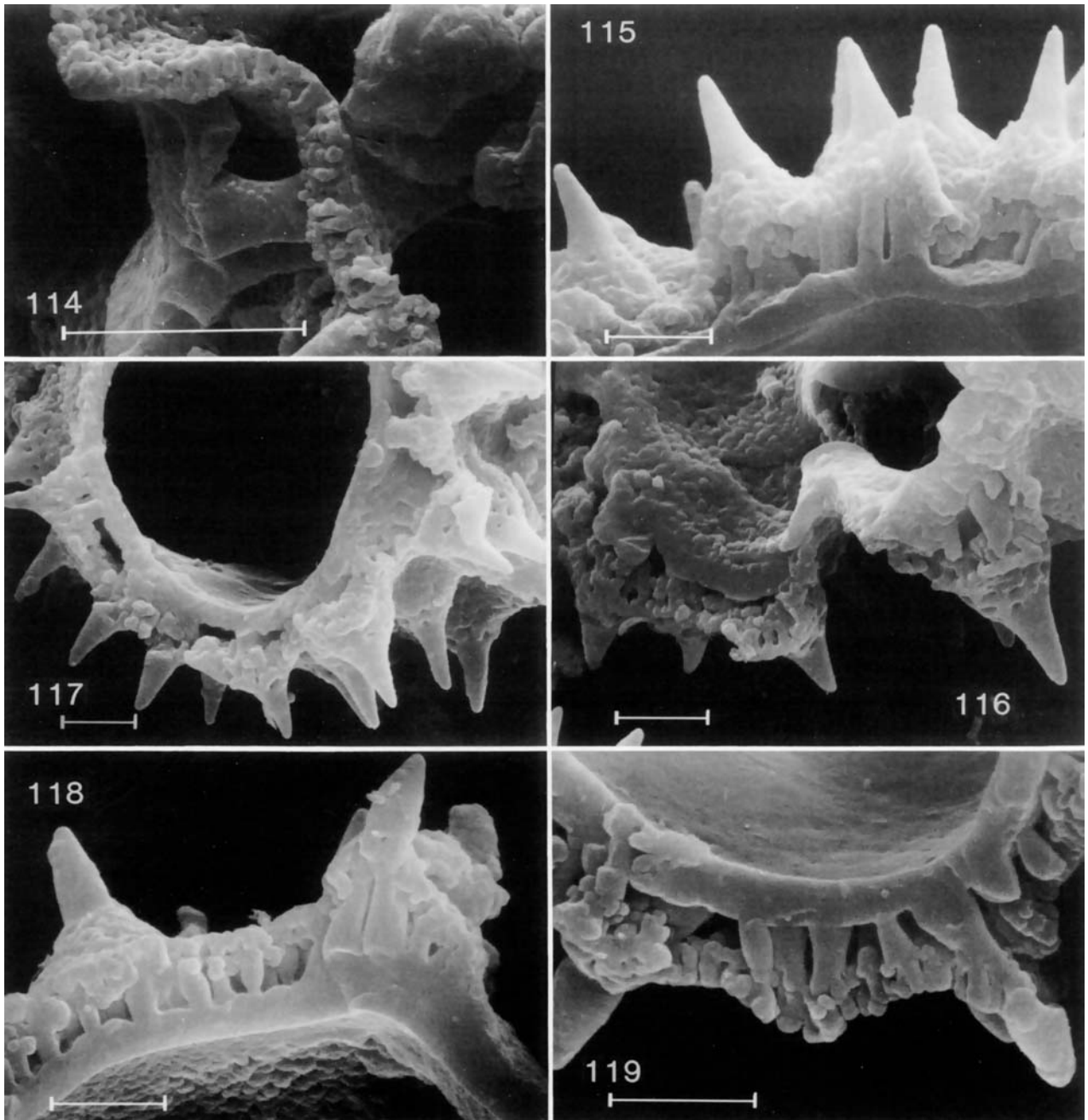
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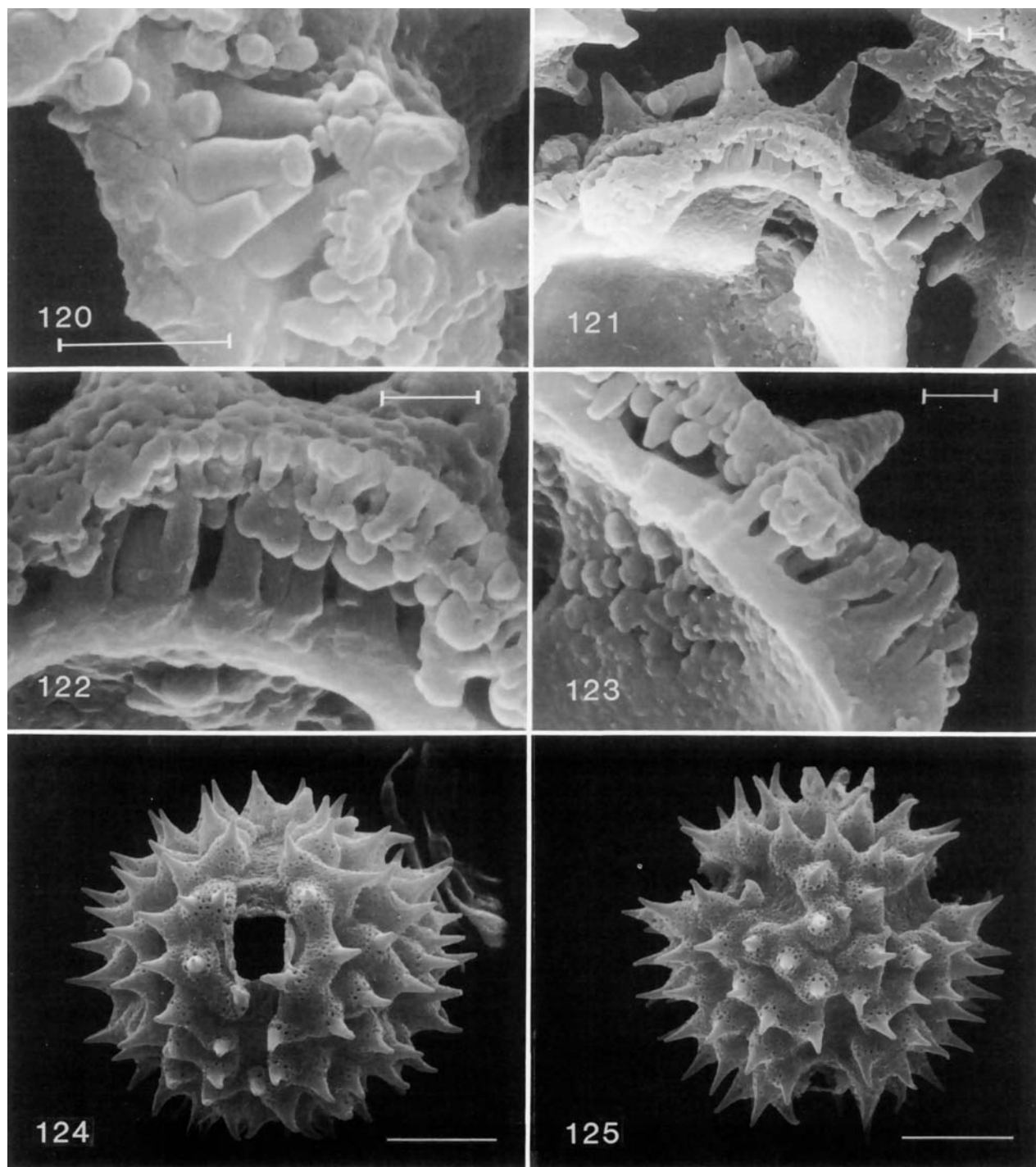
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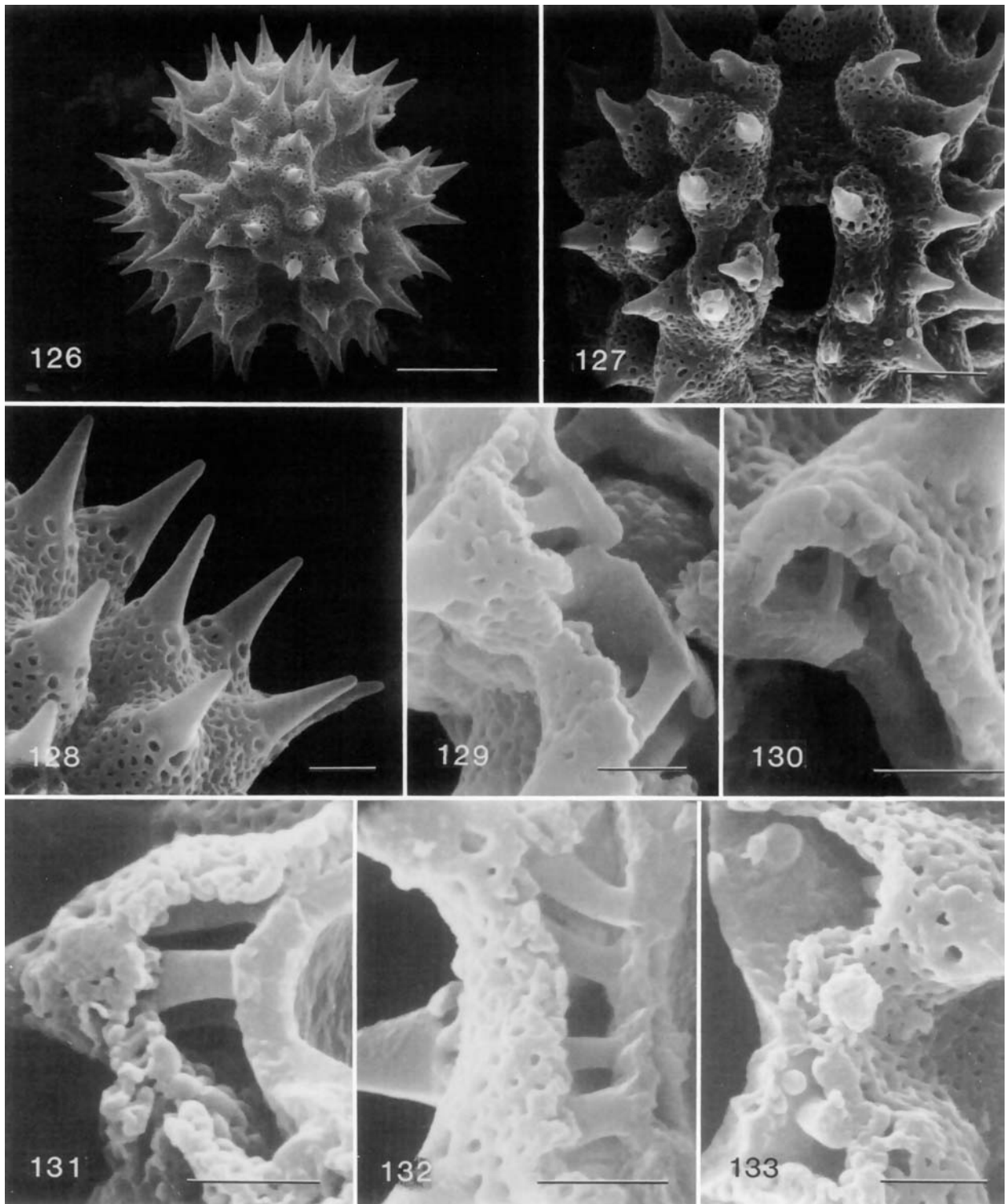
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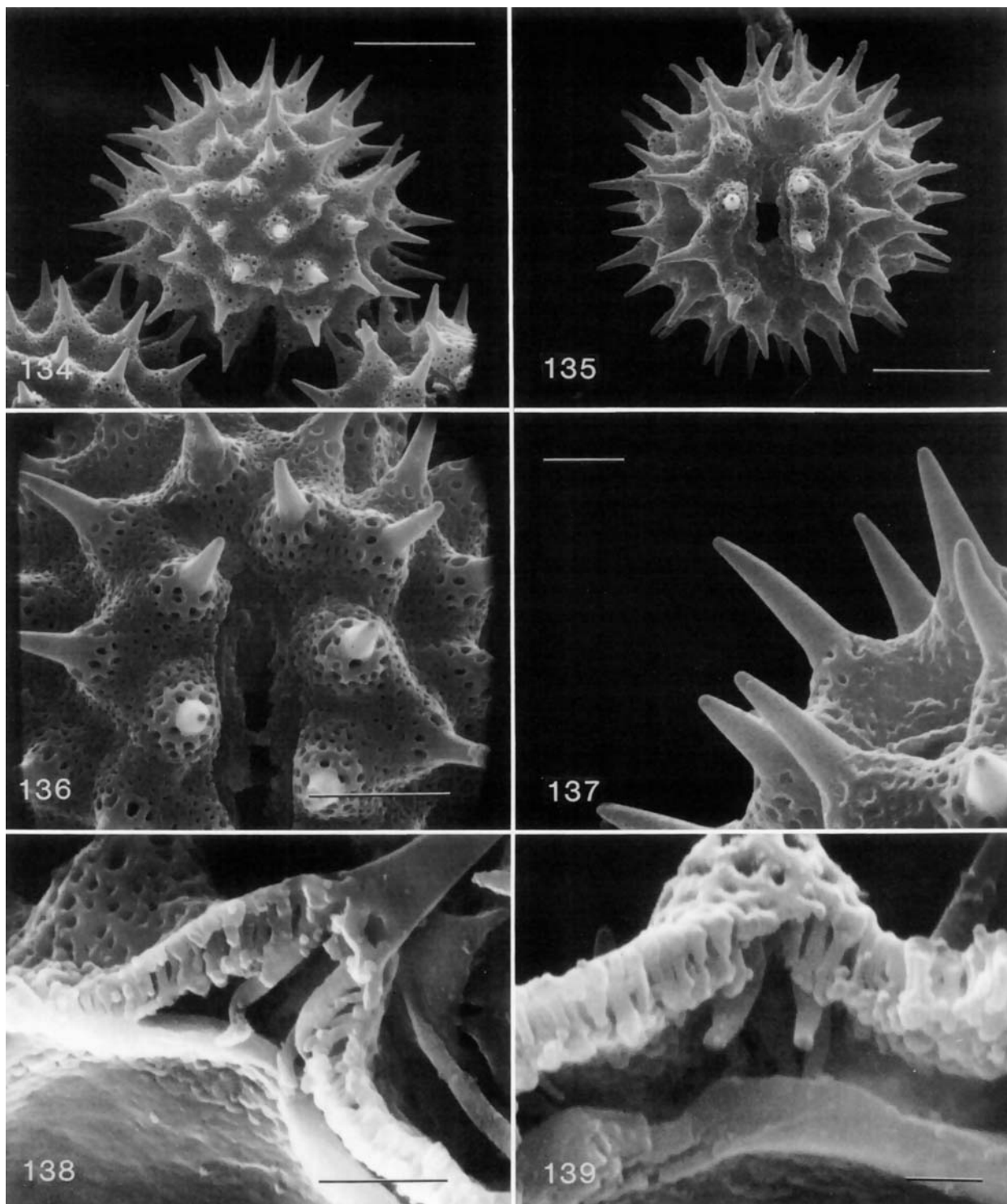
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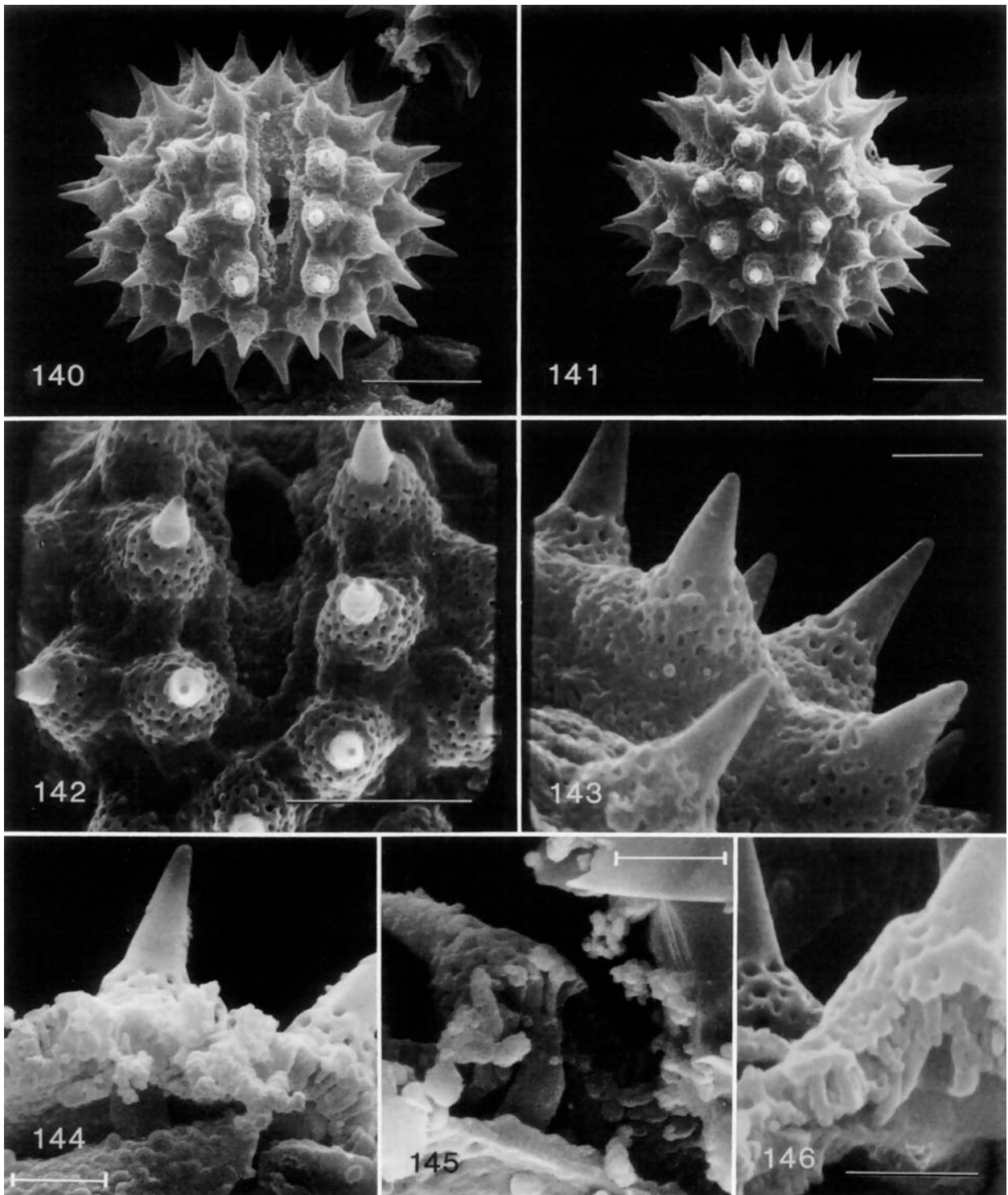
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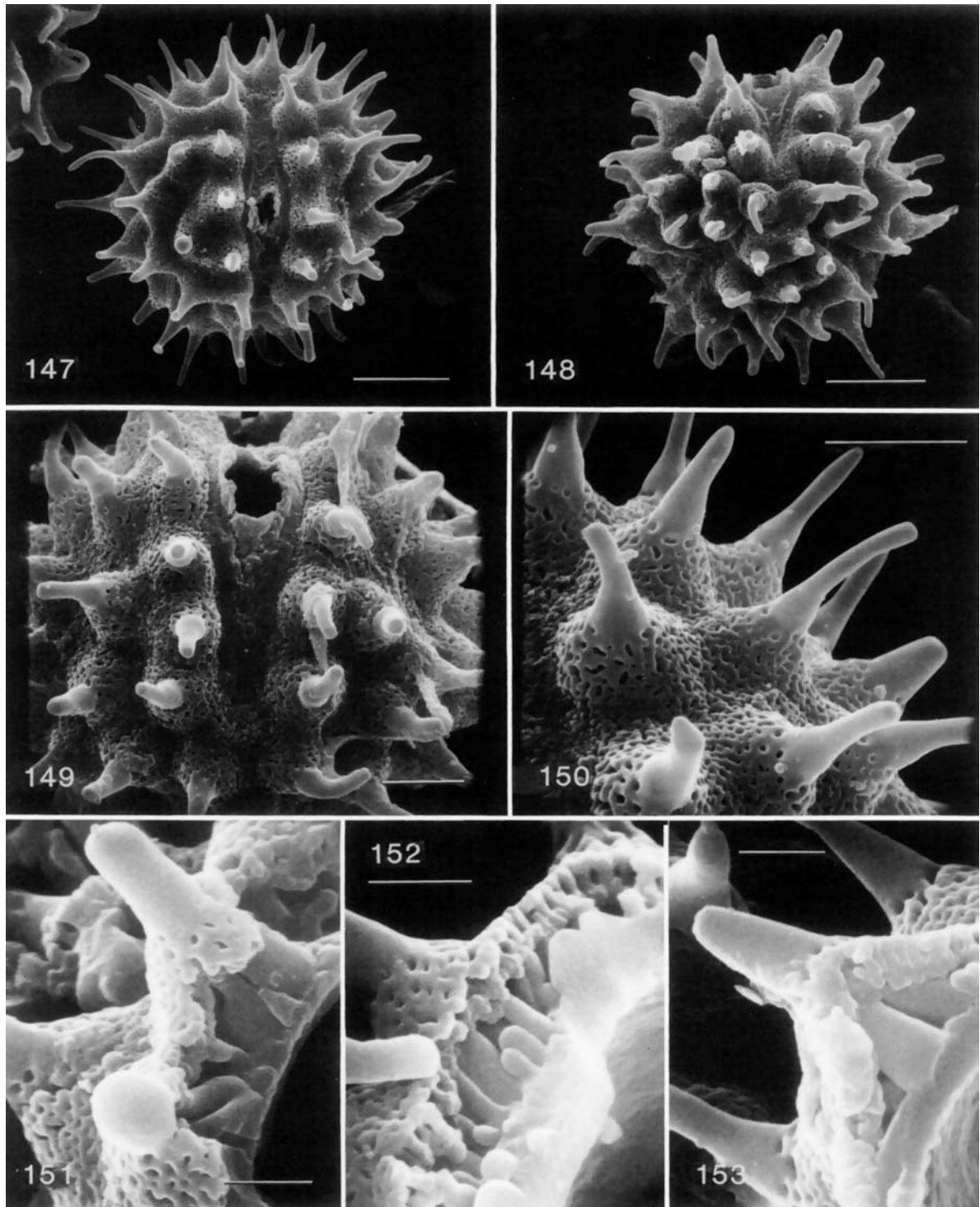
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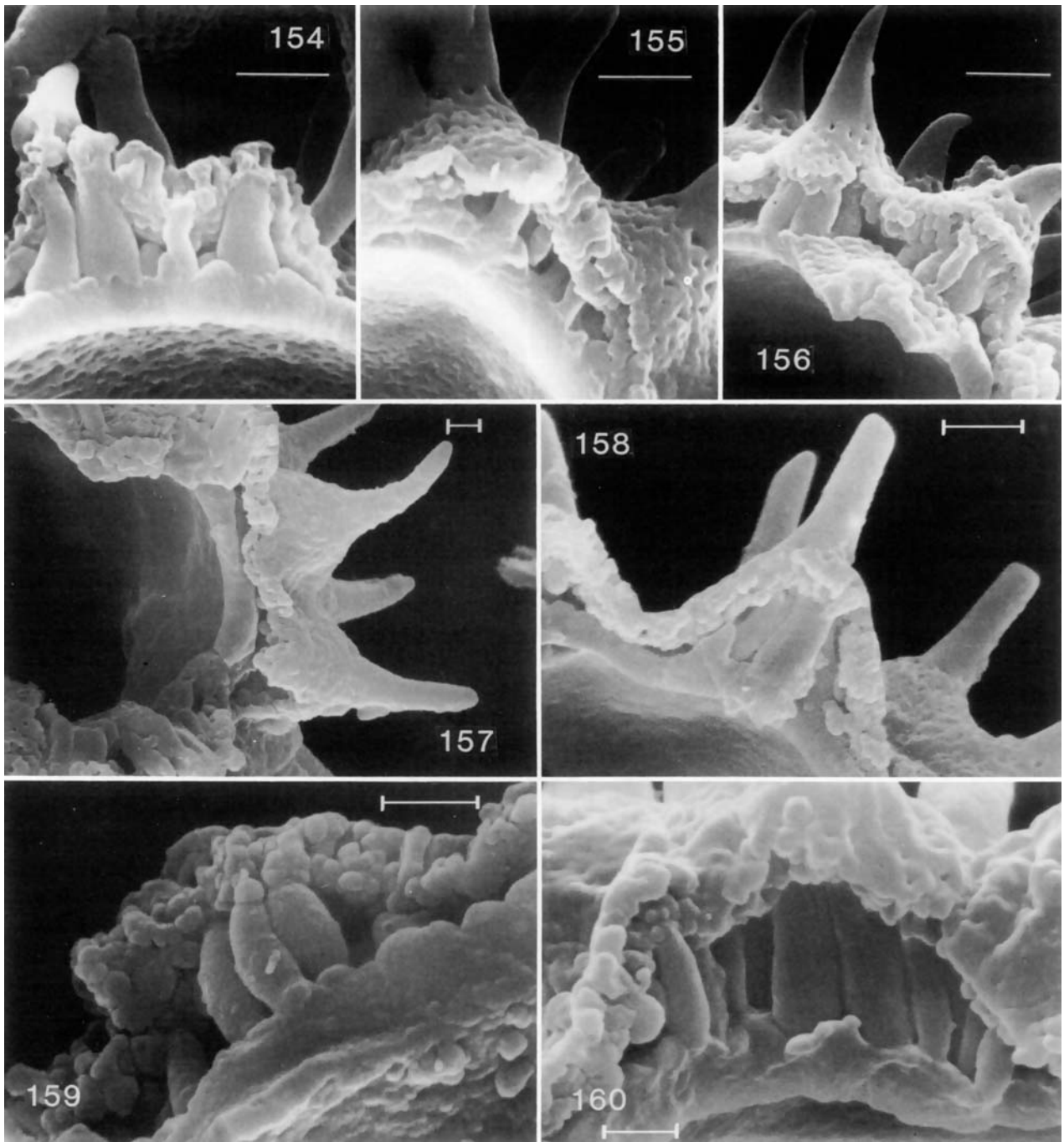
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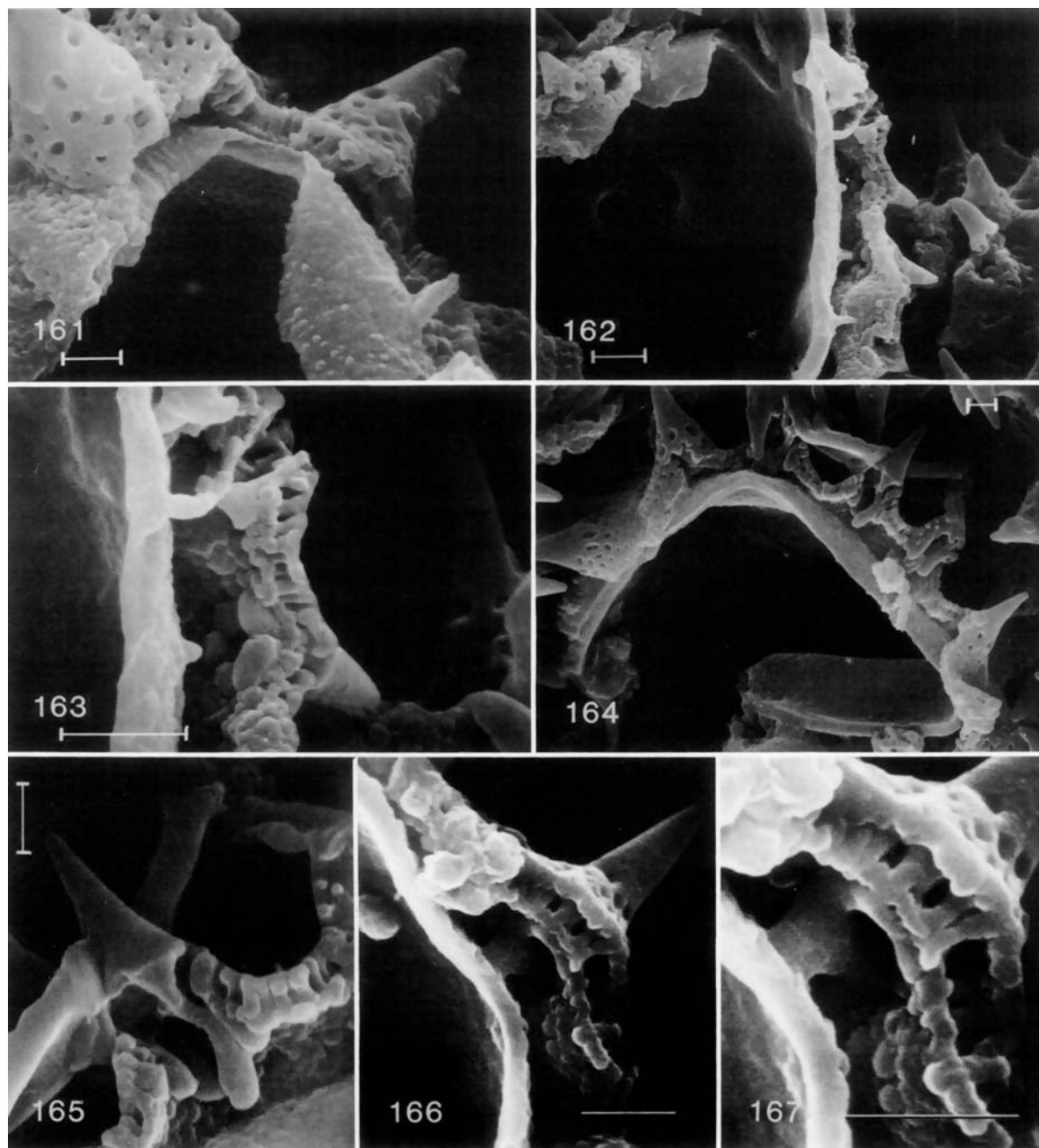
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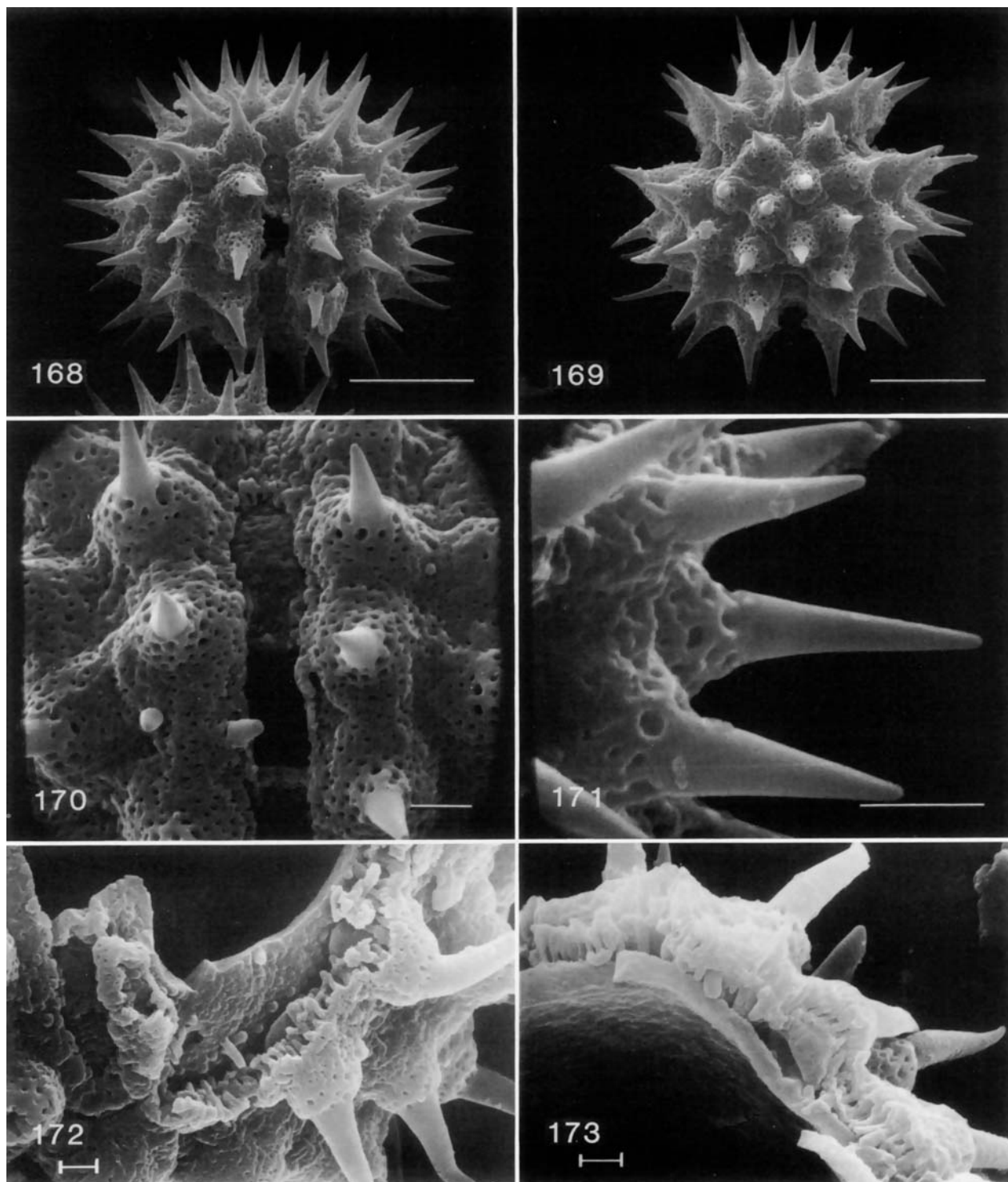
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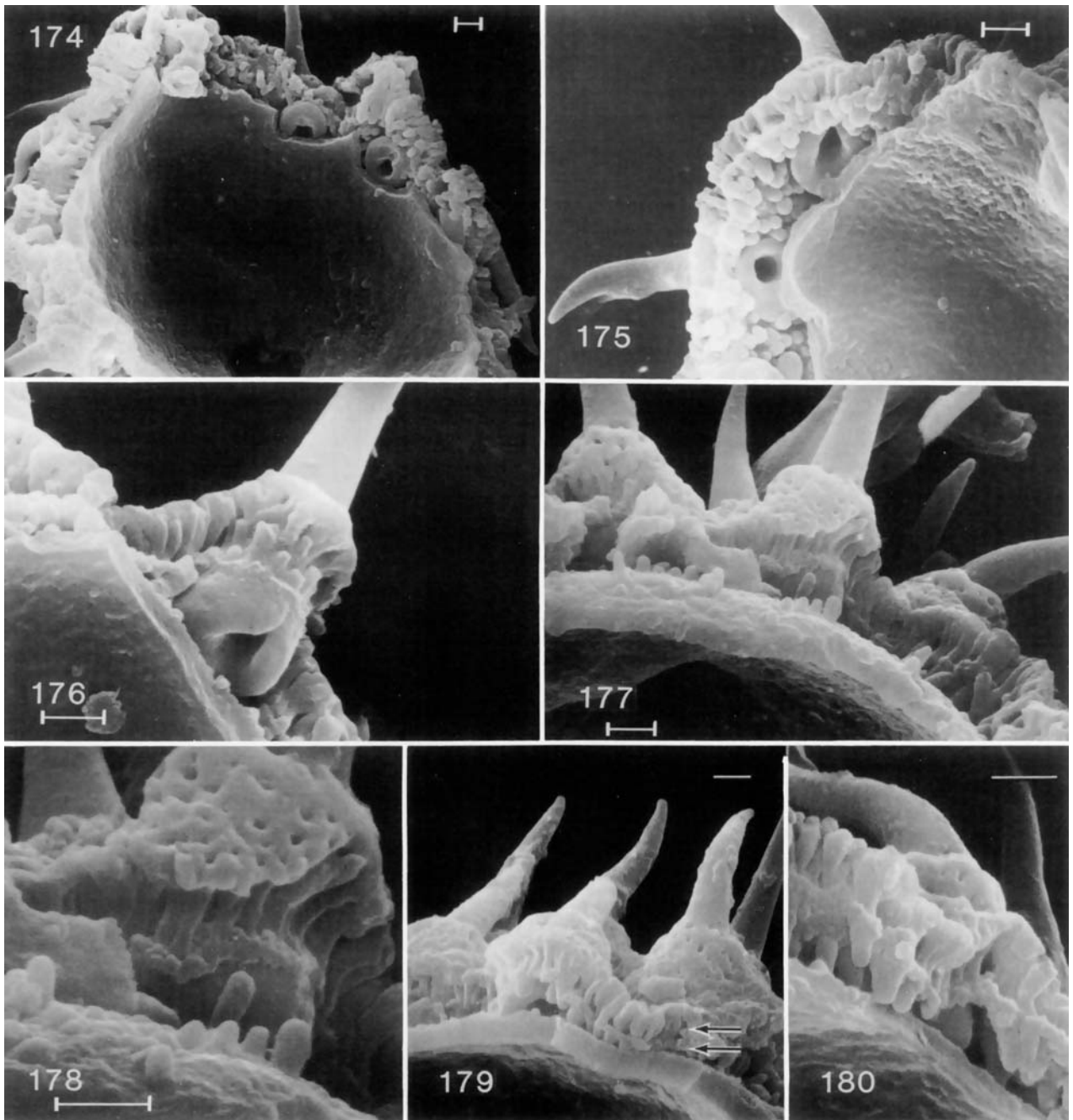
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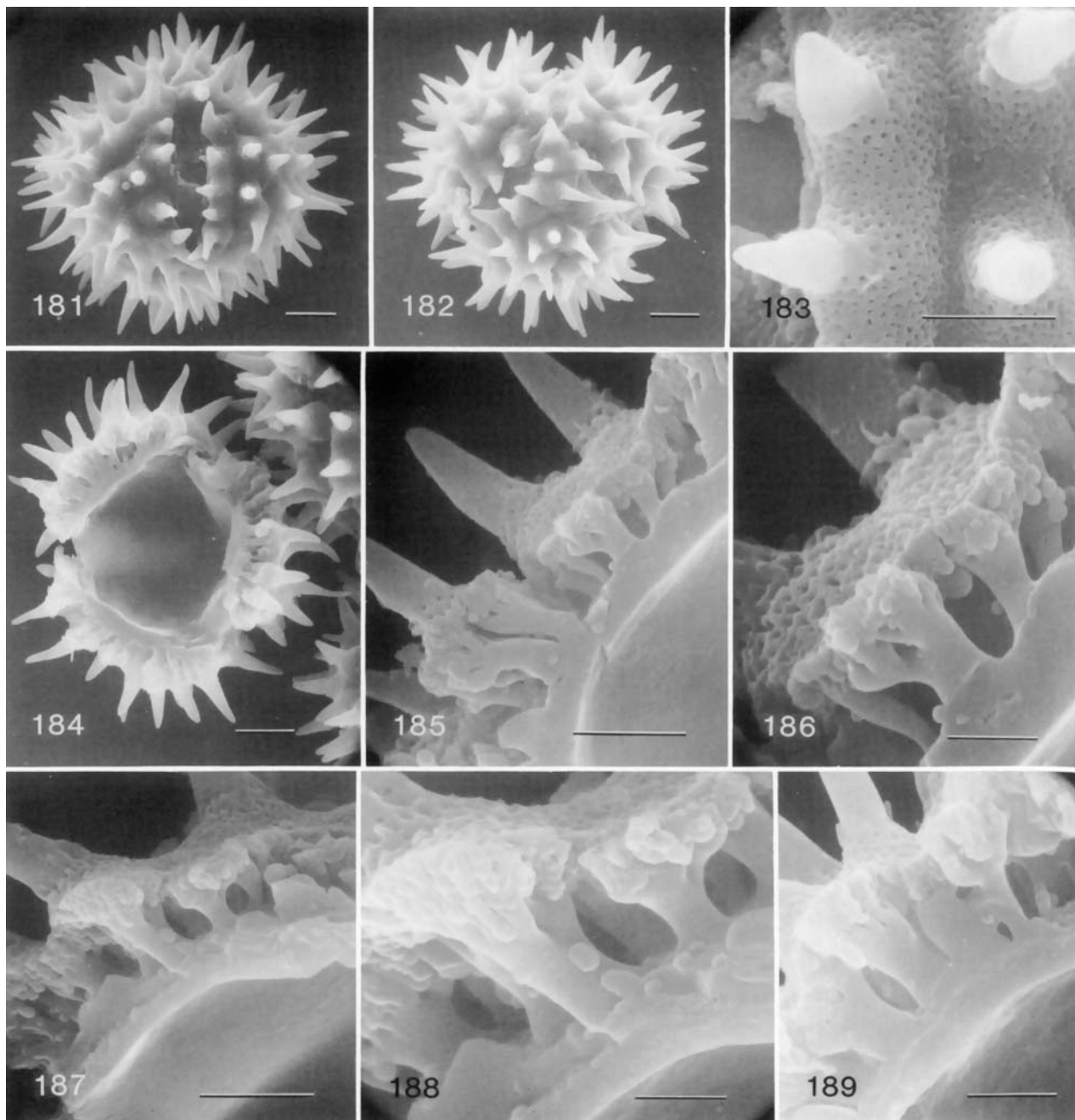
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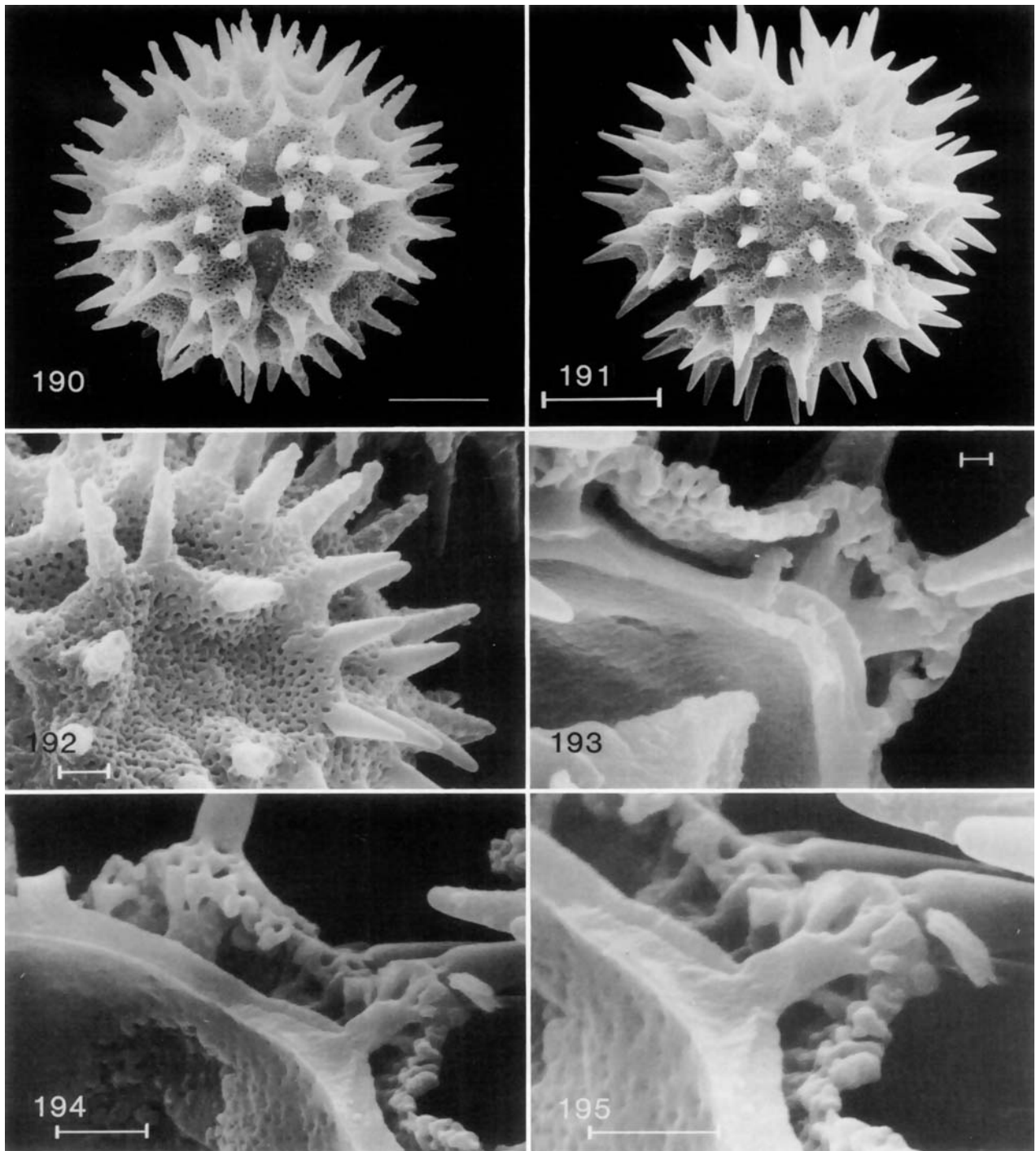
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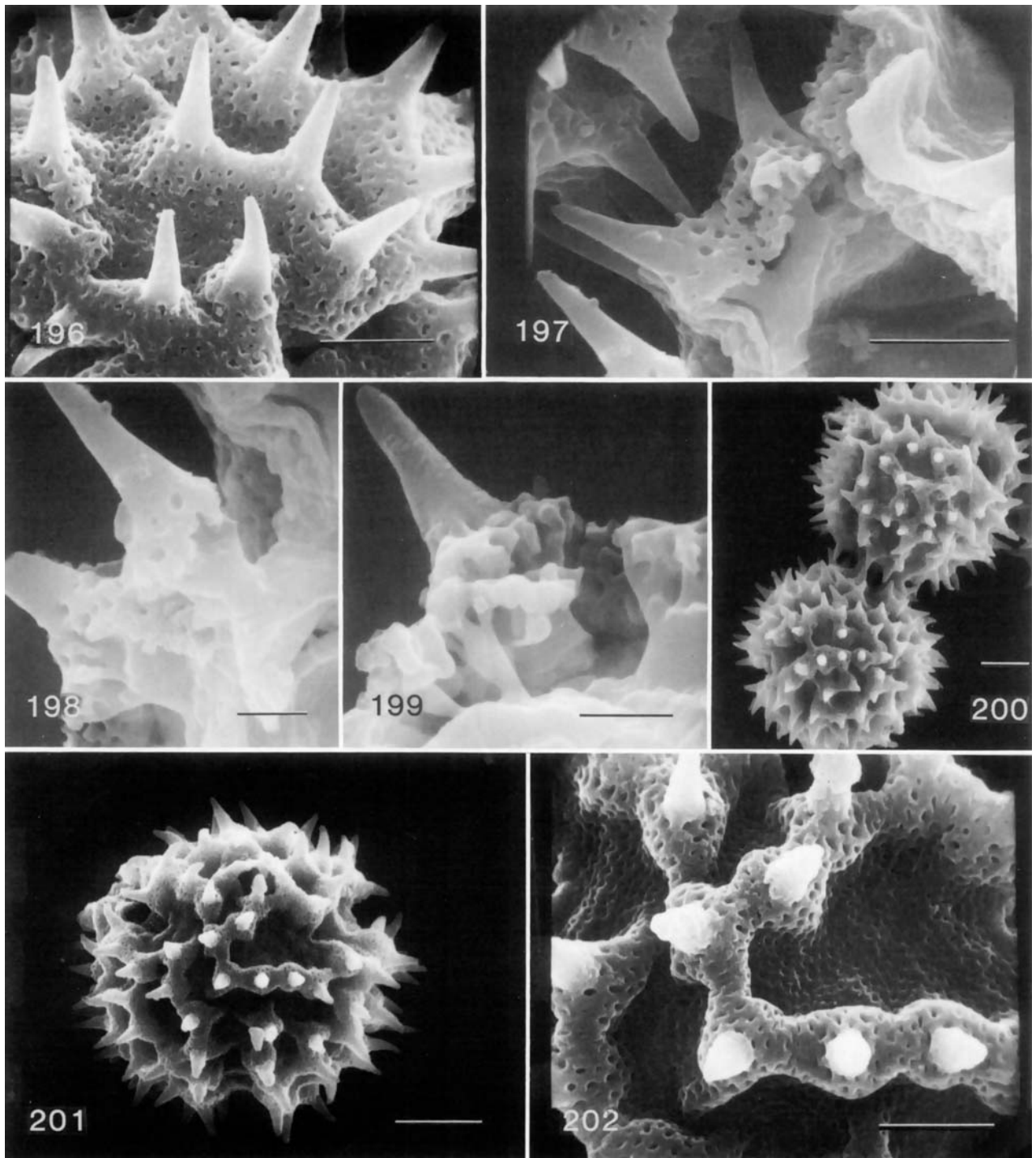
FIGURES 196–202.—SEM of tribe Vernonieae, *Blanchetia* and *Bishopalea* pollen. *Blanchetia heterotricha:* 196, surface with spines; 197–199, broken grains. *Bishopalea erecta:* 200, whole grains; 201, polar view; 202, surface. (Scale lines 196, 197, 202 = 5 μm; 198, 199 = 2 μm; 200, 201 = 10 μm.)
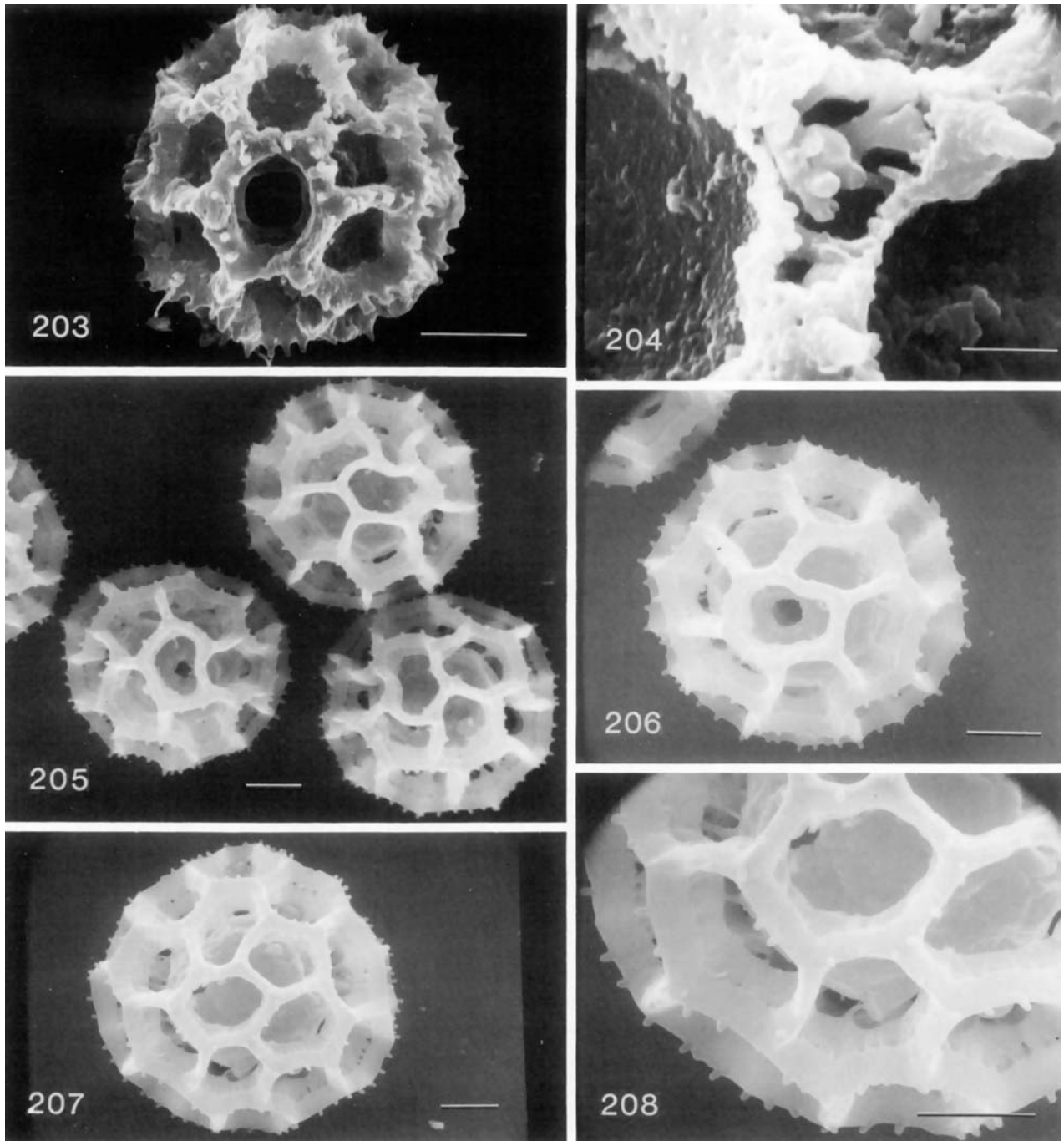
FIGURES 203–208.—SEM of tribe Vernonieae, *Heterocypsela* and *Phyllocephalum* pollen. *Heterocypsela andersonii:* 203, equatorial view; 204, broken tectum. *Phyllocephalum scabridum:* 205–207, grains; 208, reticulum, showing two strata. (Scale lines 203, 205–208 = 10 μm; 204 = 2 μm.)